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Analysis of spatiotemporal patterns of home range use and habitat selection to inform management of feral pigs on Auckland Island

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Abstract: Feral pigs (*Sus scrofa*) were introduced to Auckland Island in subantarctic New Zealand in 1807. They established and became invasive, subsequently causing substantial unwanted impacts on native biodiversity. Understanding pig movement behaviour and habitat selection can lead to focused, efficient, and effective management efforts, especially during initial knockdown of the population. Here we used location data from ARGOS telemetry collars deployed on 15 Auckland Island pigs from 2007 to 2008 to estimate seasonal home-range sizes and habitat selection. The annual home-range sizes of pigs ranged from 1.26 to 36.4 km², with a mean of 14.1 km² (SD = 11.3 km²). The variation in home-range sizes between winter and summer was generally low. We found that the pig population selected areas of their home ranges that were on average closer to the coast (though this was not necessarily selection for beaches or strandlines per se) during the spring and summer months. Pigs also selected areas closer to the coast in winter, albeit with weaker strength of selection than in spring and summer. We had insufficient data to differentiate between different coastal habitats (i.e. cliffs versus beaches and strandlines). We also found that pigs showed annual selection for tussock, hills with north-facing aspects, and rivers and streams. They avoided areas of bog-swamp and forest-scrub. Importantly, we do not know what food resources or other factors were driving habitat selection. Our results highlight areas selected by pigs that could be targeted for initial knockdown; however, staff will have to search all habitats on the island to achieve rapid eradication or a protracted mop-up of survivors. Simply targeting key accessible areas like strandlines and coastal forests will not achieve eradication. Based on these home-range sizes, eradication would require a hunter path spacing of no more than 1.4 km to ensure every pig home range was searched at least once.

Keywords: invasive species, mammalian pests, pest eradication, seasonal resource selection, subantarctic islands, sustained control

Introduction

Voyages by sailing ships could be hazardous. Shipwrecks often marooned survivors, sometimes on inhospitable islands, and captains of ships frequently needed to stop at land to reprovision food supplies. Fresh food supplies were often acquired by killing native species, perhaps most famously resulting in the extinction of the dodo (*Raphus cucullatus*) in Mauritius (Hume 2006). However, the need for fresh food for mariners also led to liberations of a number of species of domestic and wild mammals and birds, especially in the 18th and 19th centuries (Flux & Fullagar 1992; Campbell & Donlan 2005; King 2005). Included among this suite of species were feral pigs (*Sus scrofa*), with releases by Europeans occurring in, for example, the Hawaiian Islands, Galapagos Islands, California Channel Islands, and New Zealand (Coblentz & Baber 1987; Lombardo & Faulkner 2000; McIlroy 2005; Nogueira-Filho et al. 2009). Despite these often-well-intentioned liberations, invasive feral pig populations had substantial negative impacts

on native biodiversity (Courchamp et al. 2003).

Pigs are omnivorous and, as such, pose a serious threat to both native flora and native fauna (Cruz & Cruz 1987; Drake & Pratt 2001; Courchamp et al. 2003; Latham et al. 2017). They have affected the survival and recruitment of native plants through consumption, rooting, and trampling (Spatz & Mueller-Dombois 1972), dispersed exotic plant propagules (Huenneke & Vitousek 1990), and accelerated soil erosion leading to increased sedimentation in waterways (Cuddihy & Stone 1990). Pigs can affect prey populations directly by killing and eating eggs, young, and adults (see review in Russell et al. 2020), or indirectly through the process of asymmetrical apparent competition, whereby pigs provide a novel food source that can bolster predator numbers and increase predation on native prey populations (Roemer et al. 2002). Rooting and depredation by pigs can also affect ecological processes. For example, rooting can affect the physical and chemical properties of soil, thereby changing the dynamics of impacted ecosystems (Drake et al. 2011), and the destruction

of seabird colonies by pigs (see review in Russell et al. 2020) may reduce seabird-mediated nutrient transfer from ocean to land, as has been shown for rats (*Rattus* spp.) elsewhere (e.g. Fukami et al. 2006). These unwanted impacts can be mitigated if the pig population can be successfully eradicated from the target area; for example, Buller's shearwater (*Ardenna bulleri*, previously *Puffinus bulleri*) numbers increased on the Poor Knights Islands, New Zealand, after pigs were eradicated (Harper 1983). However, eradication can be challenging and expensive, especially in remote and rugged locations (Cruz et al. 2005). Understanding pig movement behaviour and habitat selection can contribute to focused, efficient, and effective management efforts. Feral pigs, probably of European rather than Polynesian origin (Robins et al. 2003), were introduced to Enderby Island and at the northern end of Auckland Island, both part of the Auckland Islands group in subantarctic New Zealand, in 1807 (Chimera et al. 1995; Taylor 2006). The purpose of this liberation was presumably as a food source for visiting ships and survivors of shipwrecks (Russell et al. 2020). Subsequent liberations occurred on nearby Davis and Shoe Islands in 1840 (McCormick 1884). Pigs were not recorded from the southern end of Auckland Island by visitors to that island in 1865 (Musgrave 1865; Norman & Musgrave 1866), but were apparently in 'large numbers' in all habitats and elevations at the northern end of that island by 1880 (Challies 1975; Russell et al. 2020). The population on Auckland Island seemed to go through an irruptive oscillation, with Challies (1975) reporting that the population crashed after reaching large numbers, presumably initiated by overshooting resource availability (Chimera et al. 1995). Pigs are currently widespread across Auckland Island, but have died out on the other islands to which they were introduced (Russell et al. 2020).

Similar to other islands that had feral pigs liberated on them, the unwanted impacts caused by pigs on Auckland Island have been high (Courchamp et al. 2003). Extensive rooting and widespread consumption of megaherbs, especially *Azorella polaris*, *Anisotome latifolia*, *Bulbinella rossii* and *Pleurophyllum criniferum*, were being reported by the mid- to late-19th century (Ross 1847; McCormick 1884). Relative to subantarctic islands free of introduced mammals, megaherbs on Auckland Island are now primarily confined to inaccessible areas (Challies 1975; Johnson & Campbell 1975; Campbell & Rudge 1984). Interestingly, however, they were still an important part of pig diet on Auckland Island in the late 1980s, comprising over 50% of the total sample by dried weight (including unidentified rhizomes and starchy plant material) (Chimera et al. 1995), despite growing mostly in inaccessible areas. Consumption of plant material appears to be spatially variable, with little evidence of consumption of plant species found in the scrub and forest zone (Challies 1975), perhaps because the palatable plants in that zone were depleted during the irruptive phase of the pig population.

Feral pigs on Auckland Island consume a wide variety of animal matter (Rudge 1976; Russell et al. 2020), but annelids appear particularly important, both in terms of percentage occurrence in dietary studies and biomass (Chimera et al. 1995). It is not known whether any of the endemic species of annelids are threatened with extinction by pigs (Chimera et al. 1995). Pigs were first noted depredating birds (burrowing petrels, Procellariidae) in 1874/75 (Krone 1900). Since then, a long list of (particularly) seabirds depredated by pigs has been observed and compiled (see Russell et al. 2020). Most accessible seabird colonies have been destroyed by pigs (and feral cats, *Felis catus*) depredating eggs, chicks, and even adults;

for example, Auckland Island shag (*Phalacrocorax colensoi* or *Leucocarbo colensoi*) and Antarctic prion (*Pachyptila desolata*) (e.g. Challies 1975; Turbott 2002). Dietary studies suggest high intraspecific variation in the occurrence of bird remains in pig stomachs, with a small proportion of the pig population, possibly those that live nearest to the seabird colonies, apparently doing the most damage (Russell et al. 2020). Pigs also eat bull kelps (*Durvillaea* spp.), other macroalgae, insects, molluscs, crustaceans, and beach-wrecked fish and marine mammals (Challies 1975; Chimera et al. 1995), which are largely coastal resources.

Eradication of pigs from Auckland Island was first discussed in 1968, but it was considered impractical at that time and its necessity has since been debated (Challies 1975; Campbell & Rudge 1984; Russell et al. 2018). Eradication has been advocated most recently by Russell et al. 2018, 2020). Successful eradication requires two rules to be met: that all target animals be put at risk of the removal techniques being used, and that animals be killed at rates faster than they can replace their losses at all densities (Bomford & O'Brien 1995; Bengsen et al. 2020). To ensure these rules are met, it may be possible to systematically cover the target area (often using fences for subdividing the area into more manageable units) and achieve rapid eradication (Parkes et al. 2010). However, this type of eradication is not always feasible, and eradication programmes including initial knockdown of the population and mop-up of survivors are often required, especially for invasive wild ungulates (Crouchley et al. 2011). The efficacy of eradication programmes, especially from geographically complex areas, may be increased by knowing where the pigs are most likely to be and how this changes seasonally (Morrison et al. 2007). This information can be used to optimise spacing between lethal removal devices, such as traps and poison bait stations, and search swaths for ground- or helicopter-based shooters (Latham et al. 2018). It can also be used to guide surveillance efforts for confidently declaring eradication, e.g. by stratifying sampling effort according to pig habitat preferences (Ramsey et al. 2009).

In this paper we used location data from Auckland Island pigs to estimate seasonal home-range sizes and habitat selection to inform management planning, particularly with regards to speculated seasonal coastal habitat use. We assessed annual selection by the pig population for landscape features except 'distance to coast', which we assessed seasonally. We quantified selection for coast by estimating whether or not pigs moved towards or away from the coast at different times of the year. As this is a continuous 'distance to' variable, it does not represent selection for the coastline per se, but rather identifies any seasonal attraction towards it, or movement away from it. We tested three competing predictions related to seasonal selection for distance to coast. First, pigs would select inland high elevation tussock grasslands during the summer but select lower elevations near the coast during winter months, as weather conditions are less severe at the lower elevation coast (Eden 1955; Challies 1975), or food availability may be higher closer to the coast in winter. Second, pigs would move closer to the coast during spring and summer months, possibly because seabird colonies (eggs and nestlings) and other coastal resources are important food sources at this time of year (Russell et al. 2020). Third, the pig population would not show any significant seasonal (monthly) pattern of selection for distance to coast. The results from these analyses could be used to inform where pig removal effort would achieve the greatest initial knockdown of the pig population, guide stratification of

surveillance effort, and, if local control became a management strategy for pigs, identify areas where the unwanted impacts of pigs might be greatest and where control of the pig population may mitigate those impacts (but see Challies 1975 & Cox et al. 2022 who argue against sustained control as a management strategy). We provide examples of how results from analyses such as this research may be useful for informing hunting or surveillance efforts within a management programme for pigs (see Cox & Macdonald 2022; Cox et al. 2022 for a review of the potential tactics and tools for eradicating pigs from Auckland Island).

Methods

Study area

We conducted our tracking study on Auckland Island (45 891 ha; 50.69°S, 166.08°E), which is the largest island in the

Auckland Islands group (56 816 ha). The islands are located about 465 km south of Bluff (Fig. 1). Auckland Island is mountainous, with several peaks surpassing 600 m. The climate is characterised by persistent westerly winds, a mean monthly summer maximum temperature of about 10.5°C in January and a mean minimum winter temperature of about 5.5°C in June, and annual precipitation of approximately 1780 mm, which typically falls over more than 300 days a year (De Lisle 1965). The vegetation on the island has been categorised into five broad classes: scrub and forest; upland tussock grassland; maritime grassland; mountain tundra; and bogs and swamps (DSL I 1991). No native terrestrial mammals exist on Auckland Island, but brushtail possums (*Trichosurus vulpecula*), mice (*Mus musculus*), cats, dogs (*Canis familiaris*), domestic sheep (*Ovis aries*), feral goats (*Capra hircus*), domestic cattle (*Bos taurus*), and feral pigs were introduced at various times, primarily in the 19th century (Russell et al. 2020). Mice, cats, and pigs are currently extant, goats were eradicated, while the remaining species died out, or, in the case of domestic species,

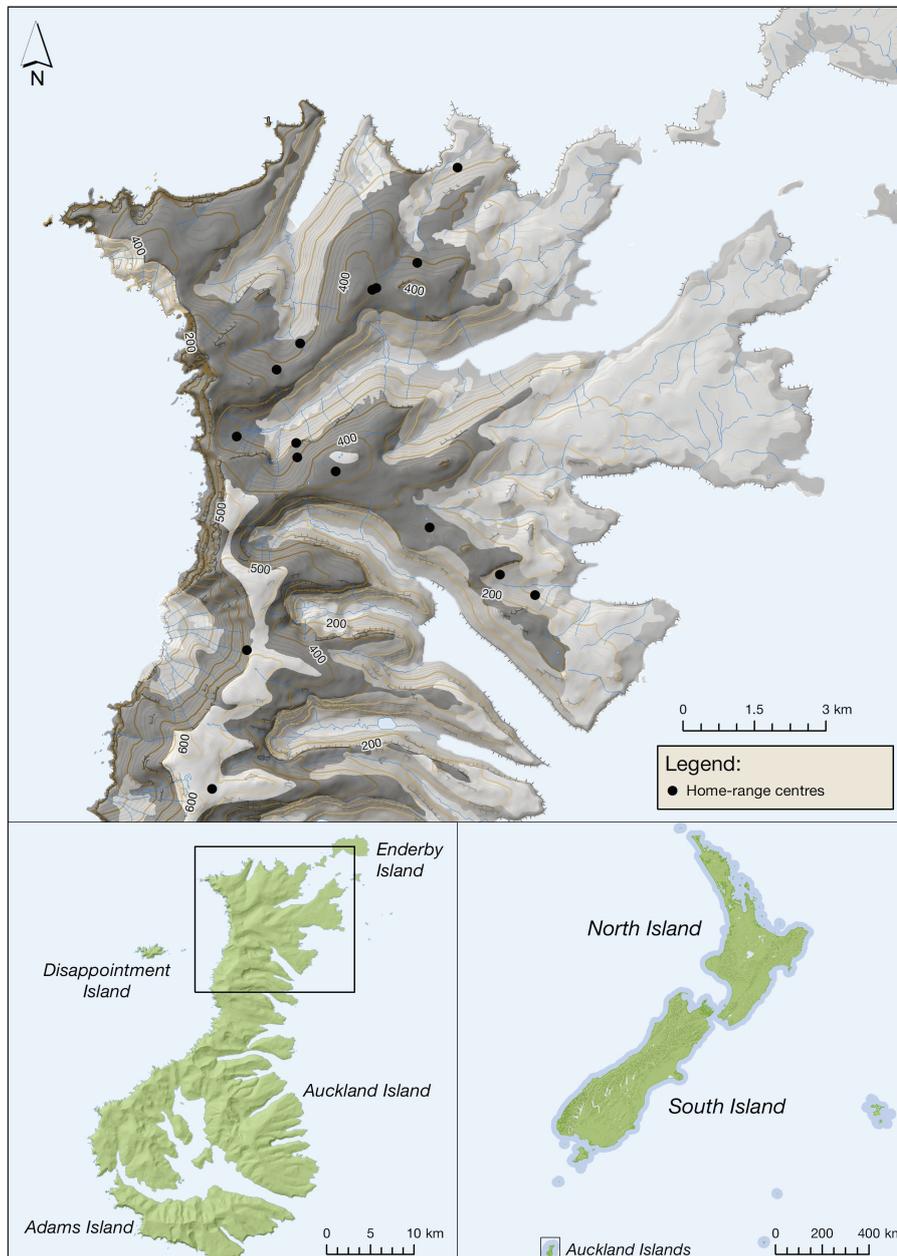


Figure 1. Map of the study location on Auckland Island, New Zealand. Tussock and forest-scrub habitat are depicted in dark and light grey, respectively. All other land covers are grouped together and depicted in white. Black circles show the home-range centres of the 15 collared pigs.

were removed (Williams 1994; Chimera et al. 1995; Russell et al. 2020; Brown et al. 2022).

Pig location data

In June 2007, 15 pigs at the northern end of Auckland Island were live captured by the Department of Conservation (DOC). Capture involved observers in a helicopter locating an adult or subadult pig and capture personnel and a trained pig dog leaping from the helicopter when close enough and restraining the pig. All pigs were captured in open tussock, but spread widely over the northern end of the island. Once physically restrained, each pig was fitted with a custom Sirtrack® ARGOS telemetry collar (Havelock North, New Zealand) and harness (Manaaki Whenua–Landcare Research animal ethics approval no. 06/07/01, 796 201 0005). Collars were active from 15 June 2007 to 1 July 2008, and were programmed to collect location data at a 14 h sample interval to avoid collecting locations at the same time of day. However, the timing of the actual location fixes that were recorded was irregular. We rarefied the data to have no more than one fix every 2 h and movement velocities not more than 1610 m h⁻¹ (97.5% percentile of raw data). The resulting median and 95% CI of movement velocity were 52 m h⁻¹ and 4–1039 m h⁻¹, respectively. Monitoring periods for collared feral pigs are shown in the Supplementary Material, Figure A1.

Landscape covariates

Explanatory variables included in our analyses were derived from a geographic information system (GIS) of the study area, using ArcGIS Pro (ESRI 2020), and included land-cover type, topography, and ‘distance to’ covariates. Recent studies highlighted that more useful insights into resource selection can be gained from considering habitat attributes at multiple discrete scales (Boyce 2006; Leblond et al. 2011), so we collected landscape covariates at two discrete spatial scales (circular buffers of 200 and 500 m radii). These were assumed to correspond to a range of hierarchical temporal (diel and seasonal) movement decisions (Leblond et al. 2011). The smallest scale corresponded to the average GPS location error, whereas the largest scale was assumed to correspond to larger ranges of perception by feral pigs. Within each buffer we derived land-cover types from the NZMS 260 series Auckland Island vegetation layer (DSL1 1991). The land-cover classes in this layer were maritime complex, low forest and mixed scrub, bog and swamp, upland tussock grassland, and tundra-like mountain summit vegetation (see Table A1 in Supplementary Material for a full description of each class). We converted land-cover types to a 15 m-resolution raster and included these in all analyses as the proportion of each land-cover type within the discrete buffers around each ARGOS location. We derived the mean aspect (computed as deviation from north) within the buffers around each ARGOS location from a 15 m-resolution digital elevation model (DEM) of the study area. Finally, we computed ‘distance to-’ variables, including the minimum distance to the nearest river or stream within the buffers, as well as the straight-line distance between each location and the coast. Note that coasts around the island include cliffs (predominantly but not exclusively on the west side of the island), drowned shorelines, and beaches. Ideally, an analysis would include each coast type as an explanatory variable in the habitat selection models. We had insufficient location data to do this analysis, and the inclusion of these additional variables would have resulted in overfitting the statistical models (Harrell 2001).

Home-range analysis

The ARGOS telemetry data were used to estimate the area of a 95% home-range kernel for each individual pig. The package ‘adehabitatHR’ (Calenge 2006) in R (R Development Core Team 2019) was used to calculate adaptive kernels. Kernel density estimators were used to create a utilisation distribution (UD) for each tracked pig, and a 95% home range area was then estimated based on the UD. Kernel density methods are flexible and require two major choices to estimate the UD. The first is the overall shape of the animals’ distribution (the density kernel) and the second determines how the size of the distribution (bandwidth) is calculated. We used a bivariate normal density kernel using a reference bandwidth (Worton 1989). Small sample sizes tend to overestimate kernel home range sizes (Seaman et al. 1999; Borger et al. 2006), so we discarded two pigs for which we had less than c. 40 locations (75 202 and 75 210; Fig. A1). We estimated kernel home ranges using the full set of ARGOS locations for each animal (i.e. the annual home range), as well as over two distinct seasons: winter (May–September) and summer (November–March). The seasonal split was based on our ecological knowledge of the system (as recommended by Basille et al. 2013) and primarily took into consideration temporal variation in temperature on the island and, to a lesser extent, the breeding season of some of the seabirds present in the island (for example, Auckland Island shags and Antarctic prions breed between about early November and mid-March; Heather & Robertson 1996; Szabo 2013 [updated 2018]). Seasonal home ranges were estimated only for pigs for which we had more than c. 40 locations for a given season.

Resource selection analysis

We evaluated third-order selection (sensu Johnson 1980) by feral pigs, using resource selection functions (RSFs; Manly et al. 2002), by comparing landscape characteristics at used (ARGOS) and available (random) locations. Areas available to each pig (i.e. the domain of availability; Manly et al. 2002) were defined by 100% minimum convex polygons (MCP) for each individual pig, excluding any areas that fell on water. Within each 100% MCP, we drew 1000 random locations to describe habitat availability for each animal.

We developed a Bayesian hierarchical model and used Markov chain Monte Carlo (MCMC) techniques to estimate parameters and make inferences about the location data. The basic approach was that for every location fix, the pig could be in 1 of 1001 possible locations (1 observed location plus the 1000 random locations). Given the habitat variability across the 1001 possible locations for a single fix, the model calculates the probability that the pig was at the observed location.

We fitted the data to a null model (no covariates) and eight alternative models that included combinations of distance to coast (DCoast), deviation from a northern aspect (DevN), distance to river/stream (DRiver), and proportion cover of forest-scrub (PForest), upland tussock (PTuss) and bog-swamp (PBog). Distance to coast, deviation from north and distance to river/stream were included in all covariate models. The alternative models included the proportion of habitat cover at either the 200 or 500 m radius. The proportion of forest-scrub cover was highly correlated with upland tussock ($r = -0.76$), so only one of these two variables was included in a model. Models were compared using DIC (Spiegelhalter et al. 2002). Convergence for all fitted models was achieved following a burn-in of 5000 iterations. Posterior summaries were obtained

from 3000 samples after a thinning rate of 20. The MCMC algorithm was written in the Python programming language (Python Software Foundation 2020).

Formally, the probability of observing the ARGOS eastings and northings (Z_{ijt}) of individual i at location j at time t given the parameters was modelled as follows:

$$\Pr(Z_{ijt} | \beta, \mu, \nu, \sigma, \varepsilon, a, b) = \frac{e^{\omega_{ijt} I_{ijt}}}{\sum_{j=1}^J e^{\omega_{ijt}}} \quad (1)$$

where ω_{ijt} is the relative probability of pig i being at location j at time t , J is the total number of location points for that individual (1 presence and 1000 pseudo absences), and I_{ijt} is a presence/absence indicator, which takes a value of one for presence or zero for random locations. ω_{ijt} is a direct prediction from the following linear model:

$$\omega_{ijt} = \mathbf{X}'\beta + \beta_{n,it} DCoast_{jt} \quad (2)$$

where $\mathbf{X}'\beta$ is the matrix multiplication of habitat covariates (excluding distance to coast) and the β coefficients, and $\beta_{n,it}$ is the coefficient for distance to coast for location j for individual i at time t . $\beta_{n,it}$ is a direct prediction of the following equation:

$$\beta_{n,it} = \alpha_{0,i} + \alpha_{1,i} WRC(day_t | a, b) \quad (3)$$

where $\alpha_{0,i}$ is the intercept parameter for individual i , $\alpha_{1,i}$ is an individual-level coefficient for the temporal variable $WRC(day_t | a, b)$, which is the probability density of a wrapped Cauchy distribution with parameters a and b . The variable day_t is the day of the year in radians, which ranges from 0 (1 January) to 2π (31 December).

The $\alpha_{0,i}$ allowed the temporally variable coefficient $\beta_{n,it}$ for DCoast to change between negative and positive values depending on the day of the year (t). For clarity, a positive $\beta_{n,it}$ indicates selection away from the coast (i.e. selection for relatively high distances from the coast). This allowed us to test our predictions; for example, that selection (ω_{ijt}) for areas away from the coast was positive in the summer (pigs seek inland areas) and negative in the winter (they move to the coast).

The individual-level intercept in eqn 3 and associated hyper-parameters were distributed as follows:

$$\alpha_{0,i} \sim Normal(\mu, \sigma^2) \quad (4)$$

$$\mu \sim Normal(0, 100) \quad (5)$$

$$\sigma \sim InverseGamma(0.1, 0.1) \quad (6)$$

where the parameters μ and σ are the population-level parameters for the mean and standard deviation for α_0 .

The individual-level coefficient $\alpha_{1,i}$ (Eqn 3) for the circular day_t variable and associated hyper-parameters were distributed as follows:

$$\alpha_{1,i} \sim Normal(\nu, \varepsilon^2) \quad (7)$$

$$\nu \sim Normal(0, 100) \quad (8)$$

$$\varepsilon \sim InverseGamma(0.1, 0.1) \quad (9)$$

where ν and ε are the population-level mean and standard deviation for $\alpha_{1,i}$, which influences the population-level selection for DCoast (Eqn 3).

Results

Between June 2007 and July 2008, we captured and collared six female and eight male feral pigs on Auckland Island (information on the sex of one pig was not recorded). Females weighed 40 kg (range 31–53 kg) on average, whereas males weighed 49 kg (range 39–59 kg) on average. After data rarefaction there were 2312 ARGOS locations available for analyses.

The home-range analysis showed that pig annual home-range sizes ranged from 1.26 to 36.4 km², with a mean of 14.1 km² and standard deviation of 11.3 km² (Table 1). The smallest and largest home ranges belonged to a 44 kg male and a 53.5 kg male, respectively, both of which occurred in the northern part of the island (Fig. 2). Mean annual home-range size was similar for males and females (14.2 km² and 13.9 km², respectively). The size of home ranges was similar between the two seasons we analysed, and also relative to the annual home ranges, although there were some exceptions (Table 1). The winter home-range sizes for pigs 75 201, 75 209 and 75 211 were about half the size of those they used in summer. The opposite pattern was evident for pig 75 207, which had a summer home range that was one-tenth the size of its winter home range.

In the RSF analysis we explored four covariate models in which habitat variables were sampled at a 200 m radius, and then repeated these models but using covariates sampled within a 500 m radius. The model that resulted in the lowest DIC included the vegetation cover variables PTuss and PBog sampled at a radius of 200 m (model 3 in Table 2). The next best model (model 1) included PTuss within a 200 m radius as the sole vegetation cover variable and had a delta DIC of 11.61. This result suggests that PBog adds substantial information to understanding pig habitat use. Comparing the models with the same covariates at the 200 m and 500 m radius (i.e. 1 and 5, 2 and 6, and so on) showed that the 200 m models fitted the data substantially better than the 500 m models. The null model had a delta DIC of 3723, indicating that pigs are strongly responding to vegetation and topographic position on the island.

Pigs used the tussock habitat disproportionately to its availability on the landscape (positive coefficient) and tended to avoid bog-swamp areas (negative coefficient; Table 3). Although PForest was not in any of the top models (Table 2), it had a negative coefficient, indicating avoidance by pigs. This result was expected given the strong negative correlation between PTuss and PForest. There was a negative relationship between pig probability of use and DRiver and DevN. This finding means that pigs were generally attracted to rivers and streams and north-facing slopes.

Understanding pig attraction to the coast and how this may vary seasonally requires interpretation of the parameters influencing β_n (Eqns 3–9). At a population level, the combination of parameters a , b , μ , σ , ν and ε (Table 3) suggests that, within their respective home ranges, pigs were generally more attracted to areas that were closer to the

Table 1. Annual, winter (May–Sep), and summer (Nov–Mar) home-range areas (km²) for 15 feral pigs radio-collared on Auckland Island, New Zealand, from June 2007 to July 2008. The table also includes number of telemetry fixes, plus sex and mass for each animal. The sum of winter and summer fixes does not equal the annual sample size because April and October were excluded from the seasonal analysis. A dashed line indicates that the kernel home range could not be estimated due to low sample size. Note that because of the different sample sizes between the seasonal and annual home ranges, the kernel density estimation method can estimate the annual home range size to be smaller than a seasonal one.

Pig ID	Sex	Mass (kg)	Annual		Winter		Summer	
			n	95% UD	n	95% UD	n	95% UD
75 200	F	37	151	1.98	102	2.94	30	–
75 201	M	44	322	1.26	223	1.20	66	2.15
75 202	M	40	20	13.76	19	–	0	–
75 203	F	47.5	115	18.59	67	14.48	37	19.85
75 204	F	35	71	19.08	67	17.65	2	–
75 205	M	53.5	78	36.40	67	27.11	8	–
75 206	F	31	363	2.31	248	2.42	76	2.11
75 207	M	56	212	8.02	130	11.78	52	1.35
75 208	F	53	75	30.80	52	17.43	17	–
75 209	M	54	332	5.61	224	4.74	75	9.29
75 210	Unknown	Unknown	14	24.21	12	–	1	–
75 211	F	37	142	12.58	72	7.92	54	15.64
75 212	M	59	47	17.04	36	18.01	8	–
75 213	M	39	285	5.52	177	5.28	74	5.92
75 214	M	Unknown	85	22.99	60	19.74	17	–

Table 2. Results of nine RSF models, with associated delta DIC values, used to compare habitat selection by feral pigs in Auckland Island, New Zealand. Lower values are better, indicating that model 3 provided the best fit to the data. The variables PTuss, PForest, PBog, DRiver, DCoast and DevN were the proportion of tussock, forest-scrub and bog-swamp, the distances to river/streams and coast, and deviation from a northern aspect, respectively.

Model	Description	Radius (m)	Δ DIC
0	Null	NA	3723.40
1	PTuss, DRiver, DevN, DCoast	200	11.61
2	PForest, DRiver, DevN, DCoast	200	568.24
3	PTuss, PBog, DRiver, DevN, DCoast	200	0.00
4	PForest, PBog, DRiver, DevN, DCoast	200	162.45
5	PTuss, DRiver, DevN, DCoast	500	365.76
6	PForest, DRiver, DevN, DCoast	500	677.59
7	PTuss, PBog, DRiver, DevN, DCoast	500	362.22
8	PForest, PBog, DRiver, DevN, DCoast	500	380.85

Table 3. Posterior parameter estimates, and associated 95% credible intervals (CI), for model 3, which had the lowest DIC value (see Table 2). The habitat covariates for this model were sampled within a 200 m radius around each observed and random location.

Parameter	Mean	Low CI	High CI
PTuss	0.769	0.718	0.820
PBog	−0.132	−0.191	−0.076
DevN	−0.368	−0.411	−0.326
DRiver	−0.743	−0.807	−0.679
a	2.904	2.419	3.339
b	0.945	0.792	1.117
μ	−0.838	−0.975	−0.705
σ ²	0.03	0.015	0.055
v	0.520	−0.049	1.161
ε ²	0.081	0.037	0.153



Figure 2. Home-range estimates for each individual feral pig collared on Auckland Island, New Zealand, from June 2007 to July 2008. Home ranges were estimated from the 95% utilisation distribution of a bivariate normal kernel. The map also shows the distribution of GPS locations obtained for each collared animal. Home ranges were not estimated for pigs 75 202 and 75 210 because of the low sample size (see Table 1).

coast than those areas further from the coast, as indicated by the negative β_n throughout the year (Fig. 3). The attraction to areas comparatively closer to the coast decreased in the winter months, as shown by the β_n becoming less negative. At a population level, this result contradicts the prediction that pigs would be attracted to the coast in winter. The fitting of individual-specific parameters for $\alpha_{0,i}$ and $\alpha_{1,i}$ showed that there was some variability amongst pigs, with some selecting inland areas further from the coast within their home range (Fig. 4; Supplementary Material Table A2). Two pigs showed a positive β_n throughout the year (pigs 75 209 and 75 213), i.e. attraction to inland areas within their home range further from the coast than areas closer to the coast. This avoidance increased (i.e. became more positive) in the winter months. Pigs 75 200 and 75 201 showed a very minor increase in attraction to the coast in the winter months, as indicated by the β_n becoming slightly more negative around July relative to the other months of the year.

Discussion

The home-range sizes and movement of feral pigs are primarily determined by the seasonal abundance of food (Saunders & McLeod 1999). We found high individual variation in home-range sizes, but generally low variation in size between the winter and summer seasons. Our results support the prediction that, at a population level, pigs tend to occur closer to, but not necessarily at, the coast during spring and summer months than they do in winter. We also found that pigs showed annual selection for tussock, hills with north-facing aspects, and rivers and streams, but tended to avoid bog-swamp and forest-scrub areas. All pigs were captured in the upland tussock area, indicating that from the outset these individuals were likely to select this habitat. An attempt to capture pigs across more diverse habitats would be required to test the potential bias caused by the capture location. Further, we do not know what food resources, or other factors, were driving individual variability in home-range sizes, selection for areas closer to the coast in spring and summer, or annual selection for other habitats. The average home-range size of feral pigs on Auckland Island was large (14.1 km²) compared to average home-range sizes reported elsewhere in southern New Zealand; for example, 0.81 km² in the Murchison area, South Island (McIlroy 1989), and 3.77 km² in Marlborough, South Island (Yockney et al. 2013). It is possible that our estimates are much larger than those reported by McIlroy (1989) because of the difference in monitoring periods (88 days versus c. 1 year for our study; note that Yockney et al. (2013) monitored pigs for 14 months). Alternatively, the larger home ranges we report could be an artifact of the analytical method we used (reference bandwidth kernel density estimator). The reference bandwidth works well if the distribution of the kernel density function is normal; however, it can over-smooth the estimate otherwise. To assess this effect, we visually inspected the estimated home ranges relative to the re-locations. However, similar to other studies (McIlroy 2005), we found high individual variability in home-range size, which was not related to the sex or size of the animal. In general, the size and location of home ranges was similar between the two seasons we assessed, and seasonal home-range sizes and placement were comparable to annual home ranges. This result suggests that food and shelter resources were sufficiently available and seasonally consistent within the areas used by each feral pig.

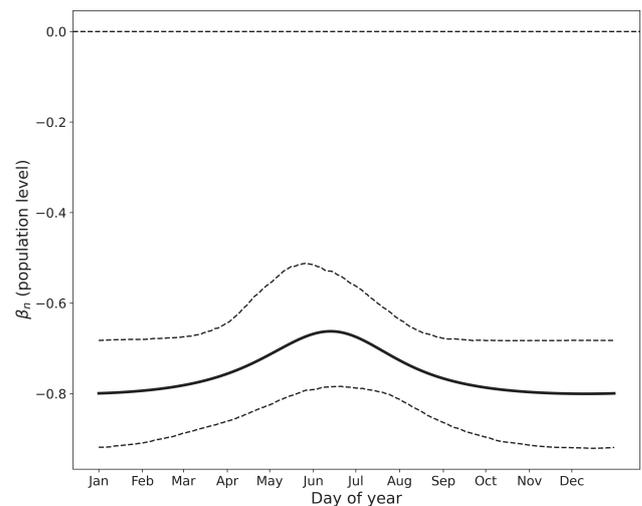


Figure 3. The mean (solid line) and 95% credible interval (dashed lines) of the population-level estimates of β_n over all days of the year. The dashed horizontal line at $\beta_n = 0$ provides a reference for values that would indicate no selection towards or away from the coast.

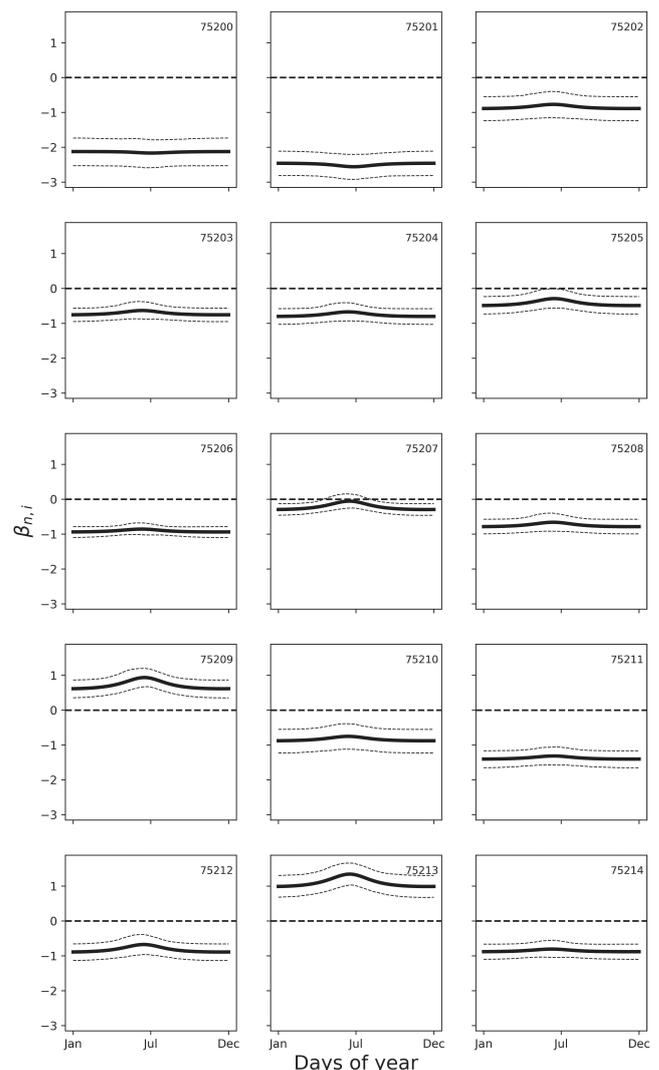


Figure 4. The mean (solid line) and 95% credible interval (dashed lines) of $\beta_{n,i}$ over all days of the year for individual pigs. The dashed horizontal line at $\beta_{n,i} = 0$ provides a reference for values that would indicate no selection towards or away from the coast.

A previous assessment of pig habitat use on Auckland Island in February (summer) 1973 found that pigs and their sign were most common in the open tussock high country above 350 m a.s.l. and in coastal forest and lowland scrub below 150 m a.s.l. (Challies 1975). At the population level, our results support strongest selection for areas closer to the coast in spring and summer, as shown by the more negative β_n coefficient for distance to coast in January–March and October–December in Figure 3. However, we also found high individual variability in selection for areas closer to the coast (Fig. 4), with some individuals selecting the open tussock high country in spring and summer (as reported by Challies 1975), rather than making elevational movements to the coast. Indeed, it is likely that some individuals were making elevational movements from the thermo-cover provided by coastal forest and lowland scrub in winter to the tussock high country in spring, possibly to feed on annelids and new plant growth at that time of year (Chimera et al. 1995).

The 1944/45 Cape Expedition survey party saw no pigs in the high country during the winter months and concluded that they were confined to lower elevations at that time of year (Eden 1955). This observation led to our prediction that pigs would move from inland high elevations dominated by tussock grasslands during the summer towards the coast and coastal forest during winter months, as weather conditions are less severe at lower elevations. Although we found that selection for areas close to the coast was highest in spring and summer, this finding does not mean that pigs selected high elevations during winter. Indeed, the annual negative relationship for distance to coast indicates that during winter the pig population is still, on average, selecting areas closer to the coast, just less strongly compared to spring and summer. Moreover, annual selection for hills with north-facing aspects suggests that pigs are negatively affected by cold winter conditions and seek thermo-cover in low-elevation forests and scrub on warmer, north-facing slopes during winter (McIlroy 2005).

Distance to coast has the potential to be misleading as it is not necessarily correlated with elevation. The west coast of Auckland Island is dominated by steep cliffs up to >500 m in height in some places, whereas the east coast has a drowned shoreline with long, narrow inlets (Challies 1975). Our analysis did not assess relative selection for cliffs versus forested shorelines or beaches, but pig selection for these features may differ based on available food or accessibility. For example, although megaherbs grow primarily on inaccessible areas, like cliffs (Challies 1975; Johnson & Campbell 1975; Campbell & Rudge 1984), some megaherbs growing on steep coastal hillsides are accessible to pigs (see Fig. 5 in Russell et al. 2020). As these plants contribute substantially to pig diet (Chimera et al. 1995), they may (partially) drive pig selection for coastal cliffs/steep coastal habitats. Depredation (or at least scavenging opportunities) of the eggs, young, and adults at colonies of white-capped mollymawk (*Thalassarche cauta steadi*), northern giant petrel (*Macronectes halli*), Auckland Island shag, and other seabirds that are surface nesters near or on cliffs may also contribute to pig selection for coastal cliffs (see Fig. 5 in Russell et al. 2020). Conversely, scavenging seaweed, molluscs, crustaceans, beach-wrecked fish and seabirds, cetacean and New Zealand sea lion or whakahao (*Phocarctos hookeri*) carcasses, and sea lion regurgitations (Challies 1975), along with opportunities to depredate seabird colonies near beaches (Russell et al. 2020), may drive pig selection for strandlines and adjacent forest. Disentangling the influence of resources available in the two contrasting

coastlines would require fine-scale delineation of different coastal zones within a GIS and more accurate pig location data, but could identify areas where native plants and animals might be at greatest risk from pigs, as well as areas where pigs could be efficiently targeted for management.

We used ARGOS telemetry data to describe the home ranges and patterns of resource selection by feral pigs. This information has the potential to hone control and surveillance efforts conducted as part of any management programme. However, a limitation of trying to identify habitats disproportionately used by pigs is the resolution of available habitat layers. We used a land-cover map for Auckland Island that was published in 1991 and was produced at a 1:50 000 scale, which provided a one-off snapshot of the vegetation in the study area c. 30 years ago. While the resolution of this land-cover layer might not be detailed enough to reflect fine-scale selection by feral pigs (e.g. for bird breeding colonies), it is sufficient to formulate predictions about where their impacts might occur as well to guide control and surveillance efforts. We monitored 15 pigs for a period of 12 months, which meant that we did not have temporal replication in our analyses. Knowing whether there is inter-annual variation in resource selection or in the size and location of home ranges is important for eradication programmes, which can extend over several years (Cruz et al. 2005; Garcelon et al. 2005; Morrison et al. 2007). Another potential limitation of our study was that the pig locations were only collected twice a day (although the 14 h interval ensured that fixes were collected at different times of day) and that the sample of collared animals was smaller than what is often recommended for resource selection studies (e.g. 20–30 animals; Leban et al. 2001; Latham et al. 2015). This sample was further reduced by two collars that appeared to malfunction, recording few locations. Location data were also entirely absent for all of January. These issues reduced our sample size and precluded a detailed resource selection analysis (e.g. by sex and season) and from estimating summer home ranges for several individuals. Sample size limitations are difficult to overcome in most studies using GPS or satellite-based technologies, primarily because of the high cost of the hardware and the potential for units to fail before yielding data (Latham et al. 2015). Nevertheless, our results provide the most detailed assessment available to date for feral pig home-range behaviour and resource selection on Auckland Island.

Our results show that while pigs at the population level select areas closer to the coast, there is high individual variability, with pigs probably showing seasonal selection for strandlines, coastal cliffs, coastal forests, lowland scrub, and tussock grasslands. The key implication of these results is that staff involved in pig management will not be able to focus solely on pig removal in the easy-to-access coastal areas of the east coast because a substantial proportion of the pig population is unlikely to be put at risk in those areas (see Cox et al. 2022). However, this does not mean, for example, that helicopter-based shooters (perhaps using thermal-imaging equipment) should not target pigs for initial knockdown on steep, tussock-covered hillsides on the west coast, or boat-based shooters should not target pigs near strandlines. These methods may have high utility as part of the knockdown of the pig population. However, for eradication to be achieved, eradication staff will have to actively locate or target pigs in all habitats on the island (also see Cox et al. 2022; Cox & Macdonald 2022). Our results also indicate that while a more detailed analysis of pig selection for different coastal habitats would be nice to have, it would not alter the identified need

for pig removal methods to target all habitats on the island.

Ideally, any removal method chosen for an eradication operation will be used in a way that minimises education of the pig population (Morrison et al. 2007; see Cox et al. 2022 for tactical use of removal methods). For example, a hunter using a helicopter as a shooting platform should kill all individuals in a group of pigs that is detected. If this is not achievable, it is possible that habitat selection by pigs could change, with more time spent by pigs in the intermediate elevational belt of short, thick scrub and dense tussock, which might substantially increase the cost of the operation or compromise its achievability. To prevent any attempt at eradicating pigs from continuing indefinitely, it may ultimately be necessary to divide the island into fenced zones, as was done on Santa Cruz Island, California, and treat each fenced area as a smaller, more manageable eradication unit (Morrison et al. 2007). Although fencing will be logistically difficult on Auckland Island, partitioning of the island into manageable eradication units has been proposed by Cox et al. (2022) as a tactic to aid eradication.

Results from our home-range and habitat selection analyses can be used to inform the knockdown phase of an eradication programme in two ways. First, having information on home-range sizes of feral pigs, and the related variability, permits a search strategy to be delineated, with spacings between traps, bait stations, or hunter paths defined so that the removal method will not miss detecting any pigs. If we assume the average home range radius for pigs on Auckland Island is 2 km (derived from a circular home range of 14 km² area), hunter paths would have to be no more than 4 km apart to ensure that the average pig was put at risk of being detected. In reality, however, an eradication programme must detect and kill all individuals (Bomford & O'Brien 1995). For pigs on Auckland Island this would require hunter path spacing of no more than 1.4 km (a conservative estimate based on the diameter of the smallest home range we describe) to ensure every pig home range was searched once (but not more than that). Likelihood of detection could be further increased by reducing the distance between search transects, such that all home ranges have two or more transects in them (i.e. instances of being searched), and these could be stratified to habitats most likely to be selected by pigs, although these changes could also significantly increase the effort required. Knowing how home-range size and habitat selection vary across the landscape and how these change as population size decreases, allows the strategy to be adapted according to local conditions. Second, once eradication is believed to have been achieved, the same principles related to removal efforts can be applied to guide surveillance efforts for confidently declaring eradication (Ramsey et al. 2009; Anderson et al. 2013), although careful consideration must be given to potential density-dependent changes in home range size and habitat selection.

Author contributions

PM designed the initial field and research plan, supervised and undertook field work; DPA and MCL developed the ecological models and analysed the data; and ADML wrote the manuscript with input from DPA, MCL and PM.

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Supplementary material

Additional supporting information may be found at the Manaaki Whenua – Landcare Research DataStore: <https://doi.org/10.7931/kjtp-mn13>

Table A1. Land-cover types found on Auckland Island, New Zealand.

Table A2. Results of RSF model 3 for the individual level estimates of $\alpha_{0,i}$ and $\alpha_{1,i}$. The mean and 95% credible intervals (CI) are shown.

Figure A1. Monitoring periods for 15 collared feral pigs (*Sus scrofa*) on Auckland Island, New Zealand, from June 2007 to July 2008.

Pig ARGOS location data.

Pseudo-absent location data within MCPs.

Python scripts for analysing data.

Python scripts for processing the results of the MCMC analysis.