



RESEARCH

Spatial distribution of probable ship rat reinvaders in a pest-fenced ecosanctuary

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Abstract: Managers of ecosanctuaries often need to make decisions in the face of uncertainty. Model-based tools which aim to assist this process, for example proof-of-absence models, are underpinned by assumptions about the behaviour of target animals, including their spatial movements. In some cases, however, there are few empirical data to draw on to inform these models. The movement behaviour of individual pests in low-density environments, as well as the dispersal of juveniles away from their natal location, is poorly understood for many species, including the ship rat (*Rattus rattus*). We document probable ship rat incursions and a breeding event within a pest-fenced ecosanctuary in Nelson, New Zealand. A comparison of genetic profiles suggested breeding had taken place, with 13 of 18 rats captured likely to be a family group (mother and likely three litters of offspring). Straight line distances from the recovery location of the putative mother to those of her probable offspring ranged up to a maximum of 1510 m, but were mostly within 200 m. No significant effect of sex, weight or head-body length on movement distance was found. Rat captures and detections appeared to be concentrated around waterways. The presence of unrelated rats in the capture sample points to eradication survivors, several separate incursion events, or a combination of both. Contributions of new data, such as this, help ecosanctuary managers by guiding better design of efficient pest detection networks, and improve models that aid their decision-making.

Key words: dispersal, juvenile, pest-fenced ecosanctuary, predator free New Zealand, *Rattus rattus*, reinvasion, surveillance

Introduction

The Predator Free Aotearoa New Zealand by 2050 movement aims for the eradication (i.e. “complete and permanent removal of all wild populations...”; Bomford & O’Brien 1995; Genovesi 2001) of invasive rats (*Rattus* spp.), brushtail possums (*Trichosurus vulpecula*), and mustelids (*Mustela* spp.) from mainland Aotearoa | New Zealand by 2050 (PF2050 2023). At present, the Aotearoa landscape is a patchwork of areas of intensive predator control effort and large areas where pulsed control is achieved via aerially broadcast toxic baits, with extensive areas of little or no control effort in between (Innes et al. 2024). An ecosanctuary is “...a project larger than 25 ha implementing multi-species pest mammal control for ecosystem recovery objectives, and usually with substantial community involvement” (Innes et al. 2019; Innes et al. 2024). Some ecosanctuaries aim to suppress predator or mammal pest species to low population densities to protect native biota, while others seek to completely remove these species. Reinvasion of pests from adjacent areas (where pest densities are typically higher) is a constant threat for all mainland ecosanctuaries, but especially critical for those aiming to remove all mammalian pests and keep them out.

For this reason, ecosanctuaries protected by pest-exclusion fencing (hereafter pest-fenced ecosanctuaries) are typical where complete removal and exclusion of pest mammals is the goal (Innes et al. 2024), although alternatives relying on strong natural boundaries such as mountain ranges or large rivers are being developed (Nichols et al. 2021). Despite these protections, pests do breach the barriers occasionally (Connolly et al. 2009; Maitland 2011) so systems to rapidly detect and remove invading individuals or family groups are a critical component of the ongoing management of both pest-fenced and unfenced ecosanctuaries.

Optimal design of detection networks in ecosanctuaries requires a good understanding of target species movement and invasion behaviour to inform detection models (Tompkins & Ramsey 2007; Monks & Tompkins 2012). Proof-of-absence modelling (Gormley et al. 2021; Ramsey et al. 2023) and rapid eradication assessment (Samaniego-Herrera et al. 2013; Russell et al. 2017; Kim et al. 2020) are related applications which rely on spatial behaviour parameter inputs to assess the probability of successful eradication given a specified spatial arrangement of detection tools and the duration of detection effort. However, empirical data to inform these models is sometimes limited, especially as it relates to pest movement

behaviour in low-density environments, and juvenile movement behaviour (Nathan et al. 2020).

Here, we report on probable ship rat (*Rattus rattus*) incursions and a breeding event that occurred in the pest-fenced Brook Waimārama Sanctuary in Nelson, New Zealand in 2019. We use genetic profiling to assess the relatedness of ship rats captured during this event and describe the spatial distribution of related and unrelated individuals. We contribute new empirical data to the small body of knowledge about juvenile ship rat movements in the wild that can be used to inform detection network design for surveillance and proof-of-absence applications in ecosanctuaries.

Methods

Field site

Located in Nelson, New Zealand, Brook Waimārama Sanctuary (abbreviated as BWS) covers 690 ha of predominantly mature beech forest, with some regenerating broadleaved forest in the southern part of the site (Smith & MacKay 2015). The site was formerly used as a waterworks reserve for Nelson City Council. The Brook Waimārama Sanctuary Trust was established in 2004 with the vision of creating a refuge for native birds, lizards and invertebrates through control of mammalian pests and weeds, and BWS was opened to the public in 2007.

In 2016, a 14.4 km pest fence (Xcluder®, Rotorua) surrounding the site was completed, creating the largest pest-fenced ecosanctuary in the South Island (Innes et al. 2019). The subsequent eradication attempt aimed to completely remove all pest mammal species from inside the pest-fenced area. To target rodents, toxic bait (Pestoff 20R rodent bait, 10 mm, 0.02 g kg⁻¹ brodifacoum; Orillion, Wanganui) was distributed by helicopter throughout BWS three times in 2017 (applied at a rate of 16 kg ha⁻¹ on 2 September, and 8 kg ha⁻¹ on 5 October and 18 October). Complementary methods were used to remove non-rodent pest mammals (these are not detailed here, given the scope of this paper is on rodents). Intensive detection and mop-up operations commenced three weeks after the final toxin application.

Post-operation proof-of-absence surveillance

A detection network consisting of 2041 white corflute tracking tunnels on a 50 × 100 m grid, along with 306 single-set DOC200 traps in wooden boxes, 73 Victor rat traps in white corflute trap boxes, 160 cat-sized white corflute tracking tunnels, and 34 single-set DOC200 traps in hedgehog trap tunnels (large timber tunnels with wide entrances at both ends) was serviced weekly for an eight-week period. This was followed by a further four months servicing the same detection network plus an additional 370 peanut-butter lured chew cards monthly. This proof-of-absence effort made it over 95% likely, given reasonable assumptions (see Discussion and Appendix S1 in Supplementary Material) that the campaign had been successful in eradicating rats (*Rattus rattus* and *R. norvegicus*). Mice (*Mus musculus*) may have also been eradicated (there were no detections during the six-month period) but have since re-established (RS, unpub data). Other pest species removed via direct or secondary poisoning included mustelids (*Mustela spp.*), brushtail possums (*Trichosurus vulpecula*), feral cats (*Felis catus*), hedgehogs (*Erinaceus europaeus*), feral pigs (*Sus scrofa*), lagomorphs, and browsing mammals. BWS was re-opened to the public on 15 July 2018.

Incursion detection surveillance

While pest fences are highly effective at keeping the majority of potential re-invaders out of pest-fenced ecosanctuaries, there is always a risk of incursion (Innes et al. 2019) and ongoing surveillance is required so that any reinvading pest species can be quickly detected and removed. During the time period covered in this study, the standard pest detection network at BWS (Appendix S2) consisted of 2420 white corflute tracking tunnels and 305 single-set DOC200 traps in wooden boxes distributed across the entire fenced area. These devices were laid out on lines spaced approximately 100 m apart, with tracking tunnels placed every 50 m (effectively creating a 100 × 50 m grid) and DOC200 boxes every second line at 200 m spacing approximately (effectively creating a 200 × 200 m grid). Additionally, there were 287 fortnightly-serviced Victor™ rat traps in white corflute trap boxes placed along two inner fence perimeter lines at approximately 100 × 25 m spacing. The array along the perimeter lines also included tracking tunnels and DOC200 trap boxes (included in the aforementioned totals for these device types). Traps and tracking tunnels were lured with either chocolate-hazelnut spread, peanut butter, Eggsellent (Connovation, Auckland), or Erayz (Connovation, Auckland). In addition to the standard detection network, additional detection devices such as trail cameras were sometimes temporarily deployed in locations of interest.

Areas which were considered to be relatively high-risk (e.g. fence perimeter tracks, public loop walk, around entry gates) were serviced at least fortnightly. Sanctuary-wide surveys, i.e. servicing the entire detection network, were carried out 3–4 times per year. If any sign of rats was detected, additional Victor™ rat traps in white corflute trap boxes and white corflute tracking tunnels were added to increase device density to 25 × 25 m spacing within 50 m on all sides of the detection, and servicing frequency was increased to twice per week for two weeks followed by once-weekly checks for six weeks. Traps and tracking tunnels were lured with either chocolate-hazelnut spread, peanut butter, Eggsellent or Erayz.

Rat incursions and response

During the period from April 2018 to January 2020 there was a series of rat detections and captures within BWS, most likely representing several separate incursion events (see discussion). For all captured rats, weight, sex and head-body length were recorded and a necropsy was undertaken (where condition of the carcass permitted). Carcasses were then labelled with retrieval date and location and preserved in a freezer. Later, genetic samples (ear tissue) were taken from each preserved rat and stored in individual labelled vials of 95% ethanol.

The presence of juveniles indicated breeding had almost certainly taken place within BWS. Based on the spatio-temporal pattern of captures BWS managers believed this was due to a single breeding female. In addition to ongoing trapping, managers responded to the assumed breeding event by initiating a targeted hand-laid brodifacoum operation on 17 September 2019. Pestoff 20R bait (Orillion, Whanganui) was applied at a rate of 8 kg ha⁻¹ over an area of 3.52 ha centred where breeding was suspected. Hand-baiters walked lines 25 m apart and stopped every 10 metres to throw toxic pellets up to a distance of 12.5 m to one or both sides depending on which part of the area they were working in. At each stop point, hand-baiters distributed 100 g of bait to cover the surrounding 125 m².

On 5 October 2019, 18 days after the hand-baiting operation, a field worker found and collected an adult female rat carcass in a stream within the baited area. This rat was necropsied and its weight, sex and head-body length were recorded. Because the rat was in condition indicating it had recently birthed young (lactating), BWS managers speculated that this was the breeding female suspected to be resident.

Genetic profiling and relatedness assessment

To assess relatedness of the suspected mother to the other rats captured, we used a genetic profiling approach. Genotyping was conducted by EcoGene® (Auckland, NZ), a business unit of Manaaki Whenua-Landcare Research, using the rat ear tissue samples we provided. Genetic profiles of each sampled individual were produced, using nine microsatellite loci (Abdelkrim et al. 2005a,b), originally developed for *Rattus norvegicus* (Jacob et al. 1995), and a sex-linked locus (Peakall et al. 2006).

We compared the genetic profile of the suspected mother rat (hereafter mother) to that of all other sampled individuals, and distinguished probable offspring and non-offspring on the basis of private alleles. This approach allowed us to rule out non-offspring with certainty, because if an individual had no alleles in common with the mother at one or more loci it could not be her offspring (Miller et al. 2010). It is not possible to confirm parentage with absolute certainty using a private alleles approach. However, in practice it is highly unlikely that an unrelated rat would have alleles that are consistent with it being the possible offspring of the mother. For that to occur, at each microsatellite locus, one of the individual's two alleles must be the same as one of the two that the mother has; across nine loci and with high polymorphism this is unlikely

(estimated 1 in 400 chance, Appendix S3). We also inferred the genotype(s) of the unknown father(s) by subtracting alleles that could have been inherited from the mother from the genotypes of probable offspring to ascertain which alleles must have been inherited from a father.

Results

Rat detection and capture history

In the Brook Waimārama Sanctuary between April 2018 and November 2019 there were a total of 49 rat detections in tracking tunnels, 1 detection on a trail camera, 17 rats caught in traps, and 1 rat carcass recovered fortuitously after toxic baiting. A rodent detection dog team searched targeted areas of BWS for a three-day period from 8–11 May 2018, but did not find any rat sign. Table 1 is a summary of all captured and recovered rats. Note that the exact date a rat was trapped is unknown because traps were not serviced daily. However, the date of capture can be narrowed down to the range between the carcass recovery date, and the date that the trap was previously serviced (Table 1).

The first rat detections were a series of eight tracking tunnel detections beginning early in April 2018. On 23 April 2018 a female rat was recovered from a trap located near the public entrance to BWS. In July 2018, a male rat was captured at the other end of BWS (2800 m away from the April capture location), 21 days after a treefall event destroyed a short section of the fence (the rat was captured 450 m away from the fence breach location). There were no further detections or captures until April 2019, when rat tracks were discovered in tracking tunnels on two occasions (7 and 14 April). Subsequently, there was a period of more than three months with no further detections; before a rat was found in a trap on 28 July 2019,

Table 1. All rats captured in the Brook Waimārama Sanctuary from April 2018 to November 2019. Distance to the location where the mother's carcass was recovered is shown for probable offspring only, as determined by private allele analysis. The table is ordered by genetic analysis result, then by distance to mother's location. ^ Approximate age range based on weight as a proxy, after Bentley & Taylor 1965, * Sex indeterminate - genetic and phenotypic sex assignments were in disagreement. † Carcass lost, phenotypic characteristics not confirmed.

ID	Date recovered	Date of previous trap service	Sex	Weight (g)	Head-body length (mm)	Genetic analysis result	Distance to mother's location (m)	Age range estimate (months)^
1	5/10/19	n/a	Female	159	165	Mother		>9
15	23/09/19	19/09/19	Male	114	155	Probable offspring	1510.4	3–9
5	5/08/19	2/08/19	Female	98	145	Probable offspring	553.0	3–9
10	2/09/19	26/08/19	Female	123	176	Probable offspring	553.0	3–9
4	1/08/19	Unknown	Female	84	135	Probable offspring	331.7	1–3
7	23/08/19	20/08/19	*	63	125	Probable offspring	179.7	1–3
9	28/08/19	Unknown	Female	94	145	Probable offspring	156.3	3–9
3	28/07/19	Unknown	Female	86	145	Probable offspring	118.5	1–3
6	11/08/19	9/08/19	Female	103	145	Probable offspring	118.5	3–9
16	2/10/19	25/09/19	Male	33	100	Probable offspring	75.2	0–1
12	3/09/19	31/08/19	Female	86	140	Probable offspring	58.3	1–3
13	30/08/19	28/08/19	Male	66	115	Probable offspring	1.0	1–3
11	3/09/19	31/08/19	Male	99	155	Probable offspring	1.0	1–3
18	23/04/18	20/04/18	Female	103	150	Not offspring	–	3–9
2	28/07/18	14/07/18	Male	112	155	Not offspring	–	3–9
8	23/08/19	19/08/19	Female	132	160	Not offspring	–	3–9
14	13/09/19	10/09/19	Female	148	175	Not offspring	–	>9
17	27/11/19	12/11/19	†	†	†	Not sampled	–	–

with a tracked tunnel found the same day 1039 m away. From this point, detections were frequent with 25 tracking tunnel detections, 1 trail camera detection, and 11 trap captures from 1 August until the hand-laid brodifacoum operation on 17 September (Fig. 1, Table 1). Topographic data sourced from the LINZ Data Service and licensed for reuse under the Creative Commons Attribution 4.0 International License.

Following the toxin operation, two rat carcasses were recovered from within the baited area: the suspected mother as described in methods, and a very young juvenile male (33 g weight) found in a Victor rat trap. Both the mother and the juvenile showed evidence of being poisoned (green dye in stomach and evidence of haemorrhaging).

Outside of the baited area, post-toxin rat detections ($n = 12$) and captures ($n = 2$) continued sporadically until 18 Jan 2020. Of all the female rats captured, only the putative mother was shown to have ever been pregnant at necropsy.

The next rat detection within BWS (a capture in a Victor rat trap less than 50 m from the western fenceline) did not occur until 19 Feb 2022, more than two years later. This and following detections are considered to represent a separate incursion(s) and are not further considered here.

Relatedness assessment

Comparison of the putative mother's genetic profile to that of all other captured rats except one (one rat carcass had been lost and was therefore not available to be sampled) revealed that 12 of the captured rats were her probable offspring, and 4 could not be her offspring (Appendix S4).

There was evidence of multiple paternity within the probable offspring, with one of the juvenile rats found to have private alleles at two loci, indicating a different father from the other 11 probable offspring. The inferred fathers' genotypes did not match any of the genetic profiles in our sample showing that the fathers of the probable offspring were not captured (unless the lost rat carcass was one) (Appendix S4). The possibility that individuals classed as probable offspring were otherwise closely related to the mother (e.g. siblings, nephew or niece) is considered less likely on the basis of age estimates (Table 1), and because necropsies found no evidence that any other adult female had ever been pregnant.

Of the four rats shown not to be the mother's offspring, two were captured in 2018 and were among the earliest post-eradication attempt detections within BWS (Table 1, Fig. 1). The other two were caught within the same timeframe as the

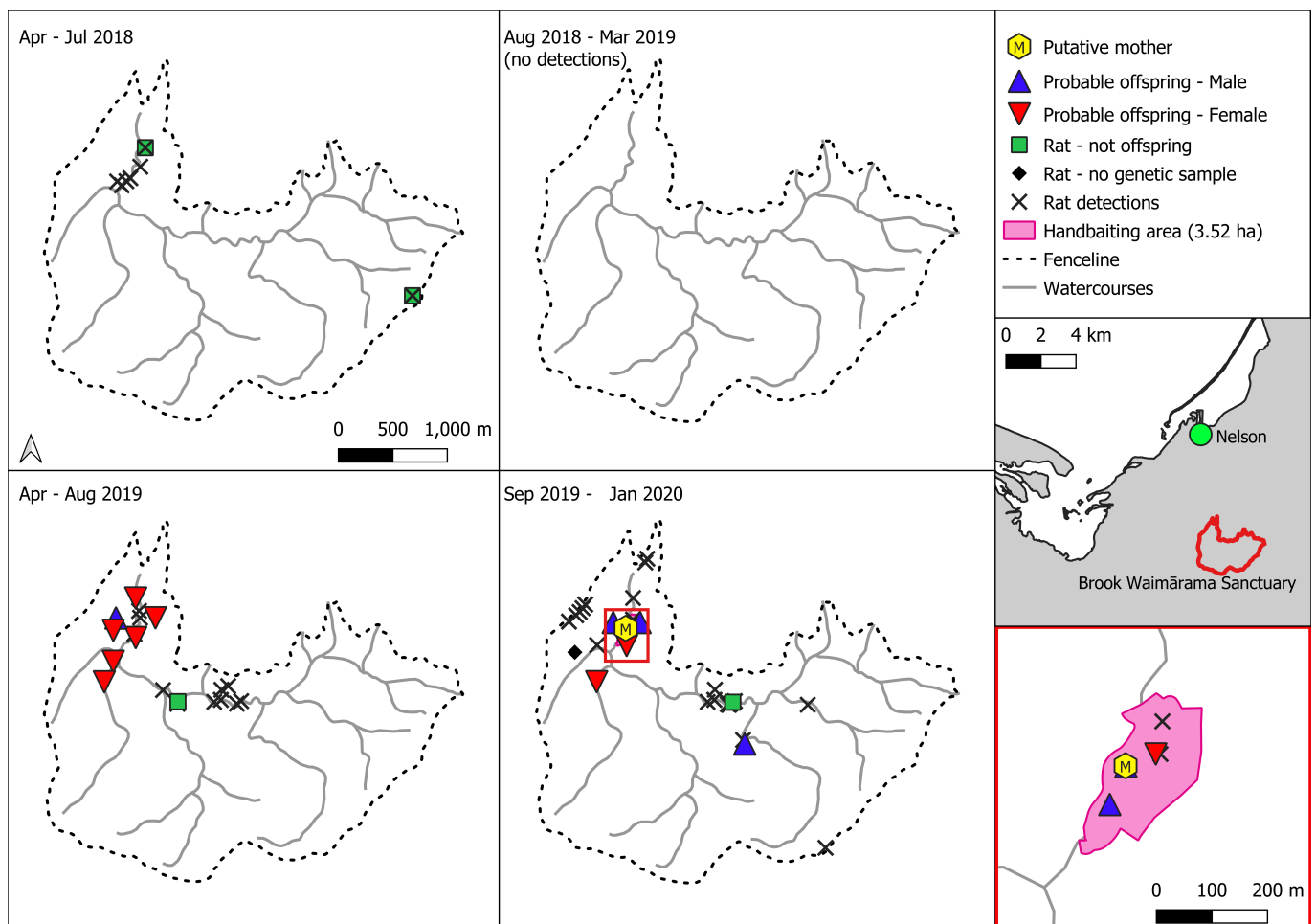


Figure 1. Rat detections and captures in Brook Waimārama Sanctuary, April 2018 to January 2020, including recovery locations of the putative mother, probable offspring, and non-offspring. Overlapping rat capture locations have been slightly offset for display. Inset panels show the position of the research site relative to Nelson, NZ (middle right), and the area over which brodifacoum baits were sown in response to the rat breeding event (bottom right). Contains data sourced from the LINZ Data Service licensed for reuse under CC BY 4.0.

probable offspring. It is notable that all four of the non-offspring were ruled out by private alleles at four or more microsatellite loci, supporting the assumption that a genetic profile that is consistent with a putative parent by chance is rare.

Juvenile movement

Distances from the recovery location of the mother to those of her probable offspring ranged from 1–1510 m (Table 1, Fig. 1). Note that these measurements represent minimum distances because it is highly likely that the rats roamed more widely than their trapping location indicates, or would have if they had not been trapped. A 100% minimum convex polygon encompassing the locations of all related individuals covered an area of 58.7 ha (QGIS v3.16.7, QGIS.org 2023).

The distribution of mother-to-offspring distances was highly skewed towards shorter distances. Eight probable offspring were caught within 200 m of the mother's location (three males and five females), and a further three (all female) were caught within 300–600 m (Fig. 2). One probable offspring (male) was caught 1510 m from the mother's location, making it an outlier amongst its full or half-siblings.

After removing the data point for the male that moved 1510 m (which was causing heteroscedasticity in linear model residuals), neither probable offspring weight (linear model, $r^2 = 0.25$, $F(1,9) = 2.9$, $p = 0.12$), nor head-body length (linear model, $R^2 = 0.25$, $F(1,9) = 3.0$, $p = 0.12$) was significantly related to the distance between the mother and probable offspring's recovery locations (see also Appendix S5 for alternative models tested). Sex also had no significant effect on the distance between mother and probable offspring (generalised linear model, $R^2 = 0.02$, $F(1,9) = 0.2$, $p = 0.67$) after removing the data point for the rat of indeterminate sex.

Discussion

Limitations

Here we report on probable incursions of wild ship rats into a pest-fenced ecosanctuary. All data were incidentally collected and observational, which means that there are several unknown factors to consider when drawing inference from our observations. Most importantly, the actual location of the natal nest (or nests) is unknown. We assume that the location of the mother's carcass was indicative of a central location within her home range, and that her nest site(s) was nearby. We judged this assumption to be reasonable, given the location and timing of detections observed, and that Nathan (2016) found that ship rat den sites were within 20 m of their home range centre on average.

It follows that the distances between probable offspring and mother capture locations that we report are only indicative of the distance the juveniles moved away from the (unknown) true natal location. Furthermore, the mother-to-offspring distances are based on trapping locations. This means that we cannot strictly interpret these juvenile movements as dispersal distances—where dispersal is defined as the net movement between an individual's point of origin and the site of first breeding (Howard 1960)—because the juveniles may have moved further from the natal area before settling if they had not been killed. Despite these limitations, there are so few reports on juvenile ship rat movements that all new information is valuable (Nathan et al. 2020; Innes & Russell 2021).

A further limitation is that the rats represented in the capture record are almost certainly not a complete sample of the rats that were present in BWS throughout the period from April 2018 to January 2020. Based on the relatedness analysis,

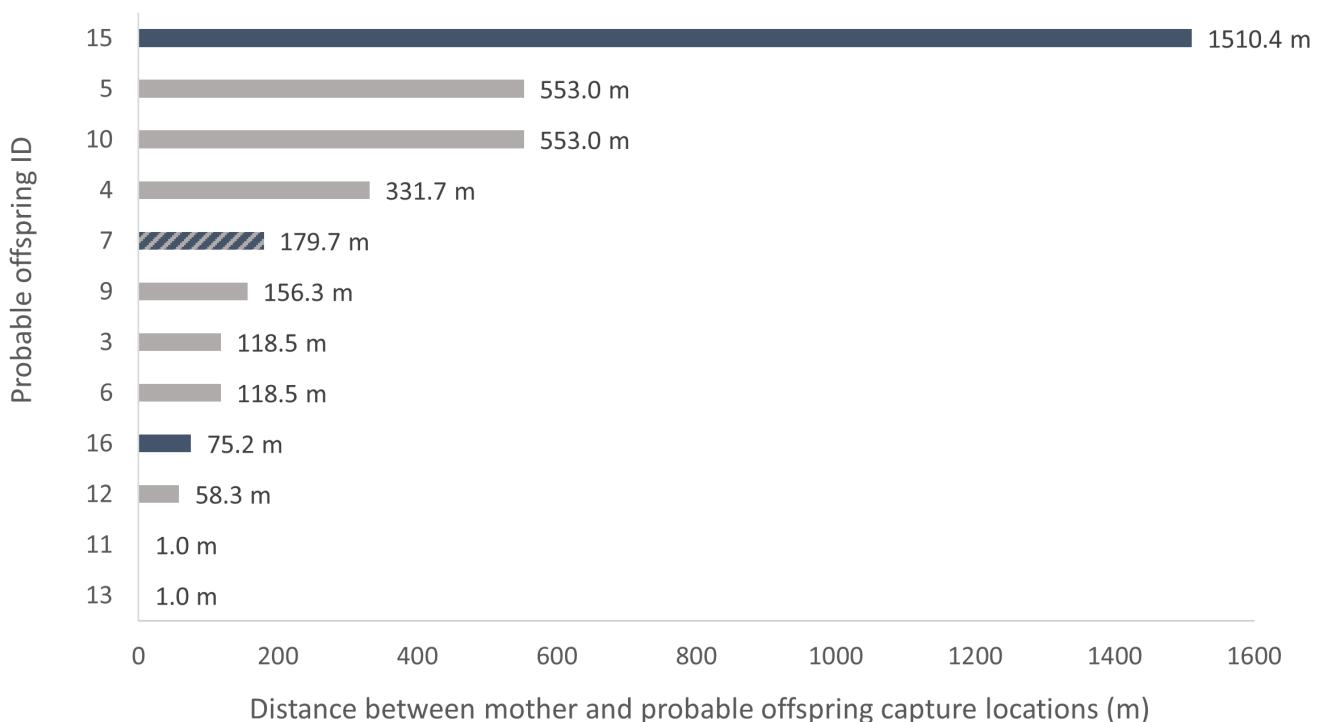


Figure 2. Distance between probable offspring capture locations and the mother's recovery location (m). Dark-shaded bars represent males (includes ID 11 and ID 13) and light-shaded bars represent females. The striped bar represents an individual of indeterminate sex.

we can infer that there is at least one father missing from the captured sample, and possibly a second (depending on whether the lost carcass was one of the fathers). Some individuals may have been killed during the brodifacoum operation. The capture of one very small rat (33 g, with evidence of toxin ingestion) indicates that there was a recently- or near-weaned litter of juveniles present at the time of the brodifacoum operation. As ship rat litters consist of 3–10 individual pups (Innes & Russell 2021) it is highly likely that several very young rats were killed in the toxin operation. Further individual rats may have died of natural causes, or even exited BWS as pest fences are only designed to prevent entry (Innes et al. 2011). Consequently, it is possible that some juvenile rats moved further than the maximum distance we recorded.

It is also worth emphasising that, despite our best efforts to provide supporting evidence and quantification of likelihood, we cannot be completely certain that the captured rats were re-invaders (or offspring of re-invaders) rather than survivors of the 2018 eradication attempt. We suggest that the use of non-toxic biomarker baits outside of pest-fenced ecosanctuaries to assess the rate of reinvasion may be a fruitful area for future research, as finding a marked animal inside a pest-fenced area provides certainty of origin outside of the fenced area (finding an unmarked individual, conversely, does not provide certainty of origin inside the fenced area). We note however that the logistic difficulties and costs associated with this type of research mean it may be more suitably led by academic or other research institutions than by pest-fenced ecosanctuary managers as an in-house project.

Juvenile movement behaviour

Typical home range lengths for adult ship rats range from 103–171 m for females, and 159–550 m for males (Dowding & Murphy 1994; Hooker & Innes 1995; Pryde et al. 2005), but very little is known about juvenile movement behaviour. Where long-range movements (>1 km) have been reported, it has usually been in the context of a low-density population. Innes et al. (2011) recorded a translocated adult male moving 1100 m after being released within pest-fenced Maungatautari Sanctuary. Similarly, the translocated mother in Nathan et al.'s (2020) aforementioned study ranged over at least 1625 m within an area that had been recently treated with aerial 1080 toxin, and where no rat activity had been detected for the two months prior to the release. In that study, where no or very few adult conspecifics were present, the wide-ranging behaviour was hypothesised to be exploratory, and likely driven by the search for resources and mates in an unfamiliar environment (Nathan et al. 2020). Carpenter et al. (2023) also reported on the movements of adult ship rats in a low-density environment, but in a different context. They wild-captured 10 ship rats in Fiordland on the edge of an area where rats had been suppressed using aerial 1080 and attached radio-transmitters to them. Three rats in their sample (all female) made long-distance movements of 1000, 1515, and 1516 m into the treated area. The authors had evidence that rat population density in the un-treated area where their subject individuals were caught was extremely high, and hypothesised that the long-distance movements they observed may have represented dispersal induced by resource limitation and high intraspecific competition in the area of origin (Carpenter et al. 2023).

Our findings contribute to a growing body of evidence that long-distance movements do occur in low-density environments, and that young rats are capable of these movements as well as adults. However, it is equally notable

that not all of the juveniles in our sample made these large movements. As far as we were able to determine based on trapping locations, over half ($n = 8$ of 12) of the probable offspring of the mother remained within 200 m of their assumed natal location, a few ventured a medium distance up to 600 m ($n = 3$), and only one travelled a distance exceeding 1500 m, with no statistically significant relationship found between body size metrics and distances moved. That there is no relationship between body size and distance may be because of the small sample. Again, we acknowledge that the juveniles may have moved further away from the assumed natal location if they had not been trapped, so these distances should be considered as minimal. Nathan et al. (2020) released a translocated mother ship rat and her pre-weaned litter of juveniles into South-Westland beech-kamahi forest and reported on the movements of three of the juveniles away from a known nest location (four additional siblings were not re-captured). Distances between capture locations and nest/release site were 164 m for one female juvenile, and 128 m and 675 m for two males. Although a very small sample, those measurements are not inconsistent with our findings, with small mother-offspring distances more commonly recorded than medium range ones. Carpenter et al. (2023) reported similar findings for adult rats, with the majority of their radio-collared rats ($n = 6$ of 10) ranging over less than 200 m, and the remaining four subject rats covering distances of 657–1516 m. Similar to our findings, Carpenter et al. (2023) detected no effect of sex on movement distances. Although data are still few, we speculate that a pattern is beginning to emerge whereby, in low density cases, the majority of ship rats (adult and juvenile) tend to move only short distances, some make medium-range movements of around 2–3 times a typical home range length, and a minority of individuals make long-distance movements well in excess of what would be considered to be standard settled behaviour. Further support is found in Abdelkrim et al. (2010) that investigated fine-scale genetic structure of the ship rat population in Puketi Forest Conservation Reserve, in which family groups living in proximity manifested as patches of high genetic relatedness in the landscape. To further investigate this hypothesis, a study which does not rely on lethal detection would be preferable. For instance, a mark-recapture approach using PIT-tags and/or dye-marking (e.g. Nathan 2016; Carpenter et al. 2022), although difficult to execute in the wild, would allow juveniles to complete their dispersal.

A final observation was that the pattern of rat captures and detections appeared to be concentrated around waterways, leading the BWS team to speculate that the dispersing juveniles were tracking along these landscape features. While we did not formally test for any such effect, the pattern of captures being disproportionately close to waterways is clear from Fig. 1. Waterways have been suggested as one of several potential reinvasion route types between forest fragments in pasture (King et al. 2011). Audy and Harrison (1951) found that a river seemed to act as an access point through an otherwise limiting mountain range for rat-borne typhus mites. We suggest that further investigation of rat dispersal behaviour in relation to waterways and other significant landscape features may be informative.

Incursion history and implications for incursion detection

Even in pest-fenced ecosanctuaries, there is always a risk of incursion (Innes et al. 2019). Damage to fences, for example due to treefall, landslides, flood scour, or sabotage may result in incursions (Connolly et al. 2009). Many pest fences have

some points that are more permeable such as vehicle or pedestrian gates which are occasionally open for short periods, or waterway gates for streams (Day & MacGibbon 2007). At BWS, the areas considered to be of highest risk for incursion are those adjacent to the pest fence, the pedestrian and vehicle access gates, and four automatically opening culverts which present a high risk during and after high water flow events (RS, unpubl. data).

Taken together, the detection record from BWS and the relatedness analysis we present here suggest multiple incursion events occurred in the period from April 2018 to January 2020 (i.e. 18–39 months after the last aerial baiting). Best practice for island eradications recommends waiting for two reproductive seasons (i.e. two years in New Zealand) before conducting final monitoring and declaring eradication (Broome et al. 2017), and we cannot rule out the possibility that some rats survived the initial aerial eradication attempt. However, considering the intensive post-eradication attempt detection effort, as well a delay of six months between the end of the aerial brodifacoum programme and the first rat detections, we consider that the two rats trapped in April and July 2018 are likely to have been recent invaders rather than eradication attempt survivors (Appendix S1). We also consider it likely that these two rats died without any offspring, given the lack of detections for more than eight months after their captures. These captures suggest the sentry detection and capture network is sufficiently effective to prevent re-establishment.

Given the eight-month gap (i.e. 28 July 2018 to 7 April 2019) in the detection record, as well as the results of the relatedness analysis suggesting no relation to the two previously captured rats, the mother rat most likely represents a separate incursion event. She may have entered BWS already pregnant. If not, there must have been a further incursion(s) by at least one adult male that was not captured (or that was captured but the carcass lost) who mated with the mother in-situ. We were unable to definitively confirm either of these scenarios.

When taken together, the broad ranges of retrieval dates (28 July to 2 October 2019) and weights (33–123 g) of the 12 probable offspring show that there were at least two, probably three different litters represented in the captured sample. Although ship rat littermates do not always have similar weights at the same age (Bentley & Taylor 1965) the smallest individual, a 33 g male retrieved on 2 October 2019, would have been just-weaned or even not quite weaned (Innes & Russell 2021) and is very unlikely to have been a littermate of any of the other individuals represented in our sample. Given that ship rat litters are thought to consist of a maximum of 10 pups (Innes & Russell 2021) the remaining 11 probable offspring are likely to represent two litters.

There were at least two fathers represented in the mother's probable offspring, which could indicate an adult male incursion after the mother's arrival, or that the female mated with one of her own male offspring once it was mature. A further two female rats were captured in August and September 2019 that were found not to be the offspring of the mother. A known fence breach event on 15 May 2019 is considered by BWS managers to be the likely source of these rats (RS, unpubl. data), with the breach located 251 m and 604 m from the capture locations. We found no evidence that either of these two females had ever birthed young (based on their necropsies).

The events at BWS emphasise the need for robust detection and response strategies in ecosanctuaries, even those that are protected by pest fences. Occasional incursions are to be expected, and sometimes these will result in the birth of

offspring within the protected area. When this occurs, rapid detection and response is required to remove the new population while it is still small and spatially restricted, and to avoid the need for a large-scale removal operation. Although we found no evidence that any of the captured female rats (other than the mother) had ever been pregnant, at least some of them were of reproductive age (based on sexual maturity characteristics at necropsy). Presumably, these would have soon begun to breed if mates were also available, so if treatment had been delayed much longer a larger operation may have been necessary.

In this case, a very small (3.52 ha) hand-laid toxin operation was sufficient to remove the breeding population of rats (in combination with existing trapping infrastructure). This is a notable success, given that the minimum footprint of her probable offspring extended over 58.7 ha. The fact that the mother bred and birthed within BWS at least once and evaded being trapped in the standard detection network for several months before being poisoned speaks to how critical the toxin operation was in ending the incursion. King et al. (2014) suggested that breeding female ship rats may be relatively sedentary, so the mother may have infrequently encountered trap infrastructure. A hand-laid (or aurally dispersed) toxic bait pellet can effectively target individual rats that have restricted movements, or that may be trap-shy. On the other hand, juveniles and naïve individuals may be particularly open to investigating new objects and therefore more trappable (Thorsen et al. 2000; Gronwald & Russell 2022), which may explain the success of the standard detection network in trapping the probable offspring.

The movement data reported here are instructive, particularly given the scarcity of such data in the literature. Adult and juvenile ranging and dispersal distances are key parameters in proof-of-absence modelling (Gormley et al. 2021; Ramsey et al. 2023) and rapid eradication assessment (Samaniego-Herrera et al. 2013; Russell et al. 2017; Kim et al. 2020) which aim to show, with a high degree of probability, that an area is free of target pest species. Due to a paucity of empirical data, these parameters have often been estimated based on expert opinion (Driscoll et al. 2014). However, recent publication of a synthesis of existing spatial detection parameter data for ten mammalian pest species in New Zealand will facilitate improved model parameterisation in the future (Vattiato et al. 2023).

A related application is the design of pest detection networks. Landscape-scale predator elimination operations (Bell et al. 2019; Nichols et al. 2021; Latham et al. 2022) are being trialled on the New Zealand mainland as part of the push towards a Predator Free New Zealand by 2050 (PF2050 2023). Due to the very large areas and often inhospitable terrain encompassed by these projects, it is logistically and financially infeasible to operate detection networks at the same intensity as the one in BWS. Sparser detection networks necessarily target breeding populations rather than individuals and thus rely on a strong understanding of target species movement behaviour. The BWS invasion contributes valuable new information to the models underpinning this research. Contributions of empirical data which inform research and development, such as we present here, will be invaluable in the work to achieve a predator-free Aotearoa New Zealand.

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Author contributions: RS led the field work at Brook Waimārama Sanctuary and all associated data collection. HN conceived the study and lead-authored the manuscript. NM authored Appendix S1 to estimate likelihood of initial rat eradication from BWS, and Appendices S3 and S4 to support our relatedness analysis. HN and NM collaborated on data analysis and interpretation and discussed potential applications of the data along with RS. The first draft of this manuscript incorporated elements of a presentation given by NM. All authors contributed substantive detail to the manuscript and reviewed and approved the final version.

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Supplementary Material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Rapid eradication assessment for ship rats following Brook Waimārama Sanctuary eradication attempt.

Appendix S2. Brook Waimārama Sanctuary surveillance network.

Appendix S3. Frequency of number of loci consistent with the mother.

Appendix S4. Genetic profiles of all genotyped rats and inference on relatedness.

Appendix S5. Head-body length (mm) and weight (g) of probable offspring and distance to mother's location.

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