

# Recovery of introduced Pacific rats following a failed eradication attempt on subtropical Henderson Island, South Pacific Ocean

A.L. Bond<sup>1,4</sup>, R.J. Cuthbert<sup>1,5</sup>, G.T.W. McClelland<sup>1</sup>, T. Churchyard<sup>1</sup>, N. Duffield<sup>1</sup>, S. Havery<sup>1</sup>, J. Kelly<sup>2</sup>, J.L. Lavers<sup>1</sup>, T. Proud<sup>1</sup>, N. Torr<sup>1</sup>, J.A. Vickery<sup>1</sup> and S. Oppel<sup>3</sup>

<sup>1</sup>RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK. <a.bond@nhm.ac.uk>. <sup>2</sup>Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, SG19 2DL, UK. <sup>3</sup>RSPB Centre for Conservation Science, Royal Society for the Protection of Birds, David Attenborough Building, Pembroke Street, Cambridge, CB2 3EZ, UK. <sup>4</sup>Present address: Bird Group, Department of Life Sciences, The Natural History Museum, Akeman Street, Tring, Hertfordshire, HP23 6AP, UK. <sup>5</sup>Present address: Conservation Solutions, 9 Prospect Drive, Belper, Derbyshire, DE56 1UY, UK.

**Abstract** Rodent eradications in tropical environments are often more challenging and less successful than those in temperate environments. Reduced seasonality and the lack of a defined annual resource pulse influence rodent population dynamics differently than the well-defined annual cycles on temperate islands, so an understanding of rodent ecology and population dynamics is important to maximise the chances of eradication success in the tropics. Here, we report on the recovery of a Pacific rat (*Rattus exulans*) population on Henderson Island, South Pacific Ocean, following a failed eradication operation in 2011. We assessed changes in the rat population using capture rates from snap-trapping and investigated seasonality by using capture rates from live-trapping. Following the failed eradication operation in 2011, rat populations increased rapidly with annual per capita growth rates,  $r$ , of 0.48–5.95, increasing from 60–80 individuals to two-thirds of the pre-eradication abundance within two years, before decreasing ( $r = -0.25 - -0.20$ ), presumably as the population fluctuated around its carrying capacity. The long-term changes in rat abundance may, however, be confounded by short-term fluctuations: four years after the eradication attempt we observed significant variation in rat trapping rates among months on the plateau, ranging from 36.6 rats per 100 corrected trap-nights in mid-June to 12.6 in late August. Based on mark-recapture, we also estimated rat density fluctuations in the embayment forest between 20.4 and 42.9 rats ha<sup>-1</sup> within one month in 2015, and a much lower rat density on the coral plateau fluctuating between 0.76 and 6.08 rats ha<sup>-1</sup> in the span of two months. The causes for the short-term density fluctuations are poorly understood, but as eradication operations on tropical and subtropical islands become more frequent, it will be increasingly important to understand the behaviour and ecology of the invasive species targeted to identify times that maximise eradication success.

**Keywords:** introduced species, island restoration, Pitcairn Islands, rodents, spatially explicit capture-recapture

## INTRODUCTION

The removal of introduced rodents from islands is an increasingly important tool for the conservation of island biodiversity, and has been successful in hundreds of cases (Lorvelec & Pascal, 2005; Howald, et al., 2007; Bellingham, et al., 2010; Russell & Holmes, 2015). Introduced rodents have been eradicated from >580 islands (Keitt, et al., 2015; DIISE, 2016) and rodent eradications are one of the most cost-effective methods of preserving island biodiversity (Howald, et al., 2007; Jones, et al. 2016).

The success rate of rodent eradications has improved as eradication tools and methods become more refined. However, failures still occur, especially on tropical islands where conditions that can increase the risk of eradication failure, such as aseasonal breeding, are more likely (Varnham, 2010; Holmes, et al., 2015). While undesirable, these unsuccessful projects still provide an opportunity to advance conservation science, often through *post hoc* review of operational planning and implementation (Keitt, et al., 2015). However, they also present potentially unique occasions to further understand invasion biology. For example, the population dynamics of surviving rodent populations following such failed eradication attempts are seldom studied (Hein & Jacob, 2015) despite being useful for predicting population dynamics during new invasions (Nathan, et al., 2015).

In particular, there is currently little knowledge on how much time elapses before tropical rodent populations can reach an island's presumed carrying capacity after a severe population bottleneck, but such information could be useful to inform the post-operation monitoring interval that determines whether an eradication operation has been successful or not (Samaniego-Herrera, et al., 2013).

On temperate islands, two years encompasses two rat breeding seasons, and is typically sufficient to determine an eradication operation's success. In the tropics, rats have a less constrained timing of breeding, and a breeding cycle as short as four months, so a shorter time may be required to reliably detect a recovering rat population, particularly in wetter conditions (Keitt, et al., 2015).

For many widespread invasive rodents, however, there is a lack of basic ecological knowledge about densities, and the factors affecting the large variation in abundance that is evident for highly versatile invasive rodents (Harper & Bunbury, 2015). Henderson Island (24°20'S, 128°19'W), in the subtropical Pitcairn Islands of the South Pacific, was subject to an aerial poison bait-based eradication attempt of the introduced Pacific rat (*Rattus exulans*) in 2011 (Torr & Brown, 2012). The eradication was unsuccessful, but the cause of the failure was neither operational shortcoming nor due to resistance of rats to brodifacoum pellets (Torr & Brown, 2012; Amos, et al., 2016, Brooke, 2019).

Here, we report on the population recovery of *R. exulans* on Henderson Island up to four years following a failed eradication attempt, and provide information on short-term seasonality in density of Pacific rats using live trapping and a spatially explicit capture-recapture (SECR) framework. We use the obtained estimates in a rapid eradication assessment (Russell, et al., 2017) to provide guidance on the length of a post-operation monitoring period after which an eradication could be considered successful with 95% certainty. These data provide a robust overview of the short- and long-term population variability on an aseasonal sub-tropical island that will inform future conservation management.

## MATERIALS AND METHODS

### Study area

Henderson Island, a UNESCO World Heritage Site, is a 43 km<sup>2</sup> raised coral atoll in the Pitcairn Islands, South Pacific Ocean, with a tropical climate (Spencer, 1995; Weigelt, et al., 2013). The island was subjected to an unsuccessful aerial eradication attempt of the introduced Pacific rat (*Rattus exulans*) in 2011 (Torr & Brown, 2012). While the ultimate cause of the eradication failure remains unknown, resistance of rats to brodifacoum pellets or operational errors are not considered factors (Torr & Brown, 2012; Amos, et al., 2016).

We conducted our study at the northern end of the island's plateau and along the two accessible beaches, North Beach and East Beach. The plateau substrate is fossilised coral with a uniform, dense native vegetation consisting of mostly of *Pandanus tectorius*, *Xylocarpus muellerianus* and *Psychotria odorata* (Waldren, et al., 1995). The beach and embayment forest ("beach back") areas have a sandy substrate with a mixed low vegetation and small stands of introduced coconut (*Cocos nucifera*) (Waldren, et al., 1995).

### Rat snap-trapping and long-term abundance indices

We estimated rat abundance indices in 2009 (September), 2012 (May and November), 2013 (August), and 2015 (October and November) on the plateau and embayment forest areas of North and East beaches of Henderson using snap-traps, though the precise methods differed because of logistical and time constraints. In all years, however, we set traps between 16:00–18:00 h (all times UTC-8), and checked the following morning between 08:00–10:00 h (Table 1).

We recorded the traps' contents (rat, crab, or snapped and empty) to calculate an index of abundance as the number of rats caught per 100 corrected trap-nights (100 CTN; Nelson & Clark, 1973), where

CTN = Total trap-nights – Trap-nights lost (equation 1);

Trap-nights lost =  $\frac{1}{2} \times (\text{crab captures} + \text{snapped traps})$  (equation 2).

### Estimating long-term rat population change

Based on the rat abundance indices derived from snap-trapping, we estimated the annual per capita growth rate,  $r$ , using the formula:

$$r = \frac{\log\left(\frac{N_t}{N_{t-1}}\right)}{t}$$

(equation 3), where  $N$  is the population estimate at time  $t$  and  $t-1$ , and  $t$  is the elapsed time, in years, between the two estimates.

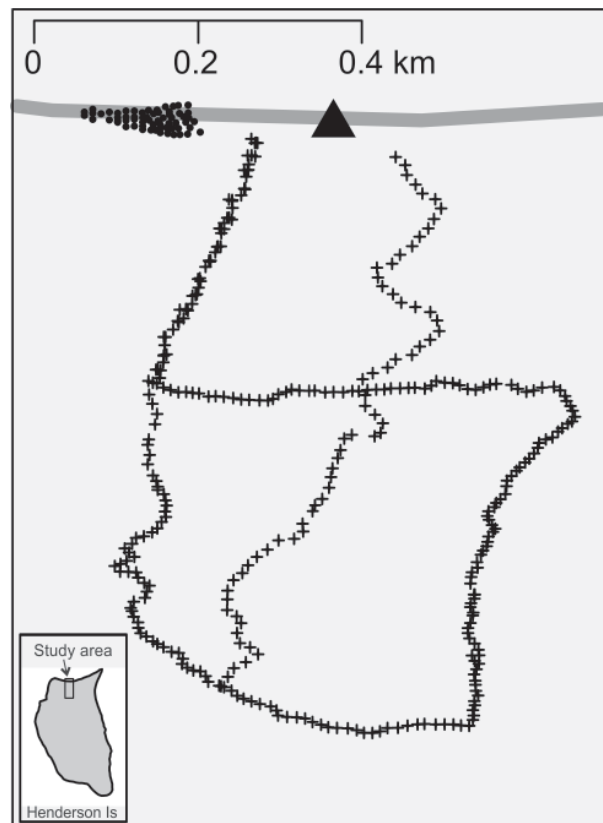
To estimate a population growth rate, which requires non-zero values in each time interval if no immigration is assumed, we scaled abundance indices derived from snap-trapping to an island population size. This approach allowed us to have all the population estimates on the same scale, and to include the very small population size in 2011. We extrapolated population size based on live- and snap-trapping data from 2009: based on live-trapping, there were approximately 28 rats/ha (95% confidence interval: 23–40 rats/ha) in the embayment forest of North Beach on Henderson (Cuthbert, et al., 2012), which corresponded to 31.7 rats 100 CTN<sup>-1</sup> in the same habitat. We extrapolated the density estimate to an approximate population size of 120,000 (range: 104,000–172,000) rats on the island, assuming equal density across all habitat types, and used the relationship between this extrapolated population

size and the snap-trapping rate to extrapolate population sizes in other years. For 2011, when no snap-trapping data were available, we used the population estimate of 60–80 individuals that was estimated to have survived the eradication attempt in 2011 based on genetic markers (Amos, et al., 2016). In each year, we proportioned the total population to the three different habitats in which we measured rat abundance based on their relative area: North Beach embayment forest (7 ha), East Beach embayment forest (7 ha), and the island plateau (4,290 ha), and the initial population based on the abundance indices in these three habitats in 2009. We assumed that trapability was constant among years.

### Rat live trapping and density estimation

To obtain a robust estimate of rat density and to document short-term fluctuation in rat density over six months, we implemented a spatial capture-mark-recapture programme in 2015 (Oppel, et al., 2019). Rats were live-trapped on the plateau from 28 May to 16 October 2015 during seven primary sessions of 10 consecutive trap-nights each, followed by a window of 10–15 days with no trapping between primary sessions. We established a trap network placed along 3.5 km of cleared paths (Fig. 1), and traps were arranged at distances from 3–20 m along 343 locations, with a different subset of 250 trap locations used during each primary session. Because our original traps (Sherman and Elliott aluminum boxes; model LFA, 23 × 9 × 8 cm, H.B. Sherman Traps Inc., Tallahassee, Florida, USA) were easily damaged by crabs, they were replaced by larger and more robust Tomahawk cage traps in September (27 × 16 × 13 cm, Key Industries, Auckland, New Zealand).

In the embayment forest at North Beach, rats were live-trapped during three primary occasions of 6–10 trap-nights each between 1 August and 19 September 2015 using 38



**Fig. 1** Map of the path network on the north end of Henderson Island showing the locations of all live traps used in 2015 (+), snap-trapping grid on North Beach (•) and the location of the research camp (▲).

**Table 1** Snap trap arrangements and bait used on Henderson Island from 2009–2015.

Habitat	Start date	End date	Bait	Trap spacing
Embayment forest – East Beach	12 Sep 09	21 Sep 09	Coconut, peanut butter, rolled oats	10–15 m
	14 Aug 11	23 Aug 11		
	23 Nov 12	30 Nov 12	Peanut butter, coconut	10–15 m
	21 Aug 13	28 Aug 13	Peanut butter, coconut	10–15 m
Embayment forest – North Beach	12 Sep 09	21 Sep 09	Coconut, peanut butter, rolled oats	10–15 m
	14 Aug 11	23 Aug 11		
	03 May 12	06 May 12	Peanut butter, rolled oats, chocolate	8–10 m
	23 Nov 12	30 Nov 12	Peanut butter, coconut	10–15 m
	21 Aug 13	28 Aug 13	Peanut butter, coconut	10–15 m
	21 Oct 15	31 Oct 15	Coconut, <i>Pandanus</i>	20 m
	01 Nov 15	14 Nov 15	Coconut, <i>Pandanus</i>	20 m
Plateau	12 Sep 09	21 Sep 09	Coconut, peanut butter, rolled oats	10–15 m
	14 Aug 11	23 Aug 11		
	03 May 12	06 May 12	Peanut butter, rolled oats, chocolate	8–10 m
	23 Nov 12	30 Nov 12	Peanut butter, coconut	10–15 m
	21 Aug 13	28 Aug 13	Peanut butter, coconut	10–15 m
	21 Oct 15	31 Oct 15	Coconut, <i>Pandanus</i>	20 m
	01 Nov 15	14 Nov 15	Coconut, <i>Pandanus</i>	20 m

traps arranged in a  $6 \times 6$  configuration with traps spaced 10 m apart, and we expanded the trapping grid to 63 traps in a  $7 \times 9$  configuration for the last primary session.

Before the first primary session in each habitat, traps were deployed, but not opened, for approximately five days to allow rats to overcome neophobia. For each ten-day trapping period, traps were baited with a small (approximately  $1 \times 1$  cm) cube of fresh coconut between 16:00–18:00 h, and checked the following morning between 08:00–10:00 h.

During trap checks each captured rat was fitted with a uniquely numbered ear tag, or the number of an existing ear tag was recorded, and the rat was released next to the trap. We recorded the trap location for each capture and recorded whether traps were available to capture rats or had been rendered ineffective (e.g. by crabs). We estimated a capture index (rats/100 corrected trap nights) for the plateau and the embayment forest for each trap-night using the same equation as above to correct for inactivated traps.

To estimate rat densities, we used spatially-explicit capture-recapture models, which have been used successfully for other rat density estimations on islands (Russell, et al., 2011; Ringler, et al., 2014; Harper, et al., 2015). We assumed that rat home ranges were randomly located with respect to trap locations and stationary within a given primary session, and that the central location of the home range was adequately described by a homogenous Poisson distribution (Efford, 2004; Borchers, 2012). Capture probability of rats at a given trap was based on the distance of the rat's home range centre from the trap and was modelled with a half-normal function in the embayment forest (Borchers & Efford, 2008; Harper, et al., 2015) and a negative exponential function on the plateau where the distribution of rat movements included a long tail of some very large movements  $>500$  m. We estimated density using the function 'secrefit' in the package 'secre'

(Efford, 2016) using R 3.2.5 (R Core Team, 2017) for each habitat and primary session separately, thus allowing for density, capture probability, and the movement parameter,  $\sigma$ , to vary over time and habitat. We did not consider trap dependence. We report estimates of density, capture probability and  $\sigma$  with 95% confidence intervals.

### Rapid eradication assessment

During the eradication operation in 2011, a team remained on the island for three months after the bait drop (from August to November), and any future eradication operation will require a similar post-operational period to monitor non-target species (Oppel, et al., 2016). We therefore estimated whether rat monitoring at all 406 trap locations of our two networks could conclude that an eradication had been successful with 95% certainty if no rat was detected during three 10-day trapping sessions up to three months after the bait drop. We also explored whether certainty could be increased if a larger area was covered with traps, and simulated a  $30 \times 30$  m trapping grid over 10%, 30%, and 50% of Henderson Island. We used our empirical estimates of population growth rate and rat roaming behaviour in a rapid assessment tool (REA Shiny; Russell, et al., 2017) assuming a prior probability of success of 83.9% (Russell & Holmes, 2015), no reinvasion (Amos, et al., 2016), and rat dispersal distances of up to 500 m (Oppel, et al., 2019). We present the probability of successful eradication that could be inferred given that no rat was detected during the specified survey effort.

## RESULTS

### Rat abundance estimates and long-term population recovery

We trapped rats from 11 August to 21 September 2009, catching 233 rats in 734.5 corrected trap-nights overall, or 31.7 rats/100 CTN, with little difference among habitats

(29.0–33.4 rats/100 CTN; Table 2). The eradication attempt in August 2011 reduced the Henderson rat population to 60–80 individuals (Amos, et al., 2016), and eight months after the eradication one rat was caught on the plateau in 96.5 corrected trap nights. From 23–30 November 2012, we caught 9.2–14.8 rats/100 CTN across all three habitats (Table 2).

In 2013, we caught 20.0–73.2 rats/100 CTN, and the abundance index exceeded the pre-eradication estimate in the embayment forest (by more than 100% on North Beach), while the population on the plateau was 62% of pre-eradication levels.

In October 2015, we caught again more rats/100 CTN in embayment forest habitat on North Beach (42.9 rats/100 CTN) than on the plateau (13.2 rats/100 CTN) corresponding to an abundance index similar to pre-eradication conditions in the embayment forest, but only 41% of pre-eradication levels on the plateau (Table 2).

Based on these rat abundance indices, the rat population appears to have recovered rapidly, with annual per capita growth rates ranging from 0.48 to 5.95 (Table 2) during the recovery phase. The estimated number of rats reached peaks of 113%, 219%, and 62% of pre-eradication levels on East Beach, North Beach, and the plateau, respectively, by 2013 (Table 2), two years after the eradication attempt. The annual population growth rate has decreased since 2013 and was slightly negative between 2013 and 2015 (Table 2).

### Short-term fluctuation in rat density

Overall in 2015, we recorded a total of 2,826 rat captures in 7,552 corrected trap-nights in our live-trapping network on the plateau and 319 captures in 684 corrected trap-nights in the embayment forest. Trapping rates in the embayment forest were much higher than on the plateau and less variable over time (Fig. 2). On the plateau, the trapping index declined from 36.6 rats/100 CTN in early July to 12.6 rats/100 CTN in late August (Fig. 2). The subsequent increase to 75.8 rats/100 CTN occurred after switching Sherman traps with Tomahawk traps, and any population increase is therefore confounded by a potentially more effective trap type. To account for habitat- and time-specific variation in capture probability, we estimated rat density using spatially explicit capture-recapture models for each primary session.

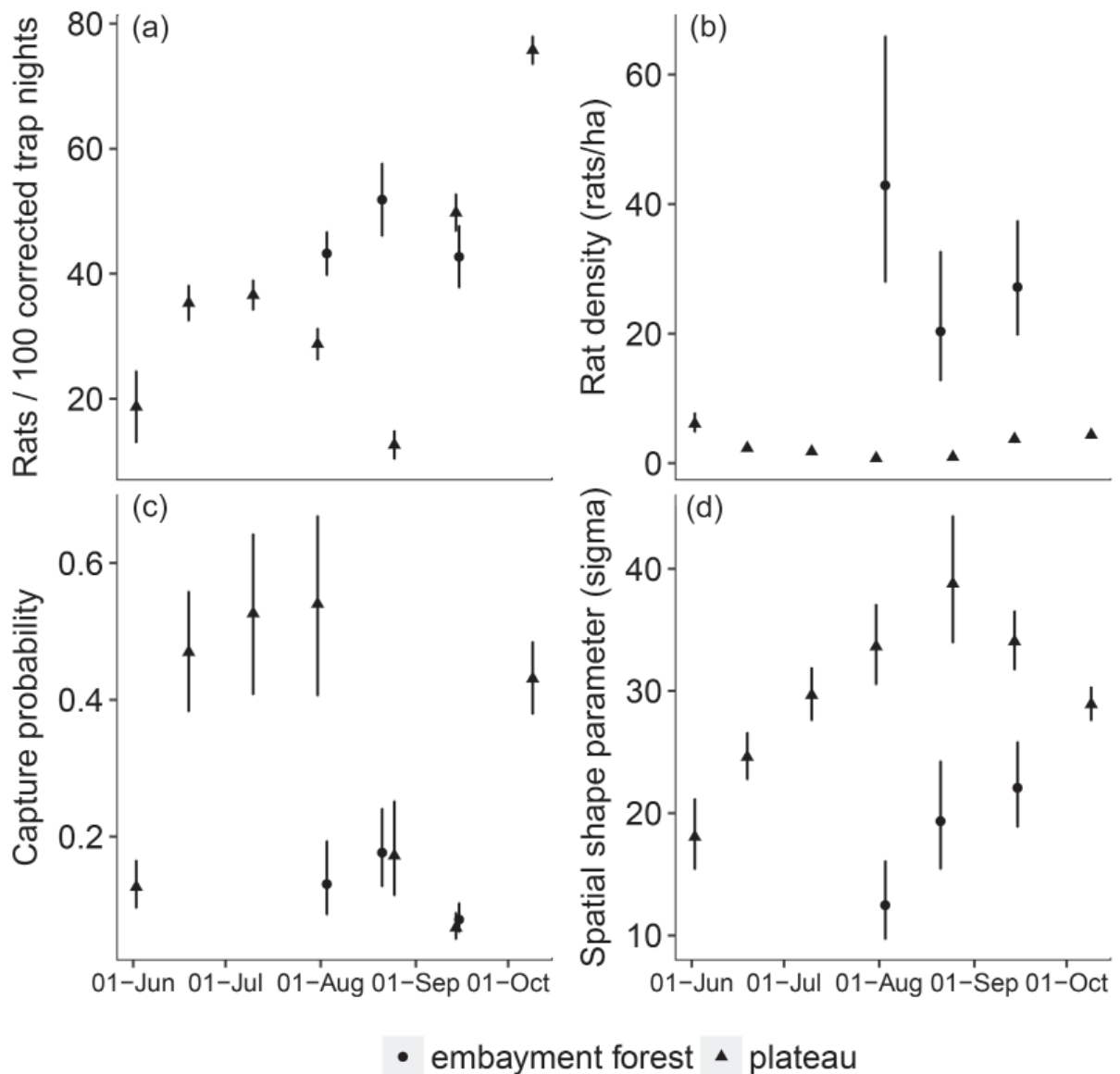
Rat density in the embayment forest was about 10× higher than that on the plateau (Fig. 2), and there were significant temporal fluctuations in both habitat types: apparent rat densities declined by 50% within one month in the embayment forest, and by 85% within two months on the plateau before recovering to 80% of the original density another three months later (Fig. 2). Lower rat densities on the plateau coincided with increased rat roaming distances ( $\sigma$ ), which were generally larger on the plateau than in the embayment forest (Fig. 2). Despite some very long rat movements on the plateau, only three individuals were recorded in both the embayment forest and on the plateau (Fig. 1).

**Table 2** Abundance indices of *Rattus exulans* on Henderson Island increased markedly following an eradication attempt in August 2011. August 2011 population estimate from Amos, et al. (2016); 2009 rat population from Brooke, et al., (2010a), and resulting population estimates are calculated from the relationship between rats/100 corrected trap nights (CTN, see text for details) and population size. Annual per capita growth rate,  $r$ , is based on exponential population growth.

Habitat	Start – end date	Corrected trap nights	Rats caught	Rats 100 CTN <sup>-1</sup>	No of rats <sup>a</sup>	% of original popn	Time between surveys (months)	Annual growth rate $r$
Embayment forest – East Beach	12 – 21 Sep 2009	252	73	29.0	210	-	-	-
	14 – 23 Aug 2011	-	-	-	5	2%	22.8	-
	23 – 30 Nov 2012	83	11	13.3	96	46%	15.0	2.36
	21 – 28 Aug 2013	92	30	32.6	236	113%	8.7	1.24
Embayment forest – North Beach	12 – 21 Sep 2009	374	125	33.4	210	-	-	-
	14 – 23 Aug 2011	-	-	-	5	2%	22.8	-
	03 – 6 May 2012	88.5	0	0.0	7	3%	8.4	0.48
	23 – 30 Nov 2012	67.5	10	14.8	93	44%	6.6	4.70
	21 – 28 Aug 2013	82	60	73.2	460	219%	8.7	2.21
	21 – 31 Oct 2015	49	21	42.9	269	128%	25.8	-0.25
	01 – 14 Nov 2015	149.5	36	24.1	151	72%	1.0	NA <sup>b</sup>
Plateau	12 – 21 Sep 2009	108.5	35	32.3	120,120	-	-	-
	14 – 23 Aug 2011	-	-	-	60	0%	22.8	-
	03 – 6 May 2012	96.5	1	1.0	3,859	3%	8.4	5.95
	23 – 30 Nov 2012	272	25	9.2	34,225	28%	6.6	3.97
	21 – 28 Aug 2013	703.5	141	20.0	74,633	62%	8.7	1.08
	21 – 31 Oct 2015	836.5	110	13.2	48,967	41%	25.8	-0.20
	01 – 14 Nov 2015	511.5	50	9.8	36,400	30%	1.0	NA <sup>b</sup>

<sup>a</sup>Number of rats extrapolated from the relationship between the abundance index and original population estimate and the mean (95% credible interval) from the state-space model used to calculate  $r$ . See text for details.

<sup>b</sup>Populations and population changes for October–November 2015 were not calculated because snap trapping removes individuals from the population and biases abundance indices for short time periods.



**Fig. 2** Rat abundance (a), density (b), capture probability (c), and spatial shape parameters (c) from spatially-explicit capture-recapture analysis of Pacific rats in two habitats on Henderson Island in 2015 (black circles: embayment forest, open circles: plateau).

### Rapid eradication assessment

Using the same trapping array as in 2015 for three 10-day trapping sessions at monthly intervals following a future hypothetical eradication attempt on Henderson Island would be insufficient to declare an eradication successful with 95% certainty. When we simulated a larger trapping array, we found that we could only conclude with 95% confidence that the eradication had been successful if no rat was detected within three months on a trapping grid covering at least 30% of Henderson Island. The model indicated that in order to be confident that the eradication had been successful within three months, we would require a  $30 \times 30$  m trapping grid covering one third of the island.

## DISCUSSION

### Population recovery after a failed eradication

The rat population on Henderson increased rapidly for at least the first 15 months following the eradication operation, with high annual per capita growth rates up to August 2013 (Table 2). As the population approached or exceeded pre-eradication abundances, the growth rate decreased between August 2013 and October 2015,

possibly as a result of the population fluctuating around a carrying capacity. These growth rates are broadly similar to the maximum annual growth rates of other rat species (Hone, et al., 2010), and are useful to estimate the probability of success of an eradication during follow-up monitoring (Russell, et al., 2017). Owing to variability in trapping methods and locations, there is considerable uncertainty about the exact size of the rat population; however, our density estimates in the embayment forest in 2015 indicate that rat density in this habitat was very similar to the pre-eradication density estimated in the same habitat at 24–40 rats/ha in 2009 (Cuthbert, et al., 2012). Based on the updated density estimates from the plateau in 2015, we estimate the rat population on North Beach in 2015 to be ~150–300 rats, which is similar to the estimates from the extrapolated relationship between density and abundance indices (Table 2). On the plateau, however, density fluctuated considerably throughout the year (Table 3), and extrapolating to the 4,290 ha of plateau habitat resulted in an estimate of ~3,300–26,000 rats, which is lower than the 48,000 estimate from the relationship with the abundance index. We assumed the relationship between density (rats  $\text{ha}^{-1}$ ) and the abundance index (rats 100 CTN $^{-1}$ ) was linear but, on the plateau, this is clearly not the case. Estimating

density, however, entails significant work over several months, whereas an abundance index can be determined fairly quickly, in a matter of days. Further work should investigate factors that influence the relationship between these two metrics.

There have been few studies on the recovery of *Rattus* spp. following eradication attempts. In urban Baltimore, Maryland, USA, *R. norvegicus* recovered to pre-control numbers within about 12–18 months (Emlen Jr., et al., 1948), and *R. fuscipes* in Australian eucalypt patches returned to pre-removal densities within two years (Lindenmayer, et al., 2005). In both cases, immigration was the likely cause of the rapid increase (though see Banks, et al., 2011). Genetic analysis from Henderson shows that there was no reinvasion, and that all rats present are descended from 60–80 survivors of the failed 2011 eradication operation (Amos, et al., 2016). Our results demonstrate the rapid recovery of an island population of introduced rodents in the absence of immigration. The time for rodent populations to either recover or reach pre-eradication levels (15–24 months), was similar to the experimental invasion of Saddle Island, New Zealand by mice (*Mus musculus*), where immigration may have supplemented mouse populations (Nathan, et al., 2015), and the time from arrival to near-saturation of black rats (*Rattus rattus*) on Taukihepa, New Zealand (24–36 months; Bell, et al., 2016).

### Temporal and spatial variation in rat population density

The shape of the recovery curve of the rat population on Henderson is difficult to determine from the intermittent trapping efforts and due to the high short-term variability. In 2015 we documented three-fold fluctuations in live trapping indices and even larger differences in rat density within just two months (Fig. 2), indicating that there may be pronounced seasonal changes among the rat population that could potentially mask or confound any long-term trajectories. There may also be considerable spatial heterogeneity in rat densities, and rats on Henderson do travel large distances (Oppel, et al., 2019), which further complicate interpretations from sampling a relatively small area of the available habitat. Some rats are relatively territorial, moving <200 m, and others roaming >1000 m (Oppel, et al., 2019).

Our finding that a decrease in rat density coincided with increasing movement rates of rats (Fig. 2) adds a further complication to the long-term comparison of simple trap indices that do not account for capture probability and rat movements. Tropical rodent populations are known to

undergo large population fluctuations, which can be driven by short-term changes in resource availability (Adler, 1998; Madsen & Shine, 1999) or extreme climatic events (Ujvari, et al., 2016). We did not observe pronounced plant resource fluctuations in 2015, and most tree species had individuals at various stages of flowering and fruiting between June and October 2015, though invertebrate abundance likely varied through the season (Lavers, et al., 2016). There was also neither a noticeable drought, nor an unusually heavy rainfall event during that period that could have explained the apparent intermittent reduction in the rat population. In the beach embayment forest, the major reduction of rat density between early and late August coincided with the temporal availability of Murphy's petrel (*Pterodroma ultima*) chicks, which may have led to temporary immigration of rats, but would have been unable to sustain a rat population for more than a few days (Brooke, et al., 2010b). Although we do not know whether higher mortality, lower fecundity, or both contributed to the apparent temporal fluctuation that we observed, or whether rats' probability of capture changed significantly over time, the timing of any future eradication operation should coincide with a naturally occurring nadir in the population trajectory to improve the probability of success. The eradication operation in 2011 therefore appears to have been optimally timed if rat population fluctuations are similar every year, but more research is required to examine whether rat populations exhibit predictable seasonality on sub-tropical islands such as Henderson.

The population abundance indices of *R. exulans* on Henderson (14–32 rats/100 CTN with snap-trapping, 12–75.8 rats/100 CTN with live-trapping) appear to be higher than abundance indices of other island rat population. For example, the *R. exulans* abundance index on Hawaii was only 5.65 rats /100 CTN (Sugihara, 1997), presumably because the species is subject to competition and predation (Moller & Craig, 1987); on the Marianas, the trapping rate was also much lower than on Henderson with 3.7 rats/100 CTN (Yackel Adams, et al., 2011). On Honuea, French Polynesia, indices ranged from 5–20 rats/100 CTN, often lower than conspecific *R. rattus* (up to 35 rats/100 CTN; Russell, et al., 2015). Abundance indices of the much larger *R. norvegicus* ranged from 3–9 rats /100 CTN (Drever, 2004; Harper, et al., 2005; Bond & Eggleston, 2015), and those of *R. rattus* from 1.6–35 rats/100 CTN across their range (Blackwell, et al., 2002; Shiels, 2010; Russell, et al., 2015), but reached up to 94.1/100 CTN on some nearshore islands in New Zealand (Russell & MacKay, 2005), and ranged from 60–80 rats/100 CTN on Surprise Island, New Caledonia (Caut, et al., 2009). The

**Table 3** Mean ( $\pm$  95% confidence interval) rat density, capture probability, and movement parameter,  $\sigma$ , in two habitats of Henderson Island in June–October 2015 estimated with spatially-explicit capture-recapture models. Note that different detection functions were used in the embayment forest (half-normal) and on the plateau (negative exponential), and that  $\sigma$  values are not directly comparable.

Habitat	Time period	Density (rats ha <sup>-1</sup> )	Capture probability	$\sigma$
Beach embayment – North Beach	Early August	42.92 (27.92–65.98)	0.13 (0.09–0.19)	12.48 (9.67–16.11)
	Late August	20.37 (12.67–32.73)	0.18 (0.13–0.24)	19.35 (15.41–24.29)
	September	27.2 (19.73–37.48)	0.08 (0.06–0.1)	22.08 (18.85–25.86)
Plateau	Early June	6.08 (4.76–7.76)	0.13 (0.1–0.17)	18.06 (15.39–21.19)
	Late June	2.33 (1.95–2.78)	0.47 (0.38–0.56)	24.6 (22.74–26.61)
	July	1.77 (1.49–2.11)	0.53 (0.41–0.64)	29.67 (27.57–31.92)
	Early August	0.76 (0.6–0.95)	0.54 (0.41–0.67)	33.64 (30.52–37.09)
	Late August	0.94 (0.75–1.17)	0.17 (0.11–0.25)	38.78 (33.92–44.33)
	September	3.73 (3.15–4.4)	0.07 (0.05–0.1)	34.05 (31.75–36.51)
	October	4.36 (3.92–4.85)	0.43 (0.38–0.49)	28.92 (27.56–30.34)

much higher trapping rate of *R. exulans* on Henderson is possibly because the species is smaller than congeners and is not subject to either predation or competition because no other mammals or avian predators exist on Henderson, and there is minimal dietary overlap with Henderson's birds (Brooke & Jones, 1995; Jones, et al., 1995; Trevelyan, 1995; Lavers, et al., 2016). In addition, the relatively high temperature and greater resource availability on tropical islands is generally well known to increase rat population size compared to temperate islands (Harper & Bunbury, 2015; Russell & Holmes, 2015). It is important to note, however, that abundance indices of rats exhibit a wide range depending on the rat species, environment, and the presence of competitor or predator species, seasonality, trap type, and the layout and spacing of traps.

Different approaches used to estimate densities also complicate the comparison across different islands (Harper & Bunbury, 2015). Despite the relatively high snap- and live-trapping rates on Henderson, our estimate of rat density is surprisingly low, especially on the coral plateau, where large rat movements were observed (Oppel, et al., 2019) that may have led to high trapping indices despite low density. But even the 10-times higher density in the beach embayment forest appears to be at the lower end of the range found for *R. exulans* on tropical islands (1.2–288 rats/ha; Harper & Bunbury, 2015). A potential explanation for this apparent discrepancy might be that Henderson Island is a relatively nutrient-poor coral atoll, where the maximum population size could be lower compared to more fertile tropical islands. Due to the potential nutrient limitation, the use of a highly attractive bait (coconut) may result in relatively high trapping rates, especially on the plateau where coconut is generally unavailable. Coconut has been implicated as an important factor affecting the eradication success on tropical islands (Holmes, et al., 2015). Our data also suggest that coconut may have facilitated a rapid recovery of the surviving rat population: In 2009, trapping rates were similar in the beach embayment forest and on the plateau, but on all occasions after the eradication attempt the snap-trapping rates on the plateau were considerably lower than in the embayment forest (Table 2). Rats on Henderson would often gnaw into de-husked coconuts, or those opened by land crabs on the beaches. We speculate that the lush embayment forest with abundant coconut may have facilitated a faster return to pre-eradication rat population densities than the scrubby plateau forest where coconut, though present, is scarce compared to the embayment forest.

Previous investigations using live- and snap-trapping indicated that live traps do not have a higher capture probability than snap traps for *R. exulans* and *R. rattus* (Russell, et al., 2015). We observed a much higher trapping rate with live traps than with snap traps in 2015, and our spatially explicit capture-recapture model indicated that rats living along our trail network had an almost 100% probability of being captured at least once in a trap. The variation in capture probability between different trap types highlights the need for consistent monitoring using identical approaches to facilitate valid comparisons over time.

### Assessing the probability of eradication success

The failure of the 2011 eradication attempt was opportunistically recorded eight months after the bait drop. Our assessment indicated that an intensive monitoring programme for three months following a bait drop would not have allowed the reliable conclusion that the eradication had been successful, unless at least 30% of the island were covered with a 30 × 30 m trapping grid. Such a trapping effort is unrealistic on Henderson Island. Rapid eradication assessments have so far only been conducted for small islands where the survey effort covered the entire area

habitable by rats (Samaniego-Herrera, et al., 2013; Russell, et al., 2017) but because Henderson Island is a fairly large island with impenetrable vegetation it is logistically unrealistic to install a monitoring network across an area sufficiently large to enable an early declaration of success. Depending on where rats that survive an eradication attempt occur in relation to the trap array at the northern end of the island, the potential benefit of post-operational monitoring to facilitate a rapid assessment of success is questionable. By the time surviving rats may be discovered with the limited trap array, the population would have likely grown to a size that would require a new eradication rather than allow a rapid follow-up to kill any remaining survivors. Although post-operational rat trapping on Henderson Island may be useful to rapidly discover eradication failure, it is unlikely that it would allow the confident conclusion of eradication success.

In summary, we found that rat abundance increased rapidly between the failed eradication operation in August 2011 and August 2013 before decreasing from August 2013 to October 2015. Rats on Henderson Island reached two-thirds of their pre-eradication abundance 24 months following their failed eradication, but our estimates of rat density on the plateau of the island suggest that rat density may have been substantially lower than previously assumed (Brooke, et al., 2010a). Studies of failed eradication operations, and the recovery of introduced rodent populations are rare, but of great conservation and operational importance. Our study highlights rodent population fluctuations on a relatively short time-scale, and a better understanding of the regularity and underlying drivers of these fluctuations would be useful to schedule an eradication operation so as to maximise eradication success. As eradication operations on tropical and subtropical islands become more frequent, it will be increasingly important to understand the behaviour and ecology of the invasive species targeted, and more work in this area is required if we are to replicate success on temperate islands.

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