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RESEARCH

Movement behaviour of a translocated female ship rat and her offspring in a low rat density New Zealand forest

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Abstract: Dispersal is a fundamentally important aspect of animal behaviour, but empirical data describing it are lacking for many species. Here, we report on a field study aimed at measuring post-weaning movement distances of juvenile ship rats (*Rattus rattus*) and their mother away from a known natal nest site in an area with low conspecific population density. The movement behaviour of invasive species at low density is of particular interest, as it can inform design of surveillance arrays to detect incursion into predator-free areas. Detecting a single invading individual requires intensive effort. An alternative approach is to focus on detecting newly-established breeding populations, while they are still spatially-restricted and able to be eliminated with timely and effective incursion response. We released a bio-marked rat mother and litter into an area recently treated with sodium fluroacetate (1080) and monitored their behaviour for 12 weeks. Final capture locations ranged up to 675 m from the release location for the juveniles, with 796 m between known siblings. The total range length for the mother exceeded 1.5 km. Although we found no evidence that the movements of the family as a collective extended further than those of the mother alone, the concept of targeting detection efforts to breeding populations warrants further investigation due to the improved probability of detecting at least one of multiple individuals, rather than a single invader.

Keywords: biomarker, conservation, dispersal, predator free New Zealand, *Rattus rattus*, reinvasion, surveillance

Introduction

Dispersal is broadly defined as "any movement of individuals or propagules with potential consequences for gene flow across space" (Ronce 2007), and is a fundamentally important ecological process in many animal species, with numerous potential costs and benefits to dispersing individuals (Byrom & Krebs 1999; Bowler & Benton 2005; Waser et al. 2013; Bonte et al. 2014). Nevertheless, the dispersal process is a poorly understood aspect of animal behaviour, largely due to the difficulty of collecting empirical data (Driscoll et al. 2014).

The advancement of molecular techniques has resulted in some progress in understanding dispersal. Spatial genetic variation among conspecifics can reveal indirect information about dispersal via the extent of genetic exchange between populations (Abdelkrim et al. 2010; Sarre et al. 2014). More direct genetic approaches, such as parentage analyses, population assignment tests, and genetic tagging, can produce valuable individual-level information (Peakall & Lindenmayer 2006; Waser et al. 2006; Veale et al. 2012). However, population assignment approaches require large sample sizes and substantial levels of genetic differentiation, and parentage analyses need a comprehensive pool of potential parents to infer individual dispersal distances from locations of parents and offspring confidently (Lowe & Allendorf 2010).

The dispersal process is particularly relevant to invasion biology, and in the practical management of invasive species. For instance, knowledge of how a particular species disperses across a landscape can be used to identify areas at most risk of invasion (Prasad et al. 2010), or conversely areas that may have some protection due to natural barriers (Zalewski et al. 2009; Cook 2018). Dispersal distance is also a key parameter in modelling processes such as population establishment and rapid eradication assessment (Samaniego-Herrera et al. 2013; Russell et al. 2017). As measurements of dispersal distances (in particular away from a known natal site) are frequently unavailable, expert opinion is often used where a model includes dispersal distance as a parameter (14% of studies reviewed in Driscoll et al. 2014). While expert opinion can be a useful starting point, empirical data are still needed to improve current and future modelling efforts which aim to optimise management of invasive species.

The ship rat (*Rattus rattus*) is a pervasive pest species in New Zealand, with severe and well-documented impacts on native biodiversity, and is identified as one of the target species in New Zealand's Predator Free 2050 goal (Russell et al. 2015; Murphy et al. 2019). Due to its status as a major pest species worldwide (Towns et al. 2006; Banks & Hughes 2012; Shiels et al. 2014; Harper & Bunbury 2015), a substantial amount of research effort has gone into understanding ship rat

behaviour. As such, the literature offers some useful information about dispersal, metapopulation dynamics, and long-distance movements in this species (e.g. Russell et al. 2009; Stokes et al. 2009; Innes et al. 2011). For instance, King et al. (2011) used a removal experiment to study the reinvasion of forest fragments by ship rats. Marked individuals re-colonised eradicated fragments from the outside within a few days. Importantly, the age and sex ratios of invading rats were significantly skewed towards young male animals, with few older breeding females colonising fragments from the outside (King et al. 2011). Nevertheless, despite our comparatively thorough knowledge of dispersal and movement behaviour in ship rats, there are few, if any, empirical measurements of distances moved by juveniles away from a known natal nest site.

A more specific motivation for our interest in juvenile ship rat movements was to evaluate whether a mother and litter unit could make a useful target for strategic detection efforts in the context of the large-scale predator-free landscapes that the Predator Free New Zealand goal envisages. Traditionally, best-practice surveillance and defence of rat-free island and mainland sanctuaries has been geared towards intercepting every invading individual. This approach demands an intensity of effort, particularly at borders, which would be prohibitively difficult and expensive to reproduce at scale. For instance, rat surveillance density on Te Pākeka Maud Island (318 ha) averages one device every 0.79 ha, with densest device distribution and weekly checks around sites of perceived highest invasion risk (Caldwell & Higgott 2016). Furthermore, given that impacts on prey species are generally correlated with predator density (Norbury et al. 2015), a limited number of ship rats in a spatially-restricted area of an otherwise predator-free landscape would likely cause minimal ecological damage to healthy native species populations under most circumstances. The critical aim is therefore to prevent the re-establishment of a widespread adult breeding population.

We aimed to explore the potential of an alternative strategy for efficient landscape-scale surveillance, with a focus on detecting spatially-restricted breeding events, rather than individual invaders. Empirical measurements of post-weaning ship rat movement distances are needed to evaluate the viability of this approach, especially in low to zero population density environments. It was our aim to provide measurements of this kind by simulating an invasion by a pregnant female ship rat into an area recently treated with 1080 (sodium fluoroacetate). We expected that, as a unit, a mother rat with a litter of pups would be easier to detect than a single invader for two main reasons: 1) there would be more individual animals to be detected, and 2) the spatial extent of the invasion would be larger due to the juveniles being expected to disperse away from the mother's range and each other as they attained maturity.

Methods

Location

The trial took place in beech-kāmahi forest at the confluence of the Jackson and Arawhata rivers in South-Westland, New Zealand (44°04.575′ S, 168°42.210′ E, Fig. 1). The Jackson-Arawhata site had been subject to a trial of a novel 1080 prescription, in which 2300 ha was aerially treated with 1080 on 7 July 2017 (Bell 2017). Subsequently, a 394 ha core area within the treated zone was intensively monitored over 55 nights (> 83 000 detection nights), with no rat sign detected (Bell 2017).

Animal husbandry and release

This trial was carried out under approval from the Lincoln University Animal Ethics Committee (AEC#2016-09 and amendments) and with the support of the Department of Conservation South Westland office.

Wild-captured male and female ship rats (sourced from Kaituna Valley Forest Reserve, Banks Peninsula) were paired at the ZIP captive animal facility in Lincoln. All rats were fed on a diet of laboratory rodent pellets (Fort Richard Laboratories), supplemented daily with food items such as seed mix and fresh fruit and vegetables. A litter of seven pups was born to a female (hereafter 'the mother') on 8 August 2017. The mother and her litter were transported by road to the ZIP field staff accommodation at Haast on 16 August, and were cared for in place by ZIP staff. A 20 g ball of peanut butter, seed mix and oats containing 0.1% Rhodamine B biomarker dye (RB) was fed to the mother and pups on three occasions, when the pups were 12, 16 and 18 days old. A collar-mounted VHF radio-transmitter weighing 7.75 g (PinPoint-75 custom, Sirtrack Ltd., Havelock North) was attached to the mother on 27 August (4.5% body weight). On 30 August, the mother and her litter were carried into the field site in a secure nest box (360 × 570 × 260 mm) and placed at a central location in the study area. To allow for some settling time, the nest box was left closed overnight. On 31 August, the nest box door was opened to allow the mother and the 23-day old juveniles to disperse from the release site at will. The total period of captivity for the mother was 85 days.

Rhodamine B makes a persistent stain in growing hair tissue, which is visible under a fluorescence microscope (Fisher 1999). Our intention was to use this marker to positively identify rat carcasses retrieved at the end of our study as being part of the family group. Marking can be obtained through direct consumption of food containing RB, or via the mother's milk in pre-weaned rats (ZIP, unpubl. data) and mice (Tolkachev & Bespamyatnykh 2018). Marking persistence times of up to three months in ship rats have been recorded in the field (Rahelinirina et al. 2010; Bagasra et al. 2016). To avoid any risk of RB baits entering the release site environment, the nest box was thoroughly checked and cleaned of any remaining traces of bait two days prior to being transported to the release location.

Detection

An array of non-lethal detection devices was laid out along pre-existing monitoring lines that had been used to measure outcomes of the July 2017 1080 treatment. The initial detection area was an irregular polygon shape (due to unsafe access to certain areas) covering an area of 236 ha, with the release site located centrally in this area. As the trial progressed, we progressively extended the monitored area with the intention of monitoring outside of the expanding movements of the mother and all juveniles, and in the final configuration a total area of 300 ha was being monitored (Fig. 1).

Detection lines (n = 29) were spaced at 100 m and on each line pre-weathered 'Black Trakka' tracking tunnels (Gotcha Traps, Warkworth) lured with Nutella (Ferrero Australia Pty Ltd) were placed every 50 m (n = 718) and chew cards lured with Pic's peanut butter (Picot Productions Ltd) were placed every 100 m (n = 398). In addition, motion-activated cameras (Browning BTC-6HDE, Alabama, n = 60) were placed on every second line at 250 m spacing, with some additional cameras on the edges of the detection area, and were set to record still images. These cameras were used for detection and aimed
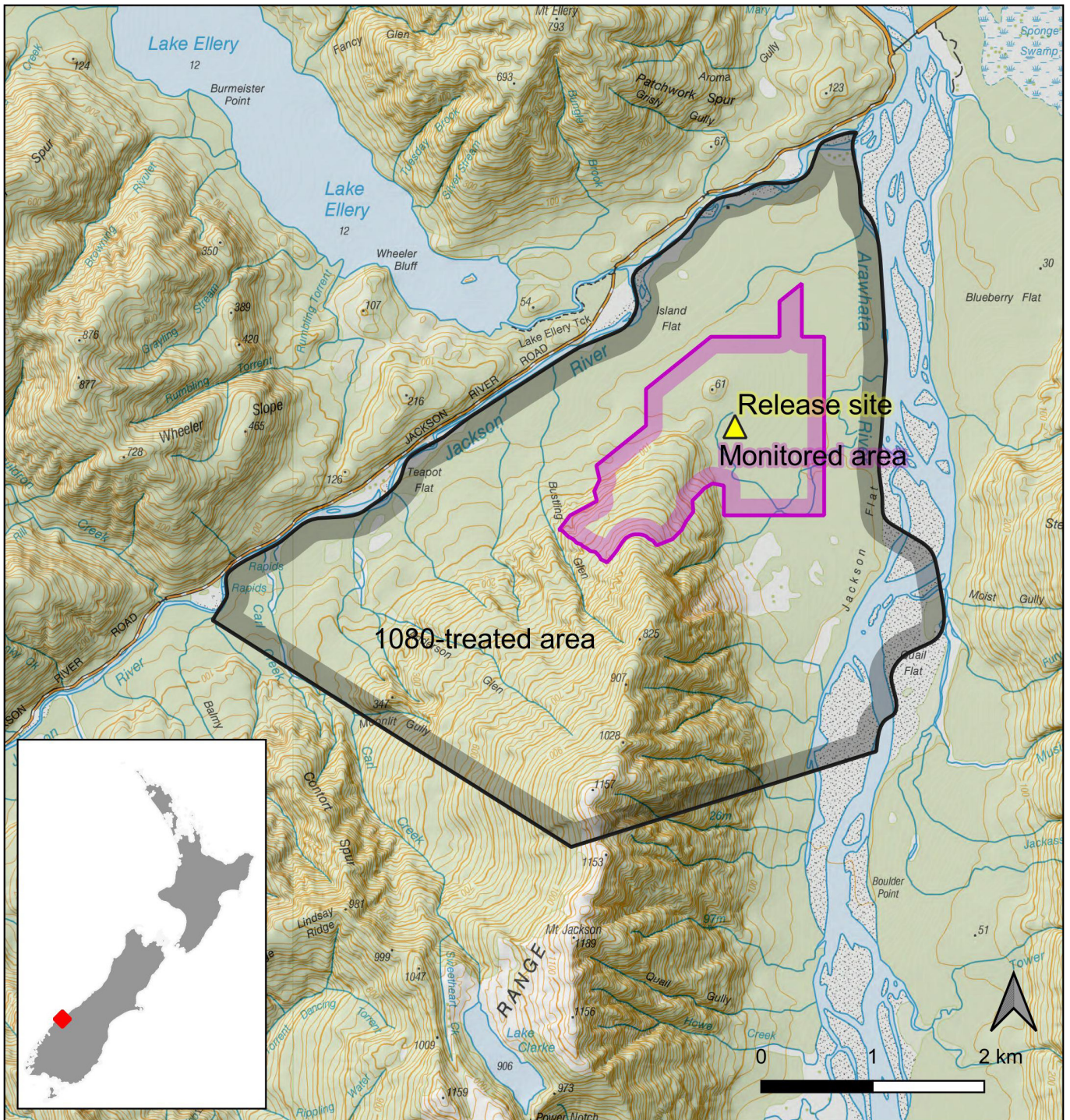
Figure 1. Location of Jackson-Arawhata field site, showing 1080-treated area, release site and monitored area. Topographic data sourced from the LINZ Data Service and licensed for reuse under the CC BY 4.0 licence.

at a chew card, allowing for comparison of body size with an object of known dimensions to assist with distinguishing between adult and juvenile rats. Upon detection of rat sign on the southern edge of the monitored area early in the trial, an additional five cameras were deployed in that area. Appendix S1 in Supplementary Materials shows the location of all tracking tunnels, chew cards, and detection cameras.

A further three cameras used for monitoring behaviour were deployed in the immediate vicinity of the release site and set to record 30 second videos. Two of these were placed 1 m

from the nest box to assist in identifying the time that pups began to emerge from the nest. The remaining camera was used to observe tracking tunnels and chew cards placed 2 m from the nest, with the intention of recording early interactions with these devices by young pups.

Detection devices were in operation from 30 August, i.e. the day before the rats were released. We aimed to service (check devices and refresh lures) all detection lines once per week, but in practice a full service of all detection lines took an average of 8.5 days due to high river-flows preventing

access to the site on some days.

In addition to passive monitoring techniques, we attempted to locate the mother by radio-tracking to her daytime den site at least once per week between 1 September and 16 October, as weather allowed. This effort resulted in 15 attempts in total.

Kill trapping and biomarker detection

Kill traps were deployed progressively throughout the trial. Figure 2 shows the location and deployment sequence of all kill traps.

Despite the lack of rat sign detected during post-1080 monitoring taking place immediately prior to our trial (Bell 2017), a large-bodied rat which was not the mother (identifiable by her radio-collar) was recorded at several camera locations near the south-west edge of the monitored area from 10 September. In an attempt to remove this suspected survivor or re-invader we deployed 42 T-Rex kill traps (Bell Laboratories, Madison WI, USA) housed in single-entry tunnels (modified Black Trakkas) and lured with a Pic's peanut butter and icing sugar blend, in the vicinity of the rat sign on 19 September (19 ha coverage).

An additional 119 T-Rex traps in tunnels were deployed progressively from 30 September, at which point the rat pups were 53 days old (34 days since last access to RB). Our intention in beginning trapping at this stage was to allow ample opportunity to trap all juveniles before they were 90 days old; the earliest point at which they may have become sexually mature (Innes 2005). Additionally, we expected RB marking to become increasingly unreliable with time elapsed since last access to the biomarker. Because sufficient traps and tunnels for complete coverage of the monitored area were not immediately available, traps were strategically placed at and around recent rat sign locations as they were progressively rolled out.

From 30 October, a further 131 T-Rex traps were deployed on the existing 100 × 50 m detection array. Instead of being placed in tunnels, these traps were nailed directly onto trees at 1.2 m height above-ground and lured with Nutella. In addition, in the near vicinity of the release site, 44 tree-mounted traps were set 20 m away from existing stations and lured with Colby cheese (Mainland Ltd.) to provide intensive trap density and an alternative lure in this area (9.5 ha coverage).

All rat carcasses recovered from kill traps throughout the trial were retained and subsequently examined for evidence of RB ingestion. A sample of 8–12 whiskers was plucked from each rat, dry-mounted on a microscope slide under a coverslip (after Purdey et al. 2003) and examined with a fluorescence microscope (Nikon Eclipse 50i microscope with NIS-Elements Software) using a blue-green excitation filter (Semrock Cy3-4040C, excitation ~510–560 nm). All whiskers were examined independently by two observers, with each individual whisker scored as positive or negative for RB marking. Any rat with at least one RB-positive whisker identified by both observers was considered to have consumed RB.
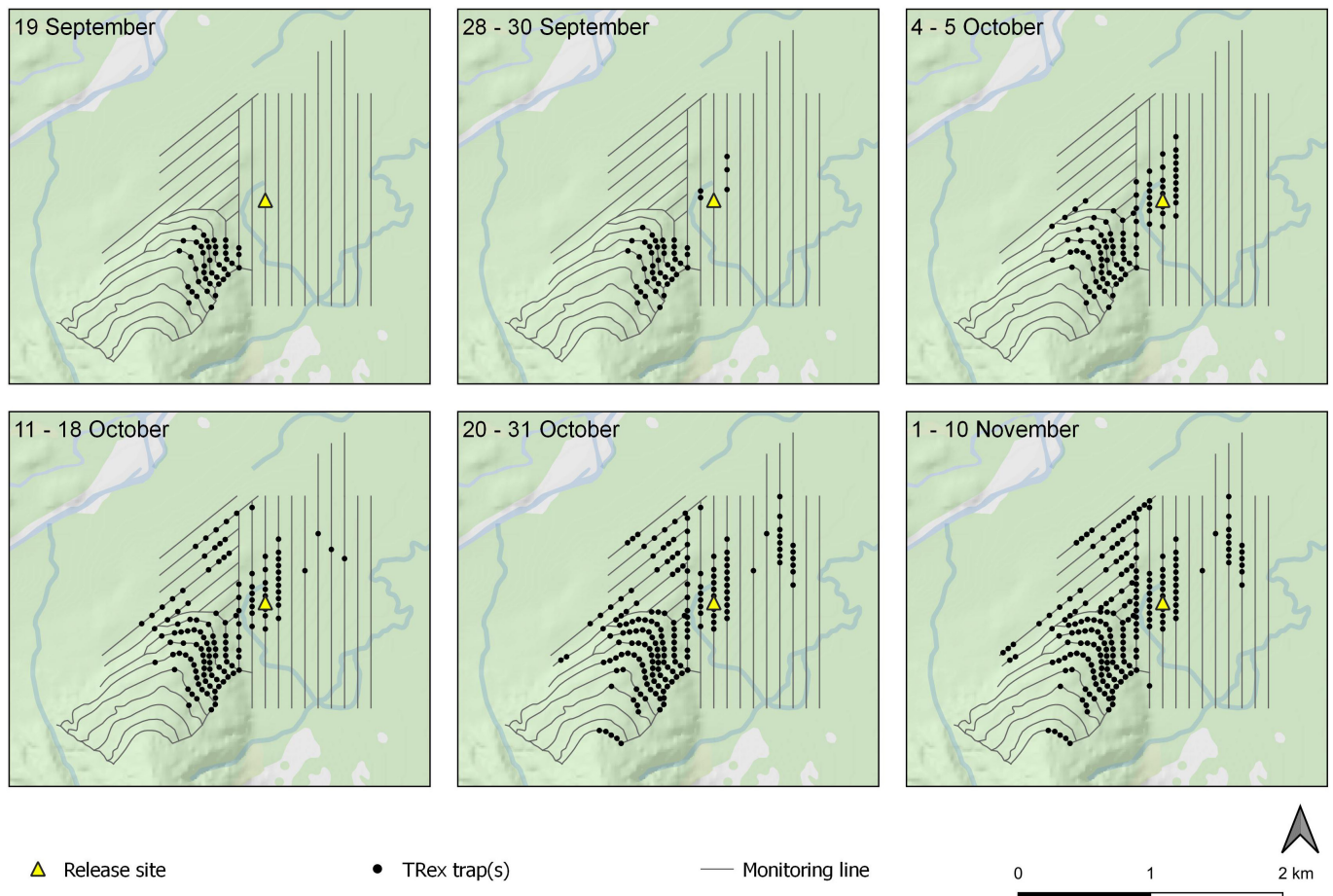
Figure 2. Sequential deployment of kill traps in the monitored area. Panels are labelled with trap deploy date ranges. Topographic data sourced from the LINZ Data Service and licensed for reuse under the CC BY 4.0 licence.

Genetic analysis

To minimise the possibility of a false negative RB result impacting our findings, we used genetic methods as a second means to assess relatedness of the mother to the other trapped rats. Genotyping was conducted by EcoGene® (Auckland, NZ), a business unit of Manaaki Whenua-Landcare Research. DNA was extracted from rat tail tissue using a DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany). Genetic profiling was performed by amplifying 10 microsatellite markers (Abdelkrim et al. 2005a, b) and a sex-linked locus (Peakall et al. 2006). Microsatellite amplicons were visualised under UV light using GelRed^{TM} and run on an ABI 3500xl Genetic Analyser (Applied Biosystems by Life Technologies). Alleles were scored using GeneMapper v5.0 (Applied Biosystems by Life Technologies).

The genetic profile of the mother was compared to that of all other sampled individuals, and non-offspring were detected on the basis of private alleles. That is, where an individual had no alleles in common with the mother at one or more loci they could not be her offspring (Miller et al. 2010).

Results

Detection

Seven complete services of the detection array were made between 4 September and 20 November 2017, along with an additional three partial services focused on areas of recent rat sign. Appendix S2 in Supplementary Materials provides a summary of rat sign detected throughout the trial. However, because unrelated individuals were discovered inside the trial area (see next section) we could not be certain which sign were attributable to the released mother and juveniles.

Captures and juvenile movement distances

Ten ship rats were kill-trapped in T-Rex traps (either in tunnels or on trees) during the study period (Table 1; Fig. 3). An adult male rat (scrotal testes) was recovered from a trap in the initially-targeted south-western area on 22 September, and was subsequently found to have no RB marking. The remaining nine rats were kill-trapped during October and November, and

included the mother, who retained her radio-collar.

In total, 4 of the 10 captured rats were positive for RB marking, including the mother (Table 1). Genotyping was carried out for all individuals except the adult male captured at trap site AA900 (sample unavailable due to a lost carcass) (Appendix S3 in Supplementary Materials). Three individuals had genetic profiles consistent with being offspring of the mother and also tested positive for RB, thus we judged that these were her juveniles. The remaining five rats could not be the offspring of the mother due to private alleles. However, similarity in the genetic profiles of four of these individuals (when compared to the prevalence of shared alleles in other New Zealand ship rat populations) indicates that they were closely related; likely half- or full-siblings (ZIP/R. Fewster, University of Auckland, unpubl. data). The fifth individual (L3, Fig. 3) had a markedly different genetic profile to any other rat sampled, and was therefore unlikely to be closely related to the other non-translocated (hereafter 'local') rats.

The three rats identified as offspring of the mother were captured 128, 164 and 675 m from the release site (Table 1; Fig. 3), and the greatest distance between two known litter mates was 796 m. These measurements represent minimum distances moved, as it is likely that the rats roamed further than their final trapping location, or would have done if not trapped. The greatest distance between individuals confirmed not to be offspring of the mother was 682 m.

Mother's ranging

Video footage from the behaviour cameras dedicated to observing the nest box showed the mother and juveniles emerging from the nest box the evening after it was opened on 31 August. Both mother and pups continued to be frequently recorded near the release site until 4 September (pups 27 days age). Subsequently, juveniles were seldom seen, but the mother was regularly recorded in the vicinity until late October. In addition to detections at the nest box, a further 18 location points can be attributed to the mother, consisting of den sites located by radiotracking, camera records where she could be identified by a visible radio collar, and the final trapping location (Fig. 4). The following text describes the mother's movements in sequence throughout the trial from all available data.

Until 14 September (pups 33 days age) the mother

Table 1. All rats trapped in Jackson-Arawhata trial. For offspring only, the distance between release site and capture location is interpreted as the minimum movement distance.

ID	Sex	Weight (g)	Rhodamine B detected?	Genetic result	Overall relatedness assessment*	Age at capture (days)†	Days since last Rhodamine B access†	Days since release†	Distance release site to capture location (m)
M	F	170	Yes	Mother	Mother	–	65–66	61–62	228.7
O1	M‡	‡	Yes	Probable offspring	Offspring	53–64	34–45	30–41	128.3
O2	M	166	Yes	Probable offspring	Offspring	86–90	67–71	63–67	675.1
O3	F	158	Yes	Probable offspring	Offspring	86–90	67–71	63–67	164.4
L1	M	135	No	Not sampled	Not offspring	–	–	–	–
L2	M	110	No	Not offspring	Not offspring	–	–	–	–
L3	M	122	No	Not offspring	Not offspring	–	–	–	–
L4	M	125	No	Not offspring	Not offspring	–	–	–	–
L5	M	169	No	Not offspring	Not offspring	–	–	–	–
L6	M	164	No	Not offspring	Not offspring	–	–	–	–

* Assessment of relatedness to the mother, taking all available evidence into account.
† Date of capture is uncertain as traps were not serviced daily. Earliest possible capture date is taken as the date of the previous service.
‡ Carcass too decayed to determine sex and weight accurately. Sex assignment taken from genotyping results
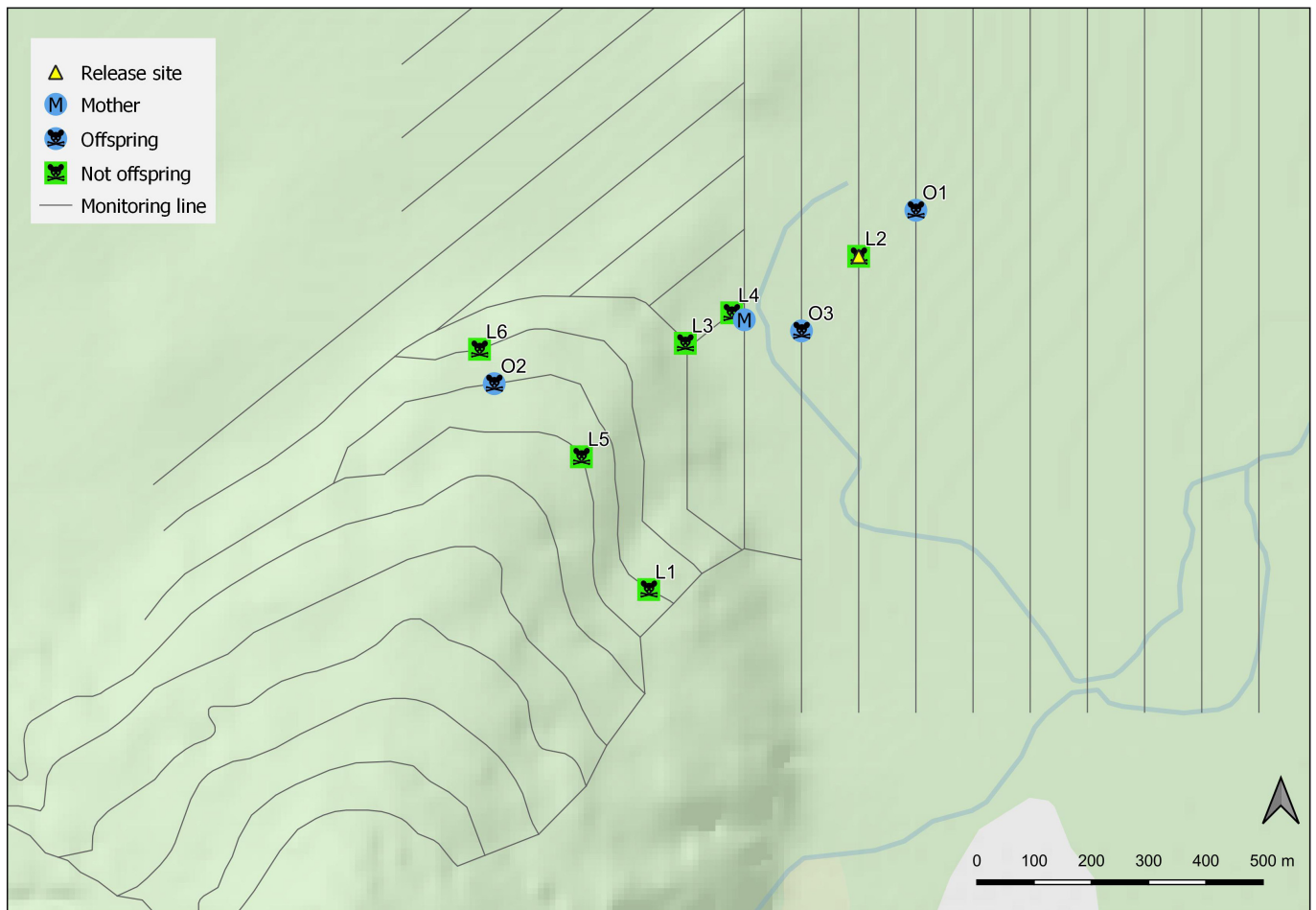
Figure 3. Trapping locations and group assignment (offspring or not of translocated mother) of all trapped rats. Labels show rat ID as in Table 1. Topographic data sourced from the LINZ Data Service and licensed for reuse under the CC BY 4.0 licence.

continued to make her den either in the nest box or within around 30 m of it (we refer to the general vicinity of these den sites as the 'eastern activity centre'). On 21 September (pups 40 days age) the mother was radio tracked to a new den site located approximately 595 m from the release site in a south-westerly direction, after prior tracking attempts on 19 and 20 September failed to locate her. The mother apparently adopted this area as the centre of her activity for a period of time, as radiotracking showed that she continued to make her den site in this general vicinity until 27 September (referred to as 'western activity centre'). However, camera records show that she was ranging much more widely, with detections approximately 300 m to the north-west and south of the western activity centre between 21 September and 2 October. The mother then appears to have relocated back towards the eastern activity centre. Although failed tracking attempts on 3, 6 and 9 October meant we could not confirm any den sites during this period, the mother was seen on camera at the nest box on four nights between 3–11 October, and was detected approximately 865 m to the north-east of the release site on a single occasion on 10 October. On the night of 15–16 October she appears to have been particularly active in the south-western part of her range, being detected four times at three separate locations. From the night of 16–17 October through till 30 October the only location at which the mother was recorded was the nest site, indicating she was predominantly using the north-eastern part of her range. The mother was kill-trapped

on 1 November, 228 m from the initial release site (Table 1). Overall, her ranging movements covered a total area of 45.8 ha (100% minimum convex polygon), and a maximum range length of 1625 m (Fig. 4). Home range area and length were calculated using QGIS v 3.44 (QGIS Development Team 2019). Outlier points were not excluded from range estimation as these are some of the most interesting points when tracking the behaviour of an invading animal in a novel environment (following MacKay et al. 2019).

Discussion

Limitations

We had intended to undertake this trial in an area that was completely rat-free, to simulate invasion behaviour in a predator-free landscape. Although rats had not been detected in the trial area for two months prior to the start of our trial, we first recorded sign attributed to an unrelated male rat within four days of the release of the mother and her litter. A further five unrelated rats were trapped over the course of our trial, and appeared to be living in close proximity to the translocated juveniles. This detection had a critical impact on our study, as it meant we could not assign rat sign from our extensive detection array of tracking tunnels, chew cards, and cameras to the translocated mother and litter with certainty. We had
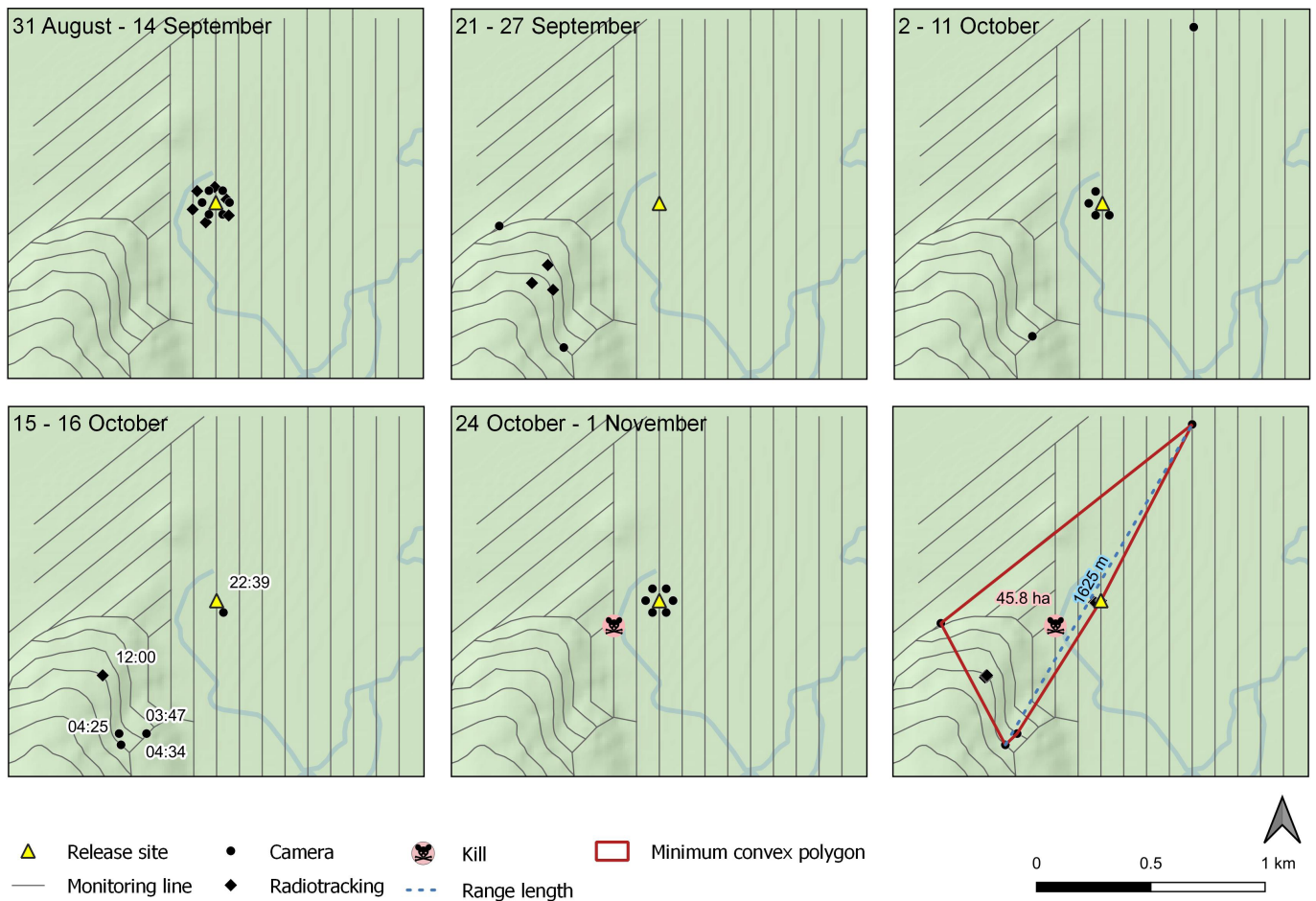
Figure 4. All detection locations for the translocated mother. Detections are grouped into clusters by dates. Multiple detections at a single location within a cluster are jittered to avoid overlapping symbols. To illustrate the extent of movement shown during a particularly active period, timestamps are shown for detections recorded on the night of 15–16 October and following evening. The bottom-right panel shows a summary of all recorded movements, with a 100% minimum convex polygon range area, and range length outlined. Topographic data sourced from the LINZ Data Service and licensed for reuse under the CC BY 4.0 licence.

intended to use these data to track the expanding movements of the family (as a unit) with a high level of spatio-temporal detail. However, we were ultimately limited to reporting the minimum distances moved between the release site and kill-trapping locations of individual juveniles as the only certain measure of movement away from the natal nest.

The use of VHF or GPS telemetry to track the juveniles would have reduced our reliance on a passive detection array to monitor their movements. However, as the juveniles were very young at the time of release it would have been unethical to fit them with radio-collars, due to weight and the risk of strangulation as they grew (Sikes & Gannon 2011). A more viable alternative could be to mark juvenile rats in a manner which allows them to be individually identifiable on camera footage, for example, with tail tattoos (after Efford & Hunter 2018), then monitor movement unobtrusively via camera detections. Genetic methods offer another approach to indirectly measure post-weaning movement distances at any population density (Waser et al. 2006). With intensive effort to trap a large proportion of the population, parentage analysis can determine distances between capture locations of parents and offspring, though an exact nest site may not be known and it may not be possible to assign siblings to litters with certainty.

A further limitation was the relatively short duration of our study, with the oldest juveniles being a maximum of 90 days old at the time of capture. Our intentions were twofold; (1) to capture juveniles within the expected persistence period of the RB biomarker, and (2) to avoid the juveniles attaining breeding age and hastening the re-population of the recently 1080-treated landscape. It is possible that we would have recorded larger juvenile movement distances if our study was longer in duration, and we would recommend that future studies should ideally track juvenile movements until first breeding is confirmed, indicating a settled home range (Howard, 1960). Ultimately, we report the behaviour of only a single mother rat and her litter. To further advance understanding of the post-weaning movements of juvenile ship rats, replications of our trial across a range of population densities and habitats are required.

Juvenile movements

We predicted that the collective dispersal extent of the juveniles would exceed that of the mother alone. We did not find evidence to support this, with only 796 m separating the three captured juveniles, and a range length of 1625 m for the mother (Fig. 5). However, an important caveat is that the movement distances we report are the minimum for each
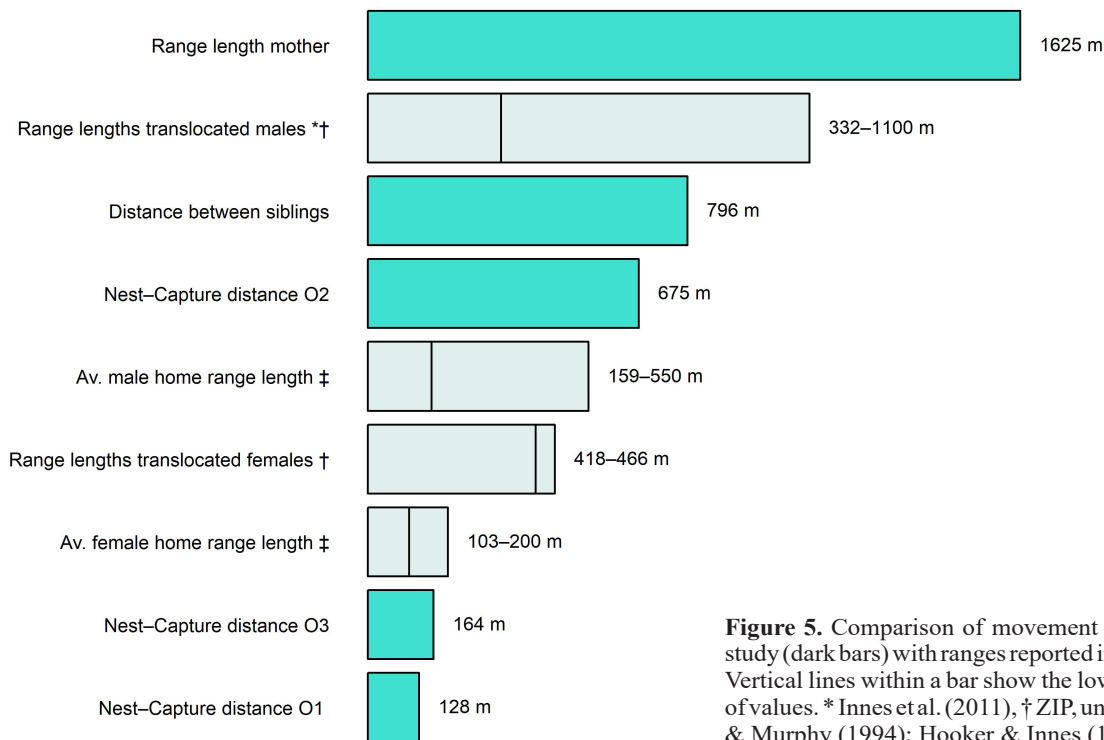
Figure 5. Comparison of movement distances recorded in this study (dark bars) with ranges reported in other sources (light bars). Vertical lines within a bar show the lower end of a reported range of values. * Innes et al. (2011), † ZIP, unpublished data, ‡ Dowding & Murphy (1994); Hooker & Innes (1995); Pryde et al. (2005).

juvenile, taken as the straight-line distance between the nest site and the final kill location. If the same measure were used to summarise the mother's movements, it would appear that she had moved only 228 m (Table 1). Furthermore, there were seven pups initially in the translocated litter and only three were re-captured, thus the movements and fates of four remain unaccounted for. It is possible that some of the juveniles did range further than their mother, but we have no way to confirm or reject this possibility.

It is notable that the maximum distance between the four local rats deemed likely to be siblings was of a similar order to that between the recaptured translocated siblings (682 and 796 m respectively). We cannot impute ages of these individuals with certainty, but the range of weights at capture leads us to speculate that they might be litter mates, born around the time of the 1080 operation in July 2017, or shortly thereafter (based on weights of ship rats of known age, Bentley & Taylor 1965). If so, it would indicate that the movement distances we recorded for our translocated juveniles are consistent with those of other juveniles born into the same environmental context. While we do not have a genetic profile for the first local rat caught (ID L1, Table 1; Fig. 3), it was unlikely to be a litter mate of the others, given its weight and obvious sexual maturity at capture. Regardless of the age and relatedness of the local rats, their presence in the trial area means either that some rats survived the 1080 operation and were not detected in 55 days of follow-up monitoring, or that re-invaders from outside the treated area dispersed into the monitored area. Neither scenario can be ruled out with the information available.

Interestingly, there was a conspicuous overlap in the distribution of the local and translocated rats, with all individuals trapped within a 20 ha area (100% minimum convex polygon, QGIS v3.44), despite the total monitored area being 300 ha and traps being available wherever rat sign was recently detected (Figure 3). This overlap may indicate

that the rats were seeking proximity to unrelated potential mates. Another explanation could be that this area comprised particularly good habitat, or that conspecific attraction was at play, with dispersing individuals using the presence of others of the same species as an indicator of good habitat (Kokko & Lopez-Sepulcre 2006).

Mother's ranging
Although ship rats are weaned between 21–28 days old (Innes 2005), all available location data for the mother suggest that she remained in the near vicinity of the release site until her litter were around 35–40 days old. This pattern is consistent with what little information is available on interactions between ship rat mothers and their offspring in the wild. Hooker and Innes (1995) reported that two juvenile rats weighing 42 g each had apparently only recently been rejected by their radio tracked mother. Based on comparison with the weights of ship rats of known ages, those pups were likely 25–35 days old (Bentley & Taylor 1965); captures of ship rats weighing less than around 40 g are rare in most New Zealand trapping datasets.

When the mother eventually did move away from the release site, she made a long-distance movement of 595 m to a new centre of activity. Average ship rat home range lengths are in the order of 103–200 m for females and 159–550 m for males in New Zealand radio-tracking studies in forest (Dowding & Murphy 1994; Hooker & Innes 1995; Pryde et al. 2005). Thus, a movement of nearly 600 m exceeds typical home-ranging behaviour (particularly of females), and resembles the exploratory behaviour of translocated rodents in the absence of conspecifics (Russell et al. 2010; Innes et al. 2011; MacKay et al. 2019). The term 'exploratory behaviour' encompasses behaviours that permit the collection of information about a novel environment (Crusio 2001), in this case wide-ranging movement.

In the most directly relevant study, male ship rats were

individually released inside predator-fenced Maungatautari Sanctuary and radio tracked (Innes et al. 2011). One individual had a final range length of 1100 m after 31 days inside the reserve, and another two had range lengths of 600 m each after seven days. Conversely, another translocation study found that movements of male ship rats released into a low (but not zero) density environment did not exceed typical home range lengths, but those of females did. In that trial, four ship rats were individually released at Bottle Rock Peninsula (Marlborough Sounds) and radio tracked daily to den sites. Minimum range lengths of two adult males were 332 and 382 m in 10 and 17 nights, respectively, whereas two adult females ranged over at least 418 and 466 m over two and ten nights, respectively (ZIP, unpubl. data). The scale of the mother's movements, and those of her offspring, in relation to key comparative measurements reported elsewhere are illustrated in Fig. 5. The total area over which the mother ranged throughout the study, 45.8 ha, was also large in comparison to average home range areas recorded in established ship rat populations (0.06–0.79 ha for females and 0.17–9.43 ha for males, Harper & Rutherford 2016).

Notably, the long-distance movement by the mother brought her activity centre to within less than 300 m of where a suspected adult male was concurrently being recorded on camera traps in the south-west of the monitored area. While we have no direct evidence that she ever came into contact with this male, the large ranging movements typically displayed by experimentally translocated rodents in low-density environments have been hypothesised to represent a mate-finding strategy (Russell et al. 2010; Innes et al. 2011; MacKay et al. 2019). This behaviour would have clear advantages for a species' ability to establish a new population upon incursion into a novel and sparsely populated environment (Nathan et al. 2015).

Overall, the behaviour of the mother was consistent with what has been observed in other studies of rodent ranging in environments with few or no conspecifics. Previous trials with translocated rats have predominantly focused on males (Russell et al. 2010; Innes et al. 2011), so evidence that females display far-ranging behaviour in low to zero-density environments is important.

Implications for landscape-scale detection

The ranging movements of the translocated mother in our trial were large compared to typical home range lengths in established rat populations. As a unit, her litter of juveniles dispersed over a distance of at least 796 m by the time they were around 90 days old and approaching the age of sexual maturity. As best we can tell with only release and kill-capture location data, this collective dispersal distance was smaller than the movements of a single individual adult in the same environment (the mother), and also smaller than the movements of one adult male introduced to rat-free Maungatautari Sanctuary (Innes et al. 2011).

Although we found no evidence that the dispersal extent of a rat litter aged 90 days exceeds that of an individual adult invader, the presence of multiple individuals in a landscape increases the likelihood that at least one will be detected. The concept of an efficient landscape-scale detection strategy targeted to breeding events therefore warrants further investigation. Such a strategy could rely on sparsely deployed detection devices intercepting at least one of an invading family and alerting managers immediately via an automated reporting system, triggering a rapid response to remove the nascent population while it is still restricted to a small area within the larger

predator-free landscape.

Clearly, the efficiency of this strategy is critically dependent on the rates of reinvasion and breeding events at a particular site, as well as the speed and social acceptability of repeated response actions. We envisage that a family-based detection strategy will be most suited to large-scale mainland areas where intensive surveillance would be prohibitively expensive and logistically difficult to achieve, and where reinvasion is infrequent due to strong protection at its boundaries; for instance significant natural barriers (Cook 2018), or an intensive 'virtual barrier' of trapping (Bell et al. 2019). We anticipate that sites meeting these criteria will become increasingly common as New Zealand progresses towards its goal to be predator-free by 2050.

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