Seasonal variation in movements and survival of invasive Pacific rats on sub-tropical Henderson Island: implications for eradication

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Abstract Invasive rodents are successful colonists of many ecosystems around the world, and can have very flexible foraging behaviours that lead to differences in spatial ranges and seasonal demography among individuals and islands. Understanding such spatial and temporal information is critical to plan rodent eradication operations, and a detailed examination of an island's rat population can expand our knowledge about possible variation in behaviour and demography of invasive rats in general. Here we investigated the movements and survival of Pacific rats (*Rattus exulans*) over five months on sub-tropical Henderson Island in the South Pacific Ocean four years after a failed eradication operation. We estimated movement distances, home range sizes and monthly survival using a spatially-explicit Cormack-Jolly-Seber model and examined how movement and survival varied over time. We captured and marked 810 rats and found a median maximum distance between capture locations of 39 ± 25 m (0–107 m) in a coastal coconut grove and 61 ± 127 m (0–1,023 m) on the inland coral plateau. Estimated home range radii of Pacific rats on the coral plateau varied between 'territorial' (median: 134 m; 95% credible interval 106–165 m) and 'roaming' rats (median: 778 m; 290–1,633 m). The proportion of rats belonging to the 'roaming' movement type varied from 1% in early June to 23% in October. There was no evidence to suggest that rats on Henderson in 2015 had home ranges that would limit their ability to encounter bait, making it unlikely that limited movement contributed to the eradication failure if the pattern we found in 2015 is consistent across years. We found a temporal pattern in monthly survival probability, with monthly survival probabilities of 0.352 (0.081–0.737) in late July and 0.950 (0.846–0.987) in late August. If seasonal variation in survival probability is indicative of resource limitations and consistent across years, an eradication operation in late July would likely have the greatest probability of success.

Keywords: home range, introduced species, island restoration, Pitcairn Islands, *Rattus exulans*

INTRODUCTION

Eradications are a powerful and frequently used management option to counter the native biodiversity loss caused by invasive species on islands (Jones, et al., 2016). Planning for an eradication requires a fundamental understanding of the ecology and movement characteristics of the target invasive species (Zavaleta, 2002; Keitt, et al., 2015). Among the most widespread invasive species on islands are three species of rat (*Rattus rattus*, *R. norvegicus*, *R. exulans*), which now occur on >80% of the world's island groups (Atkinson, 1985; Jones, 2010). Rat eradications have been successfully completed on hundreds of islands (Howald, et al., 2007), but eradications on tropical islands, where a lack of seasonal fluctuation in resource abundance allows rodents to reproduce throughout the year, still have a lower success probability than eradications on temperate islands (Holmes, et al., 2015; Keitt, et al., 2015). Detailed information on rat movements and demography from tropical islands should therefore benefit eradication planning on tropical islands (Keitt, et al., 2015).

Rodent eradications on islands larger than 100 ha are generally conducted by aerially distributing cereal-based toxic bait pellets across the island, and are only successful if every individual rodent has access to sufficient bait within its home range to consume a lethal dose of toxin (Cromarty, et al., 2002; Howald, et al., 2007; Broome, et al., 2014; Holmes, et al., 2015). Hence, a better understanding of the size of home ranges can inform the density at which bait pellets need to be dispersed on the ground. Movements of invasive rodents on islands vary by habitat, population density, food availability, individuals' age and sex (Bramley, 2014a; Ringler, et al., 2014; Harper, et al., 2015), but more information on the size of movements and their variation over time of year could contribute to eradication planning on islands.

Besides ensuring each individual has access to a sufficient quantity of bait, rodent eradications are also more likely to succeed if they are timed to coincide with a predictable period of rodent stress (e.g. mortality). On temperate islands, mortality occurs during a predictable seasonal shortage in resource availability during autumn or winter, and therefore provides a natural time window for an eradication operation when rodents are more likely to switch to palatable poison baits (Howald, et al., 2007; Russell & Ruffino, 2012). On tropical islands, with less-defined seasonality and irregular periods of resource limitation, there is still very little information on how the survival of rodents varies within a year (but see Tamarin & Malecha, 1971). Additional information on seasonal variation in survival of rodents on tropical islands can inform when an eradication operation would have the highest probability of success and therefore aid the planning of an eradication operation (Howald, et al., 2007; Holmes, et al., 2015; Keitt, et al., 2015).

Here we use data from a large spatial capture-recapture programme and conventional radio-tracking to investigate the movements of invasive Pacific rats (*R. exulans*) on an uninhabited sub-tropical island (Henderson) in the South Pacific. An eradication operation on this island in 2011 failed to kill all individuals. Among the reasons that can cause eradication failure, insufficient bait toxicity could be excluded due to follow-up experiments (Amos, et al., 2016). However, two further potential causes, namely that not all rats had access to bait and that the eradication was poorly timed and coincided with high survival, have not been investigated so far. Our study was designed to provide knowledge to better understand the 2011 eradication failure and improve the probability of success of a future eradication attempt. We estimate movement distances and home range sizes using mark-recapture and radio-tracking

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data and evaluate if the smallest rodent home ranges would contain a sufficient quantity of bait pellets based on bait distribution rates used during the eradication attempt in 2011. We further estimate survival of rats over a five-month period, examine temporal variation in their monthly survival probability, and assess whether the timing of the failed operation in 2011 was appropriate.

METHODS

Study area

Henderson Island (24º22′ S, 128º20′ W) is a flat, raised coral atoll of 4,309 ha in the sub-tropical Pacific Ocean with two distinct habitats – a central plateau roughly 25 m above sea level (4,290 ha), and a sandy beach area with a vegetated margin (hereafter referred to as 'embayment forest', 14 ha). Henderson Island has a sub-tropical climate with erratic rainfall patterns, and there are no permanent freshwater bodies on the island (Spencer, 1995; Weigelt, et al., 2013). The plateau substrate is fossilised coral with uniform, dense native vegetation consisting mostly of *Pandanus tectorius*, *Xylosma suaveolens* and *Psydrax odorata* (Waldren, et al., 1995). The beach and embayment forest areas have a sandy substrate with a mixed shrubby vegetation and small stands of introduced coconut (*Cocos nucifera*) (Paulay & Spencer, 1989; Waldren, et al., 1995).

Pacific rats were introduced to Henderson Island by Polynesians several hundred years ago (Steadman & Olson, 1985), and currently have adverse effects on native biodiversity on Henderson Island (Brooke, et al., 2010; Dawson, et al., 2015). In late August 2011, an operation using the aerial distribution of cereal-based pellets containing 20 µg/g of the toxin brodifacoum was carried out to eradicate all Pacific rats from Henderson Island. Although the baiting operation met best practice standards, had no spatial gaps in bait distribution, used bait pellets containing a sufficient amount of toxin (Torr & Brown, 2012), and used bait application densities well beyond those needed to overcome estimated hermit-crab consumption (Cuthbert, et al., 2012), the eradication operation was unsuccessful and 60-80 individual rats were predicted to have survived (Amos, et al., 2016). Rat populations recovered within 2–4 years (Bond, et al., 2019) and were at an unknown stage of expansion or fluctuation during 2013 and 2015.

Rat live trapping

To obtain a robust estimate of rat survival probability, and to document rat movements over five months, we implemented a spatial capture-mark-recapture programme in 2015. Rats were live-trapped on the plateau from 28 May to 16 October 2015 during seven primary sessions of 10 trapping nights each, with a window of 8–15 days with no trapping between primary sessions. This time frame was chosen because food availability for rats was assumed to be lower during the 'winter' months on Henderson than at other times of the year (Spencer, 1995; Brooke & Towns, 2008). In the embayment forest, rats were live-trapped between 1 August and 19 September 2015 during three primary sessions of 6–10 trapping nights each.

On the plateau we established a trap network placed along 3 km of cleared path (Fig. 1). Traps were arranged at distances from 3–20 m at 343 locations, with a different subset of trap locations used during each primary session due to gradual progression of trail clearance. In the embayment forest, we established a grid of 63 traps arranged in an oblique rectangular configuration (Fig. 1) with traps spaced 10 m apart. Traps were placed on the ground, marked with a unique number, and locations were recorded to within 5 m using a hand-held GPS device.

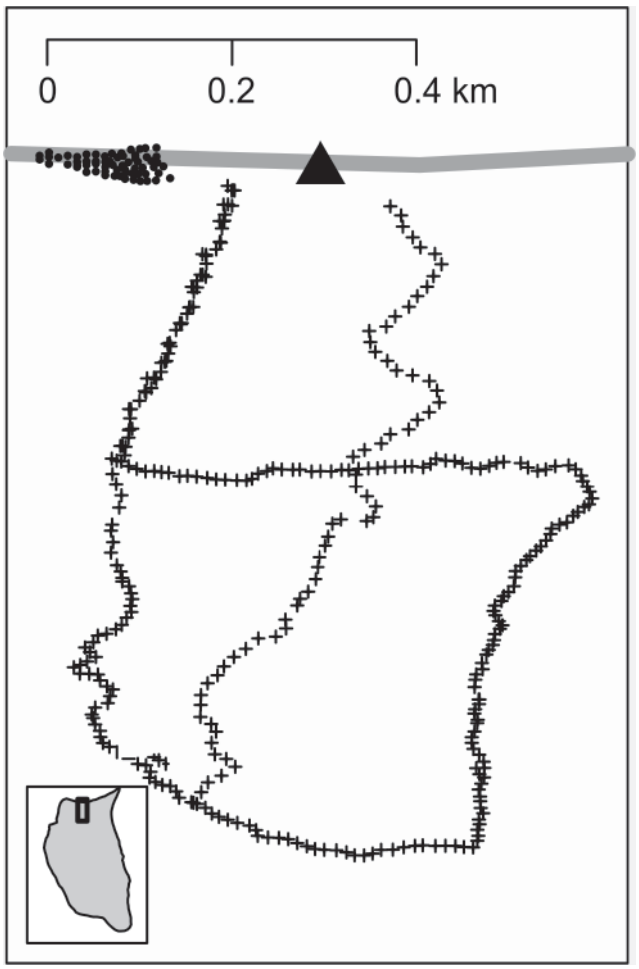

Fig. 1 Map of the trapping network used on Henderson Island in 2015. Black triangle is the research camp, the grey line is the upper margin of the beach, + indicate trap locations on the coral plateau, and black dots indicate trap locations in the embayment forest.

We used two different live trap types, a small metal box (7.6 × 8.9 × 22.9 cm, LFA Folding Trap, H. B. Sherman Traps Inc., Tallahassee, Florida, USA), and a metal cage (13 × 16 × 27 cm, Metal Rat Cage Trap, Key Industries, Auckland, New Zealand). Before the first primary session in each habitat, traps were deployed, but not opened, for approximately five days to allow rats to overcome neophobia (Yackel Adams, et al., 2011; Russell, et al., 2015). For each night in each ten-day trapping period, traps were baited with a small (1 × 1 cm) cube of fresh coconut between 1600–1800 h local time (UTC-8), and checked the following morning between 0800–1000 h.

Each captured rat was fitted with a uniquely numbered ear tag (size 1005-1; National Band & Tag Company, Newport, Kentucky, USA), and the rat was released next to the trap. We recorded the trap location for each capture, whether female rats showed signs of lactation or pregnancy, and whether traps were available to capture rats or had been de-activated (e.g., by crabs). Upon their first capture, rats were sexed by examination of external genitalia, weighed using a spring balance (± 1 g; Pesola AG, Schindellegi, Switzerland), and their body and tail lengths were measured to the nearest 1 mm using a metal ruler (Cunningham & Moors, 1996).

In November 2015, after the mark-recapture effort, we also conducted lethal snap-trapping along a subset of the locations of the live-trap locations on the plateau. This lethal trapping was designed to provide definitive age and

sex classifications and body measurements for as many tagged rats as possible.

Radio-tracking

To provide an alternative estimate of movement range not dependent on the recapture of a rat, we radio-tracked rats that were captured on the plateau in July 2013 using the same small metal box traps as mentioned above. We fitted radio-collars (pipAg393, 2.6 g, Biotrack, Wareham, UK) attached to plastic collars with rubber tubing to each rat. After fitting the collar, rats were placed back in the trap and monitored for five minutes; adjustments were made to the collar if necessary before the rat was released at the site of capture. The capture location, sex, reproductive status (males with or without descended testes; females with or without a perforated vagina) and mass were recorded for all radio-tracked rats as described above.

After release, rats were located at least twice daily during daylight hours using a three-element Yagi antenna and Telonics TR-4 receivers with each radio-collar separated by frequency. Locations were either recorded by homing using a hand-held GPS device with an accuracy of <5 m or estimated through bisection by using distance and bearing from two observation points with an accuracy of ca. 25 m (Kenward, 2001).

Calculation of movement distances

We first calculated the straight-line distance between trap locations for subsequent captures of individual rats. These distances are a conservative estimate of rats' movement distances, because they assume an unrealistic direct line of travel from one trap to the next. We summed all distances between subsequent captures and divided the total travel distance calculated for each individual by the number of captures to provide an overall estimate of mean distance moved between two capture events that is not dependent on the number of captures (Püttker, et al., 2012). We also calculated the observed range length, defined as the maximum distance between any two capture locations for a given individual (Stickel, 1954; Lindsey, et al., 1973). We present results as median ± standard deviation and range.

Analysis of home range size and survival

To estimate rat survival while taking movements into account, we used a spatially-explicit Cormack-Jolly-Seber (CJS) model adapted from similar models (Gardner, et al., 2010; Raabe, et al., 2013; Royle, et al., 2016). We considered each primary session as a capture occasion and reduced binomial capture data from trapping nights to counts of each individual at each trap location during a given primary session because robust-design formulations of the spatial CJS model (Ergon & Gardner, 2014) did not converge. We removed all rats that were captured only once from the analysis, because these transients do not provide any information on movement or survival probability (Pradel, et al., 1997), and we draw no inferences from estimated capture probabilities. We also implemented a non-spatial CJS survival model following Russell & Ruffino (2012), to compare to the spatial model. This model yielded similar mean estimates and temporal variation in survival, suggesting the spatial model results are valid, but with much greater precision by not incorporating the large variance in rat movements (ESM Fig. S1). Understanding and incorporating rat movements is critical for distinguishing survival from movement in apparent survival models (Gilroy, et al., 2012; Schaub & Royle, 2014), especially for inferring potential factors in eradication failure, and we therefore present only the results of the spatial CJS model.

Our spatial CJS model assumed that rat home ranges were circular, but that the estimated centre of a rat's home range could vary spatially based on an individual-specific correlated random walk parameter (Royle, et al., 2016), which effectively allowed rats to shift their activity centre over time. We also assumed that capture probability of rats at a given trap followed a negative exponential function based on the distance of the rat's home range centre to the trap (Ergon & Gardner, 2014; Royle, et al., 2016), and that the shape of this capture probability function varied over time and among individuals. Because exploratory analysis of rat movements indicated that neither individual nor environmental covariates could adequately capture the variation in rat movement, we assumed that the shape of the capture probability function originated from two different statistical distributions: one distribution reflected 'territorial' rats and was specified as a normal distribution with a mean of $\sigma = 30$, which corresponds to a typical home range radius for insular rats (Bramley, 2014b; Ringler, et al., 2014; Harper, et al., 2015). The other distribution reflected 'roaming' rats with a uniform distribution between $\sigma = 60 – 400$, allowing a movement radius of 1,000 m, which has been recorded for Pacific rats in other studies (Wirtz, 1972; Lindsey, et al., 1973). For each individual rat, we allowed the model to select the home range radius parameter belonging to either the 'territorial' or 'roaming' movement type, and we report the proportion of males and females that were estimated to belong to each type.

We estimated rats' survival probability between primary sessions and assumed that survival varied over time. Because the interval among primary sessions was not constant, we calculated the interval as the time difference between the mid-point of subsequent primary sessions (range: 17–25 days) and converted survival probabilities to monthly survival probabilities to allow a direct comparison among different primary sessions. In a CJS model the probabilities of capture and survival are confounded for the last trapping occasion; to allow inference on survival probability up to our last live-trapping occasion in October 2015, we included data from a final additional session of kill trapping in November 2015 in the model (sensu Nathan, et al., 2015), and allowed for a different capture probability for that trapping period. Because rat survival may vary by sex and may depend on food availability (Russell & Ruffino, 2012; Ringler, et al., 2014), we included individual sex and the Normalised Difference Vegetation Index (NDVI) as covariates affecting survival probability. NDVI is a measure of vegetation 'greenness' derived from remote sensing imagery and can serve as a useful proxy for rat food availability (Pettorelli, et al., 2011; Pettorelli, et al., 2014). We downloaded NDVI for Henderson Island at a 250 m resolution from NASA Earth Data (https://daacmodis.ornl.gov/cgi-bin/MODIS/GLBVIZ_1_Glb/modis_subset_order_global_col5.pl), and averaged NDVI over 32 days centred on the mid-point of each survival period to reflect the food availability for rats during the period over which survival was estimated. We used diffuse priors for covariate effects on survival, but used informative priors for daily survival probabilities that were based on previous studies (Tamarin & Malecha, 1971; Moller & Craig, 1987; Roberts & Craig, 1990). Time-specific priors for daily survival probability were drawn from a random uniform distribution between 0.9 and 1.

We fitted the robust design CJS model in JAGS v 3.4.0 (Plummer, 2012) using the 'jagsUI' package (Kellner, 2016) called from R 3.2.5 (R Core Team, 2016). We ran three Markov chains each with 30,000 iterations, discarded the first 7,000 iterations as adaptation and burn-in, and tested for convergence using the Gelman-Rubin diagnostic (Brooks & Gelman, 1998) as well as visual representations of all parameters of interest. We report posterior mean estimates and 95% credible intervals for

survival probability and the spatial shift of home range centres among primary capture sessions. Code to repeat the analysis can be downloaded from: https://github.com/steffenoppel/henderson/blob/master/Oppel_etal_SECR_ANALYSIS_and_DATA.zip.

To estimate a 'home range radius' from the shape of the spatial detection function, we assumed a circular exponential distribution for individual home ranges, and calculated an approximation of the home range radius that would encompass 95% of an individual's territory using the function 'circular.r' in R package secr 2.10.2 (Efford, 2016). We converted this estimate of home range radius to an estimate of home range size using standard geometry ($A = \pi r^2$). This estimate of space use, although not equivalent to a home range estimate obtained from telemetry, allowed us to compare the space use inferred from our spatial trapping approach to a similar metric estimated from radio-tracking to compare the conclusions from each approach.

To provide a comparable estimate of home range size from radio-tracking data, we first calculated the minimum convex polygon (MCP) for each tracked animal and then calculated the 95% kernel utilization distribution using the 'kernelUD' function of the 'adehabitatHR' package in R (Calenge, 2006) for all rats with >10 position fixes after capture. We parameterized our kernel density estimation model using a grid size of 1000, and a smoothing parameter of h = 10 m to avoid overestimation of home ranges due to large kernels around single locations.

Adequacy of cereal bait distribution during eradication attempt

To assess how many bait pellets would have been available to rats, we calculated the approximate number of bait pellets that would have been available in minimum home range sizes of rats during the eradication operation in 2011 based on mean bait application rates. In 2011, bait was distributed at 40–60 kg/ha in the embayment forest and 10 kg/ha on the plateau during the first of two bait applications. Given that a bait pellet weighs ca. 1.8 g, there were between 22,000 and 33,000 pellets/ha available in the embayment forest, and 5,500 pellets/ha on the plateau. For each of the home range estimates from radio-tracking and spatial re-capture, we multiplied the estimated size of the minimum home range area by the density of pellets to infer how many bait pellets would have been accessible to individual rats.

RESULTS

Rat movement

We captured and marked a total of 810 rats, of which 580 were recaptured at least once, yielding a total of 4,920 capture events at 396 unique trap locations. On the plateau, we captured 727 individuals of which 524 were recaptured at least once; in the embayment forest we captured 86 individuals of which 56 were recaptured at least once; only three individuals were captured in both habitats.

The median movement distance between subsequent captures was 17 ± 19 m (range: 0–153 m) in the embayment forest and 23 ± 70 m (0–970 m) on the plateau (Table 1). The median maximum distance between subsequent capture locations averaged across all individuals was 31 ± 23 m in the embayment forest and 54 ± 105 m on the plateau. The observed range length was 39 ± 25 m (0–107 m) in the embayment forest and 61 ± 127 m (0–1,023 m) on the plateau. The total minimum movement distance of individuals summed across all their capture events was 83 ± 100 m (range: 0–387 m) in the embayment forest and 140 ± 617 m (0–8,022 m) on the plateau; however, due to the unequal trapping effort in both time and space these basic movement distances are not directly comparable between the two habitats. Males showed generally longer and more variable movements than females in both habitats, but this effect was more pronounced on the plateau where much longer movements could be recorded by the larger trap network (Table 1). There was very little difference among females that were recorded with or without signs of current reproduction (Table 1). Of the rats recaptured at least once, 8.4% were only captured in one trap location. With the exception of one lactating female which was captured nine times in the same trap location, all rats that were captured >5 times moved between at least two different trap locations.

Table 1 Median and standard deviation (sd) straight-line movement distances (m) and observed range lengths of Pacific rats between live capture events during a spatial mark–recapture study on Henderson Island in May–October 2015. Note that the trapping effort in the two habitats had a different spatial and temporal extent (see Fig. 1 for spatial extent of trap locations). 'breed' females were classified if they had obvious signs of lactation or pregnancy.

Parameter	Embayment forest						Coral plateau					
	males		non-breed females		breed females		males		non-breed females		breed females	
	median	sd	median	sd	median	sd	median	sd	median	sd	median	sd
n individuals	32		13		20		262		201		171	
n captures	171		49		77		2010		1195		608	
mean distance between subsequent captures (m)	17.5	17.9	20.7	19.6	13.6	21.5	27.2	80.4	20.9	53.0	21.6	57.0
maximum distance between subsequent captures (m)	36.7	23.3	31.7	23.2	18.4	21.9	60.7	117.6	49.8	91.1	46.3	85.8
observed range length (m)	43.3	25.2	35.4	23.2	18.4	21.9	70.4	144.9	55.5	106.2	46.3	93.0
total minimum distance travelled (m)	93.6	105.1	108.4	102.2	23.7	56.7	172.0	793.2	115.7	367.4	85.0	204.6

Seasonal variation in survival and space use

Based on the capture and recapture of 540 individual rats on the plateau (including recapture in snap traps in November), we found seasonal variation in monthly survival probability (Fig. 2), but no evidence that survival was influenced by sex (β = -0.15; 95% credible interval -0.43–0.12) or NDVI (β = 0.44; -0.87–1.73). In June and early July, the median monthly survival probabilities of Pacific rats on the plateau were 0.794 (0.306–0.967) and 0.781 (0.471–0.933), respectively, but dropped to 0.353 (0.081–0.737) and 0.636 (0.488–0.763) in late July and early August, respectively (Fig. 2). Remaining survivors had very high survival in late August (0.950; 0.846–0.986) and September (Fig. 2), despite persisting low NDVI (Fig. S2). Similar estimates were obtained from 60 individual rats in the embayment forest, with median monthly survival probabilities of 0.361 (0.054–0.907) in early August and 0.864 (0.466–0.995) in September.

The survival estimates had very low precision due to the potential for confounding emigration, because during the times of lower mean survival probability, a larger number of rats appeared to exhibit longer movements. Rat movements were captured by two frequency distributions (Fig. 3), with the majority of rats (79.1%) belonging to a 'territorial' type that exhibited home range radii between 100 and 200 m, and a smaller proportion (19.9% of males, 22.0% of females) belonging to a 'roaming' type with highly variable and occasionally very long-distance movements (Fig. 3). The proportion of captured rats belonging to the roaming type increased from 0.8% in June to 13.8% in late July (Table 2). In the embayment forest, we estimated only marginally smaller home range radii as on the plateau in early August (Table 2).

Besides large movements around a central point in their territory, our model also indicated that, for rats that were captured in two subsequent primary sessions, the central point of their activity shifted by a median of 50 m (5–290 m) between early and late August, and by a median of 92 m (4–378 m) between September and October (Fig. 4).

Home range sizes estimated from telemetry

In 2013, we successfully tracked 19 rats (9 females, 10 males) between 1 July and 24 August with body mass ranging from 29 to 107 g (median: 71 g, SD: 32 g). The median 50% utilization distribution (the core home range) was 0.095 ± 0.08 ha (range 0.05–0.30 ha), and the 95% utilization distribution (UD) was 0.55 ± 0.37 ha (range 0.21–1.58 ha). The minimum convex polygon home range was more variable with a median of 0.36 ± 0.86 ha (range 0.003–2.99 ha). Rats used vegetation in the canopy or sub-canopy during less than 20% of re-locations. There was no relationship between the number of days a rat was tracked (range: 7–54 days) and the size of its home range (MCP: $p = 0.11$; 95% UD: $p = 0.31$). Thus, the estimates derived from radio-tracking suggested much smaller rat home range areas than those derived from spatially-explicit mark-recapture models, which ranged from 2.88 to 931.6 ha for territorial rats on the plateau, and from 0.11 to 53.6 ha in the embayment forest, assuming that these rats used a circular home range.

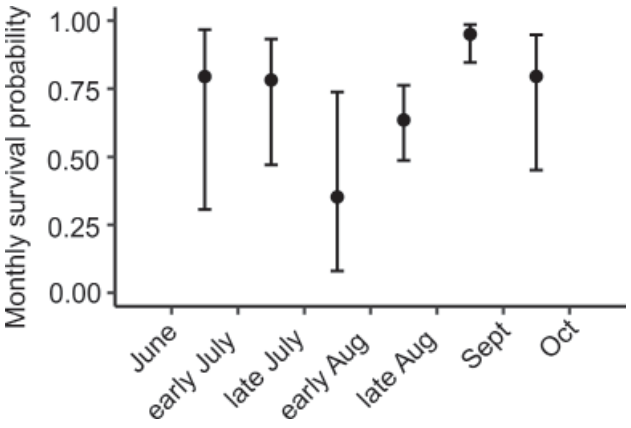

Fig. 2 Mean (95% credible interval) monthly survival probability of Pacific rats on Henderson Island between seven primary trapping sessions over five months in 2015 estimated from a spatial Cormack-Jolly-Seber model. Note that survival probability is scaled over a 30-day period due to unequal time intervals between primary trapping sessions.

Adequacy of cereal bait distribution during the 2011 eradication attempt

The lowest confidence limit for an estimated home range for any season based on our spatial capture data was 2.88 ha on the plateau and 0.11 ha in the embayment forest.

Table 2 Home range radius (m) of two different behavioural types of Pacific rats on the coral plateau and in the embayment forest of Henderson Island between June and October 2015, estimated from a spatial mark–recapture model. Median estimated home range radius and lower (lcl) and upper (ucl) 95% credible limits are given in m. 'prop' indicates the proportion of captured rats in a 10-day trapping session that belonged to one of the behavioural types. Roaming rats could not be detected in the embayment forest.

		Residential rats				Roaming rats			
		prop	median	lcl	ucl	prop	median	lcl	ucl
Plateau	June	0.99	135	107	162	0.01	399	290	584
	early July	0.91	132	103	161	0.09	776	223	1,659
	late July	0.86	133	104	162	0.14	866	279	1,725
	early Aug	0.89	135	107	165	0.11	1,038	307	1,767
	late Aug	0.93	138	110	167	0.07	1,229	619	1,774
	Sept	0.88	137	110	171	0.12	688	150	1,579
	Oct	0.77	132	102	171	0.23	724	293	1,568
Embayment forest	early Aug		96	37	228				
	late Aug		137	36	377				
	Sept		142	34	382				

Home ranges of this size would result in 15,988 toxic bait pellets being available within a rat's home range on the plateau, and 2,456 in the embayment forest. Based on radio-tracking, where the smallest 95% UD was 0.21 ha, 1,175 pellets would have been available in a rat's home range on the plateau, and 4,700 pellets in the embayment forest.

DISCUSSION

We demonstrated that invasive Pacific rats on Henderson Island exhibited substantial individual and temporal variation in their movement and survival over a five-month period. We found no evidence to suggest that rats had home ranges that would have limited their ability to encounter bait if bait was distributed with a density similar to the 2011 eradication attempt. Indeed, the movements and home range estimates that we obtained were considerably higher than those of any other published study on the same species (Table 3), including populations that have been eradicated (Bramley, 2014b). The timing of the failed eradication operation in mid/late August 2011 also appears to have been at a time of the year where we recorded naturally low survival in 2015, and the seasonal timing of the operation was likely appropriate if conditions in 2011 followed a similar phenology as in 2015 (Fig. S2).

Monthly survival probability of Pacific rats varies between 0.40 and 0.72 (Tamarin & Malecha, 1971; Moller & Craig, 1987; Bunn & Craig, 1989), with an expected life span around 8–10 months (Harrison, 1956;

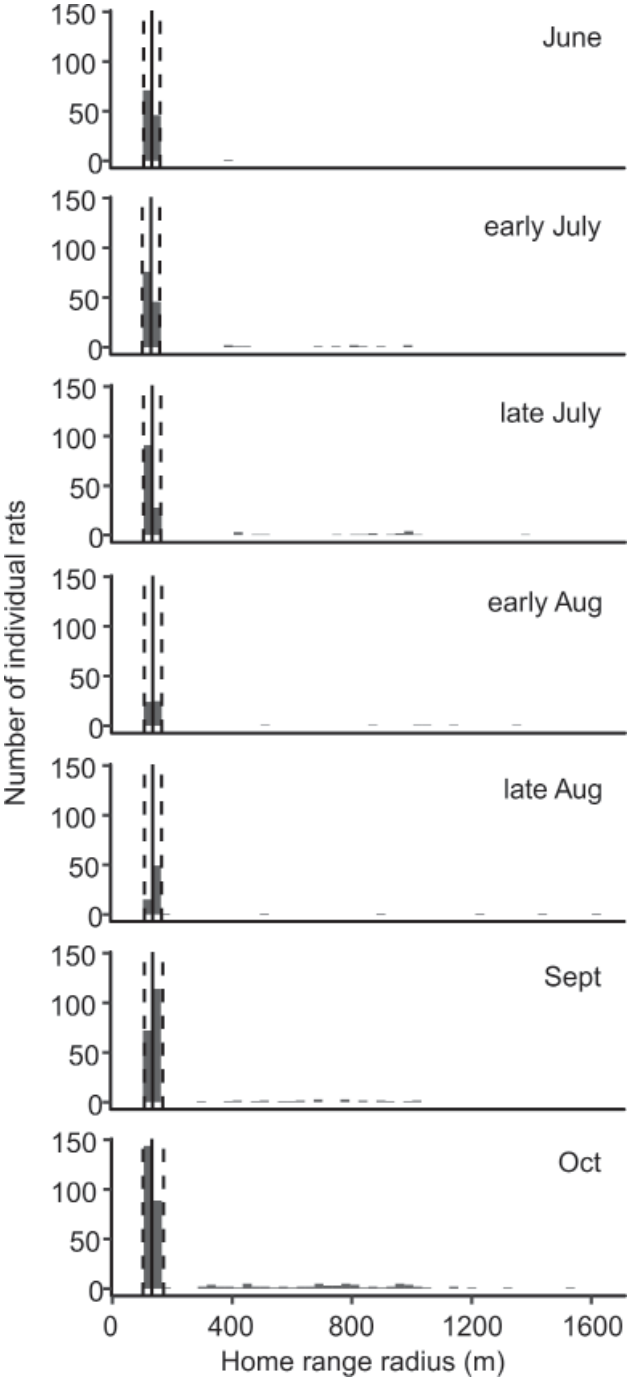

Fig. 3 Histogram of the number of individual Pacific rats having a home range of a radius estimated from a spatial Cormack-Jolly-Seber based on mark–recapture data from the coral plateau on Henderson Island during seven primary trapping sessions in 2015. Vertical lines indicate the population mean (solid) and 95% credible interval (dashed) home range radius.

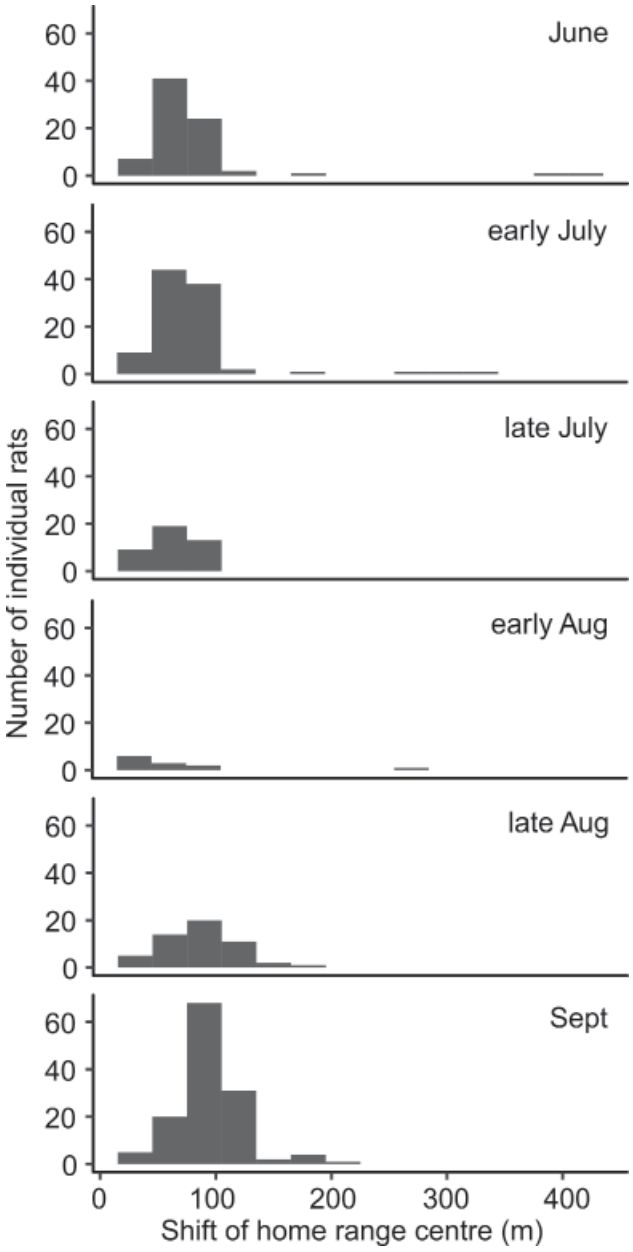

Fig. 4 Frequency of displacement distances of activity centres of male and female Pacific rats on the interior coral plateau of Henderson Island between seven primary trapping sessions over five months in 2015 estimated from a spatial Cormack-Jolly-Seber model.

Bourliere, 1959). We estimated broadly similar median monthly survival probabilities of 0.36–0.90 on Henderson Island. However, previous estimates were mostly based on raw recapture rates and did not account for recapture probabilities, and our slightly higher estimates of survival in June, early July, and late August may be due to our model accounting for low recapture probability. A higher survival probability of Pacific rats on Henderson Island might also be expected given the absence of larger competitors (*R. rattus* or *R. norvegicus*).

There was temporal fluctuation in survival probability of Pacific rats in other tropical (Tamarin & Malecha, 1971) and temperate island populations (Moller & Craig, 1987; Bunn & Craig, 1989), and we found similar short-term variability in survival on Henderson Island. We currently do not understand what may have caused the temporal decline in survival probabilities in July and August, and whether such a reduction occurs predictably every year in response to regular environmental events. As a sub-tropical island, Henderson Island experiences only moderate fluctuations in temperature and day length, which are unlikely to lead to the same predictable population fluctuations as observed on temperate islands (Russell & Holmes, 2015). The changes in both survival and movement within our five-month study period on Henderson may have reflected a period of resource shortage from late July to September that may have induced higher mortality and emigration as a larger proportion of rats belonged to the 'roaming' movement type. Assuming that the reduced survival that we observed in 2015 was caused by resource limitation (e.g. Russell & Ruffino, 2012), and that fluctuations in resource availability and survival are similar among years (Fig. S2), an operational timing in July or early August may maximise the chances of eradication success.

Our spatial mark-recapture data on the plateau, where traps were up to 1.5 km apart, revealed many long movements by rats. These movements matched or exceeded the previously estimated maximum travel distance of 1,097 m or home range estimate of 3 ha for Pacific rats (Lindsey, et al., 1973; Nass, 1977; Lindsey, et al., 1999; Clapperton, 2006; Scheffler, et al., 2012), and were similar to movements typically found in the much larger Norway rat (*R. norvegicus*) (Clapperton, 2006; Bramley, 2014b). Despite some long movements that we recorded, the extrapolated 'home range areas' from our spatial capture data are possibly biased high, because these extrapolations are based on the assumption that rats occupy a circular home range, which may not be the case (Nass, 1977; Lindsey, et al., 1999; Clapperton, 2006). In particular, our trails may have affected rat movement by providing highly nutritious and palatable coconut bait in traps that is otherwise not available on the plateau. However, our trails were characterised by an absence of vegetation between 30 to 250 cm above ground, and probably did not materially affect the movement ability of rats on the ground. Nonetheless, the maximum estimates of home range area that we provide must be considered with caution, as the areas actually exploited by rats may be significantly smaller than the assumed circular radius range.

Based on our estimates of movement behaviour from radio-tracking in 2013 and spatial mark-recapture in 2015, individual rats would have theoretically encountered hundreds to thousands of bait pellets in their typical home range, which would likely be sufficient for them to ingest a lethal dose even if crab consumption gradually reduced bait density over time (Cuthbert, et al., 2012). We therefore consider it unlikely that the eradication failed because individual rats did not have access to a sufficient quantity of toxic bait, but uncertainty remains with respect to certain life stages (e.g. nursing female rats and freshly weaned pups): the number of rats surviving the 2011 operation was very small, constituting <0.2% of the estimated rat population (Amos, et al., 2016). An eradication operation may fail if only a very small number of rats exhibit no movement and would therefore not encounter a sufficient quantity of bait. Of the 810 rats that we captured in 2015, 28% were never recaptured, and of those that were

Table 3 Summary of home range size (ha) estimates of Pacific rats (*Rattus exulans*) on subtropical and tropical islands derived from either radio tracking (TR) or spatial capture–mark–recapture (CMR); type of estimate refers to minimum convex polygon (MCP) or spatially-explicit capture recapture (SECR) and indicates what measure of uncertainty (standard deviation, SD; range) is provided with the estimate.

Location	Tracking method	Sex	*n*	Home range (ha)	Type of estimate	Reference
Hilo, HI, USA	TR	F	28	0.06 (0.01–0.18)	MCP (range)	(Nass, 1977)
Green Island, Kure Atoll, HI, USA	CMR	F	40	0.08 (0.01–0.48)	Mean minimum (range)	(Wirtz, 1972)
Kapiti Island, NZ	TR	M	6	0.14 ± 0.04	MCP (mean ± SD)	(Bramley, 2014b)
Green Island, Kure Atoll, HI, USA	CMR	M	19-40	0.17 (0.01–0.73)	Mean minimum (range)	(Wirtz, 1972)
Hilo, HI, USA	TR	M	29	0.18 (0.01-1.21)	MCP (range)	(Nass, 1977)
Kapiti Island, NZ	TR	F	5	0.18 ± 0.05	MCP (mean ± SD)	(Bramley, 2014b)
Henderson Island, Pitcairn Islands	TR	F+M	19	0.32 ± 0.38	MCP (mean ± SD)	This study
Henderson Island, Pitcairn Islands	CMR	F+M	541	0.11 –931.6	SECR (range)	This study
Hilo, HI, USA	TR	F+M	26	1.73	Circle with radius mean distance from burrow	(Lindsey, et al., 1973)
Hilo, HI, USA	TR	F+M	3	3	MCP (mean ± SD)	(Lindsey, et al., 1999)
Kahanahaiki, HI, USA	TR	Unk	1	1.8	95% kernel	(Shiels, 2010)

recaptured at least once, 8% were only captured in a single location. Because we did not record any movement for a greater proportion of rats than the estimated surviving population in 2011, it is theoretically possible that there are some individuals that move very little or move very little for a short period of time during which bait is available on the ground. Unfortunately, the probability of detecting a non-moving phenotype that exists with a prevalence of <0.2% in the population is virtually zero for any practically feasible sample size.

In summary, the rat eradication attempt on Henderson Island in 2011 failed to kill all individuals, and our work provides new knowledge to evaluate the potential causes of this failure. An eradication failure can occur if (i) not all individuals had access to sufficient bait; (ii) not all individuals died despite consuming bait; or (iii) not all individuals consumed a lethal dose of bait despite having access (Holmes, et al., 2015). We have shown that the timing of the operation was appropriate and that it is unlikely that rats did not have access to sufficient bait. Previous work confirmed that rats remain susceptible to brodifacoum, suggesting that toxicological resistance is an unlikely cause of the 2011 eradication failure (Amos, et al., 2016). A combination of factors leading to high alternative food availability and a small number of rats preferring natural food sources and disregarding bait may have resulted in the failure of the eradication attempt in 2011, and further research is required to examine whether that risk can be reduced for a new eradication attempt.

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REFERENCES

Amos, W., Nichols, H.J., Churchyard, T. and Brooke, M. de L. (2016). 'Rat eradication comes within a whisker! A case study from the South Pacific'. *Royal Society Open Science* 3: 160110.

Atkinson, I.A.E. (1985). 'The Spread of Commensal Species of *Rattus* to Oceanic Islands and their Effects on Island Avifaunas.'. In*:* P.J. Moors (ed.) *Conservation of Island Birds.* pp. 35–81. Cambridge, United Kingdom: International Council for Bird Preservation.

Bond, A.L., Churchyard, T., Cuthbert, R.J., Donaldson, A., Duffield, N., Forrest, A., Havery, S., Lavers, J.L., MacKinnon, L., McClelland, G.T.W., Kelly, J., Proud, T., Skinner, A., Torr, N., Vickery, J.A. and Oppel, S. (2019). 'Recovery of introduced Pacific rats (*Rattus exulans*) following a failed eradication attempt on Subtropical Henderson Island, South Pacific Ocean'. In: C.R. Veitch, M.N. Clout, A.R. Martin, J.C. Russell and C.J. West (eds.) *Island invasives: scaling up to meet the challenge*, pp. 167–174. Occasional Paper SSC no. 62. Gland, Switzerland: IUCN.

Bourliere, F. (1959). 'Lifespans of Mammalian and Bird Populations in Nature'. In*:* G.E.W. Wolstenholme and M. O'Connor (eds.) *The Lifespan of Animals*, pp. 90–102. London: J & A Churchill.

Bramley, G.N. (2014a). 'Habitat use by kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand'. *New Zealand Journal of Ecology* 38: 64–75.

Bramley, G.N. (2014b). 'Home ranges and interactions of kiore (*Rattus exulans*) and Norway rats (*R. norvegicus*) on Kapiti Island, New Zealand'. *New Zealand Journal of Ecology* 38: 328–334.

Brooke, M. de L. and Towns, D. (2008). *A Feasibility Study for the Eeradication of Kiore Rattus exulans from Henderson Island.* Royal Society for the Protection of Birds, Sandy, UK.

Brooke, M. de L., O'Connell, T.C., Wingate, D., Madeiros, J., Hilton, G.M. and Ratcliffe, N. (2010). 'Potential for rat predation to cause decline of the globally threatened Henderson petrel *Pterodroma atrata*: Evidence from the field, stable isotopes and population modelling'. *Endangered Species Research* 11: 47–59.

Brooks, S.P. and Gelman, A. (1998). 'General methods for monitoring convergence of iterative simulations'. *Journal of Computational and Graphical Statistics* 7: 434–455.

Broome, K., Cox, A., Golding, C., Cromarty, P., Bell, P. and McClelland, P. (2014). *Rat Eradication Using Aerial Baiting. Current Agreed Best Practice Used in New Zealand.* Internal document DOC-29396. New Zealand Department of Conservation, Wellington, New Zealand.

Bunn, T.J. and Craig, J.L. (1989). 'Population cycles of *Rattus exulans*: Population changes, diet, and food availability'. *New Zealand Journal of Zoology* 16: 409–418.

Calenge, C. (2006). 'The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals'. *Ecological Modelling* 197: 516–519.

Clapperton, B.K. (2006). *A Review of the Current Knowledge of Rodent Behaviour in Relation to Control Devices.* Wellington, NZ: Department of Conservation.

Cromarty, P.L., Broome, K.G., Cox, A., Empson, R.A., Hutchinson, W.M. and McFadden, I. (2002). 'Eradication planning for invasive alien animal species on islands – the approach developed by the New Zealand Department of Conservation'. In*:* C.R. Veitch and M.N. Clout (eds.) *Turning the tide: the eradication of invasive species*, pp. 85–91. Occasional Paper SSC no. 28. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.

Cunningham, D.M. and Moors, P.J. (1996). *Guide to the Identification and Collection of New Zealand Rodents, 2nd edition,* Wellington, NZ: Department of Conservation.

Cuthbert, R.J., Brooke, M. de L. and Torr, N. (2012). 'Overcoming hermit-crab interference during rodent-baiting operations: A case study from Henderson Island, South Pacific'. *Wildlife Research* 39: 70–77.

Dawson, J., Oppel, S., Cuthbert, R.J., Holmes, N., Bird, J.P., Butchart, S.H.M., Spatz, D.R. and Tershy, B. (2015). 'Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories'. *Conservation Biology* 29: 143–153.

Efford, M. (2016). 'secr – Spatially Explicit Capture–recapture in R. R Package Version 2.10.4'. <https://CRAN.R-project.org/package=secr>.

Ergon, T. and Gardner, B. (2014). 'Separating mortality and emigration: Modelling space use, dispersal and survival with robust-design spatial capture–recapture data'. *Methods in Ecology and Evolution* 5: 1327–1336.

Gardner, B., Reppucci, J., Lucherini, M. and Royle, J.A. (2010). 'Spatially explicit inference for open populations: Estimating demographic parameters from camera-trap studies'. *Ecology* 91: 3376–3383.

Gilroy, J.J., Virzi, T., Boulton, R.L. and Lockwood, J.L. (2012). 'A new approach to the "apparent survival" problem: Estimating true survival rates from mark–recapture studies'. *Ecology* 93: 1509–1516.

Harper, G.A., van Dinther, M., Russell, J.C. and Bunbury, N. (2015). 'The response of black rats (*Rattus rattus*) to evergreen and seasonally arid habitats: Informing eradication planning on a tropical island'. *Biological Conservation* 185: 66–74.

Harrison, J. (1956). 'Survival rates of Malayan rats'. *Bulletin of the Raffles Museum* 27: 5–26.

Holmes, N.D., Griffiths, R., Pott, M., Alifano, A., Will, D., Wegmann, A. and Russell, J.C. (2015). 'Factors associated with rodent eradication failure'. *Biological Conservation* 185: 8–16.

Howald, G., Donlan, C.J., Galvan, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y.W., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. and Tershy, B. (2007). 'Invasive rodent eradication on islands'. *Conservation Biology* 21: 1258–1268.

Jones, H.P. (2010). 'Seabird islands take mere decades to recover following rat eradication'. *Ecological Applications* 20: 2075–2080.

Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Oppel, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russell, J.C., Samaniego-Herrera, A., Seddon, P.J., Spatz, D.R., Towns, D.R. and Croll, D.A. (2016). 'Invasive mammal eradication on islands results in substantial conservation gains'. *Proceedings of the National Academy of Sciences* 113: 4033–4038.

Keitt, B., Griffiths, R., Boudjelas, S., Broome, K., Cranwell, S., Millett, J., Pitt, W. and Samaniego-Herrera, A. (2015). 'Best practice guidelines for rat eradication on tropical islands'. *Biological Conservation* 185: 17–26.

Kellner, K.F. (2016). 'jagsUI: A Wrapper Around rjags to Streamline JAGS Analyses. R Package Version 1.4.2'. <https://CRAN.R-project.org/package=jagsUI>.

Kenward, R. (2001). *A Manual for Wildlife Radio Tagging,* London: Academic Press.

Lindsey, G.D., Nass, R.D., Hood, G.A. and Hirata, D.N. (1973). 'Movement patterns of Polynesian rats (*Rattus exulans*) in sugarcane'. *Pacific Science* 27: 239–246.

Lindsey, G.D., Mosher, S.M., Fancy, S.G. and Smucker, T.D. (1999). 'Population structure and movements of introduced rats in an Hawaiian rainforest'. *Pacific Conservation Biology* 5: 94–102.

Moller, H. and Craig, J.L. (1987). 'The population ecology of *Rattus exulans* on Tiritiri Matangi Island, and a model of comparative population dynamics in New Zealand'. *New Zealand Journal of Zoology* 14: 305–328.

Nass, R.D. (1977). 'Movements and home ranges of Polynesian rats in Hawaiian sugarcane'. *Pacific Science* 31: 135–142.

Nathan, H.W., Clout, M.N., MacKay, J.W.B., Murphy, E.C. and Russell, J.C. (2015). 'Experimental island invasion of house mice'. *Population Ecology* 57: 363–371.

Paulay, G. and Spencer, T. (1989). 'Vegetation of Henderson Island'. *Atoll Research Bulletin* 328: 1–20.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jędrzejewska, B., Lima, M. and Kausrud, K. (2011). ‚The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology'. *Climate Research* 46: 15–27.

Pettorelli, N., Laurance, W.F., O'Brien, T.G., Wegmann, M., Nagendra, H. and Turner, W. (2014). 'Satellite remote sensing for applied ecologists: opportunities and challenges'. *Journal of Applied Ecology* 51: 839–848.

Plummer, M. (2012). ‚JAGS Version 3.3.0'. <http://sourceforge.net/projects/mcmc-jags/files/Manuals/>.

Pradel, R., Hines, J.E., Lebreton, J.D. and Nichols, J.D. (1997). 'Capture–recapture survival models taking account of transients'. *Biometrics* 53: 60–72.

Püttker, T., de Barros, C.d.S., Martins, T.K., Sommer, S. and Pardini, R. (2012). 'Suitability of distance metrics as indexes of home-range size in tropical rodent species'. *Journal of Mammalogy* 93: 115–123.

R Core Team (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Raabe, J.K., Gardner, B. and Hightower, J.E. (2013). 'A spatial capture–recapture model to estimate fish survival and location from linear continuous monitoring arrays'. *Canadian Journal of Fisheries and Aquatic Sciences* 71: 120–130.

Ringler, D., Russell, J., Jaeger, A., Pinet, P., Bastien, M. and Le Corre, M. (2014). 'Invasive rat space use on tropical islands: Implications for bait broadcast'. *Basic and Applied Ecology* 15: 179–186.

Roberts, M. and Craig, J. (1990). 'The demography of kiore, *Rattus exulans* in three habitats'. *New Zealand Journal of Zoology* 17: 43–53.

Royle, J.A., Fuller, A.K. and Sutherland, C. (2016). 'Spatial capture-recapture models allowing Markovian transience or dispersal'. *Population Ecology* 58: 53–62.

Russell, J.C. and Ruffino, L. (2012). 'The influence of spatio-temporal resource fluctuations on insular rat population dynamics'. *Proceedings of the Royal Society B: Biological Sciences* 279: 767–774.

Russell, J.C., Caut, S., Anderson, S.H. and Lee, M. (2015). 'Invasive rat interactions and over-invasion on a coral atoll'. *Biological Conservation* 185: 59–65.

Russell, J.C. and Holmes, N.D. (2015). 'Tropical island conservation: rat eradication for species recovery'. *Biological Conservation* 185: 1–7.

Schaub, M. and Royle, J.A. (2014). 'Estimating true instead of apparent survival using spatial Cormack–Jolly–Seber models'. *Methods in Ecology and Evolution* 5: 1316–1326.

Scheffler, P.Y., Foote, D., Forbes Perry, C., Schlappa, K. and Stone, C.P. (2012). *Population Dynamics of Introduced Rodents in Hawai'i Volcanoes National Park 1986–1990.* Honolulu, HI: Pacific Cooperative Studies Unit, University of Hawai'i.

Shiels, A.B. (2010). 'Ecology and Impacts of Introduced Rodents (*Rattus* spp. and *Mus musculus*) in the Hawaiian Islands'. PhD thesis. Honolulu, HI: University of Hawai'i.

Spencer, T. (1995). 'The Pitcairn Islands, south Pacific Ocean: Plate tectonic and climatic contexts'. *Biological Journal of the Linnean Society* 56: 13–42.

Steadman, D.W. and Olson, S.L. (1985). 'Bird remains from an archaeological site on Henderson Island, South Pacific: Man-caused extinctions on an "uninhabited" island'. *Proceedings of the National Academy of Sciences* 82: 6191–6195.

Stickel, L.F. (1954). 'A comparison of certain methods of measuring ranges of small mammals'. *Journal of Mammalogy* 35: 1–15.

Tamarin, R.H. and Malecha, S.R. (1971). 'The population biology of Hawaiian rodents: Demographic parameters'. *Ecology* 52: 383–394.

Torr, N. and Brown, D. (2012). *Henderson Island restoration project post-operational report.* Sandy, UK: Royal Society for the Protection of Birds.

Waldren, S., Florence, J. and Chepstow-Lusty, A.J. (1995). 'A comparison of the vegetation communities from the islands of the Pitcairn group'. *Biological Journal of the Linnean Society* 56: 121–144.

Weigelt, P., Jetz, W. and Kreft, H. (2013). 'Bioclimatic and physical characterization of the world's islands'. *Proceedings of the National Academy of Sciences* 110: 15307–15312.

Wirtz, W.O.I. (1972). 'Population ecology of the Polynesian rat, *Rattus exulans*, on Kure Atoll, Hawaii'. *Pacific Science* 26: 433–464.

Yackel Adams, A.A., Stanford, J.W., Wiewel, A.S. and Rodda, G.H. (2011). 'Modelling detectability of kiore (*Rattus exulans*) on Aguiguan, Mariana Islands, to inform possible eradication and monitoring efforts'. *New Zealand Journal of Ecology* 35: 145–152.

Zavaleta, E.S. (2002). 'It's often better to eradicate, but can we eradicate better?'. In*:* C.R. Veitch and M.N. Clout (eds.) *Turning the tide: the eradication of invasive species*, pp. 393–404. Occasional Paper SSC no. 28. IUCN SSC Invasive Species Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.