Successes and failures of rat eradications on tropical islands: a comparative review of eight recent projects

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Abstract Rat eradication is a highly effective tool for conserving biodiversity, but one that requires considerable planning effort, a high level of precision during implementation and carries no guarantee of success. Overall, rates of success are generally high but lower for tropical islands where most biodiversity is at risk. We completed a qualitative comparative review on four successful and four unsuccessful tropical rat eradication projects to better understand the factors influencing the success of tropical rat eradications and shed light on how the risk of future failures can be minimised. Observations of juvenile rats surviving more than four weeks after bait application on two islands validate the previously considered theoretical risk that unweaned rats can remain isolated from exposure to rodent bait for a period. Juvenile rats emerging after bait was no longer readily available may have been the cause of some or all the project failures. The elevated availability of natural resources (primarily fruiting or seeding plants) generated by rainfall prior to project implementation (documented for three of the unsuccessful projects) may also have contributed to project failure by reducing the likelihood that all rats would consume sufficient rodent bait or compounding other factors such as rodent breeding. Our analysis highlights that rat eradication can be achieved on tropical islands but suggests that events that cannot be predicted with certainty in some tropical regions can act individually or in concert to reduce the likelihood of project success. We recommend research to determine the relative importance of these factors in the fate of future tropical projects and suggest that existing practices be re-evaluated for tropical island rodent eradications.

Keywords: best practice, conservation, invasive, restoration, rodent

INTRODUCTION

Marine islands house an estimated 15–20% of terrestrial biodiversity and are home to 61% of IUCN Extinct species and 37% of IUCN Critically Endangered species (B. Tershey unpubl. data). Invasive species have been the most frequent cause of extinctions on islands and the second leading cause of Critical Endangerment (B. Tershey unpubl. data). Commensal rats (*Rattus* spp.) are considered the most damaging group of invasive species on islands because of their near global distribution and the frequency with which they cause extinctions, extirpations and ecosystem-level impacts (Towns, et al., 2006; Howald, et al., 2007; Kurle, et al., 2008). Rats can be eradicated from islands (Keitt, et al., 2011) resulting in significant species and ecosystem recovery (Bellingham, et al., 2010). Thus, rat eradication is a powerful tool with which to prevent extinctions.

Although this tool has been widely deployed, with more than 500 successful rat eradications to date (DIISE, 2017), most rat eradications have been on small, mid to high latitude islands (Howald, et al., 2007) where endemic species diversity is lower. If rat eradication is to realise its full potential to prevent extinctions, then future eradications need to be more frequently conducted where endemic species diversity is high: on larger tropical islands (Kier, et al., 2009). However, while rat eradication is being successfully conducted on increasingly large, high latitude islands, with a failure rate of less than 3% (Russell & Holmes, 2015), success on both large and small tropical islands has been more elusive, with a failure rate of 10% and very little understanding as to the underlying causes of failure (Holmes, et al., 2015; Keitt, et al., 2015).

In an attempt to better understand the mechanisms responsible for eradication failure on tropical islands and improve the rate of success of future projects, a global review of rodent eradication practice on tropical islands was instigated (Russell & Holmes, 2015). In support of the review, Holmes, et al. (2015) performed a statistical analysis on as many rat eradication attempts as possible to determine correlative factors that might pinpoint important influences on tropical rat eradication success. However, rat eradication projects are complex and multifaceted (Cromarty, et al., 2002) and, like complex projects within other disciplines, it can be challenging to determine the reason(s) for project failure. To reduce the risk that the broad-brush approach utilised by Holmes, et al. (2015) overlooked important and influential factors, we completed a second review, this time using a qualitative framework on a subset of the projects assessed by Holmes, et al. (2015).

Qualitative comparative reviews are used extensively in the social and behavioural sciences (e.g. Ragin, 1989; George & Bennett, 2005; Bennett & Elman, 2006), but also in other fields such as software engineering (Abrahamsson, et al., 2003), human resource management (e.g. Allen, et al., 1997), and political science (e.g. Bennett & Elman, 2006). A qualitative comparative review offers the opportunity to compare projects and their nuances in detail, which superficially, statistical analyses cannot do, but also allows for the possibility for making generalisations if they exist (Ragin, 1989). This approach, which we believe has greater utility in conservation biology, offered a complementary mechanism for verifying or dispelling the importance of factors identified as significant or insignificant in Holmes, et al. (2015).

We examined in depth, reported data from eight well-planned and sufficiently resourced tropical rat eradication attempts, balanced among four successful and four unsuccessful projects, to better understand: 1) the variability in factors influencing tropical rat eradication projects irrespective of outcome, 2) the factors that consistently differentiate successful from failed tropical rat eradication attempts for projects where full reported data are available, 3) what steps can be taken to improve eradication reporting and minimise the risk of failure for future tropical rat eradications.

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METHODS

Island eradication study sites

For the purposes of this study we focused on rat eradication projects that used the method shown to have the greatest chance of success, but which faced all of the challenges associated with tropical islands and described by Keitt, et al. (2015). We did not consider geographical location to be important if these conditions were met. Projects that met the following criteria were selected for our analysis:

- Rodent bait was applied by helicopter, guided by GPS. Projects that used the aerial application of bait were the focus for our study because this method has the best record of success in both temperate and tropical climates (Howald, et al., 2007).
- The project was undertaken on a tropical island or islands. Although Henderson lies just south of the tropic of Capricorn at a latitude of 24°21'S, we considered this island to be tropical in the context of rodent eradication due to the island's temperature range, vegetation and absence of pronounced seasonality (Spencer, 1995; Brooke, et al., 1996).
- The project was undertaken on an island or islands with a Precipitation Coefficient of Variance (CV) of mean monthly rainfall of less than 50% (Fig. 1). We focused our analysis not on particularly wet or dry islands, but on islands where rainfall and ecosystem productivity were more difficult to predict. We excluded projects completed on arid or semi-arid islands such as along the Pacific Coast of Mexico or North-western Australia because, for rodent eradication, these islands share the seasonality associated with temperate islands i.e. an eradication operation can be undertaken when natural food resources are scarce and breeding, within the rat population, is less likely. The island of Banco Chinchorro, Mexico was excluded from our analysis because it had a rainfall CV greater than 50%. Nevertheless, Banco Chinchorro is another well documented project and could have been a useful addition to our comparative review.
- The project was undertaken on an island or islands with land crabs. The presence of land crabs was identified as a significant influence on project success in Holmes, et al. (2015).
- Projects where reinvasion could be dismissed as an unlikely cause of failure. Projects were only included if reinvasion had been ruled out through comparative DNA analysis or were undertaken on uninhabited islands that were rarely visited and extremely remote. This excluded islands such as Denis and Curieuse in the Seychelles (Merton, et al., 2002) and the Aleipata Islands in Samoa (Butler, et al., 2011).
- Sufficiently detailed information was available to allow the project to be reviewed within the framework recommended by Keitt, et al. (2015).

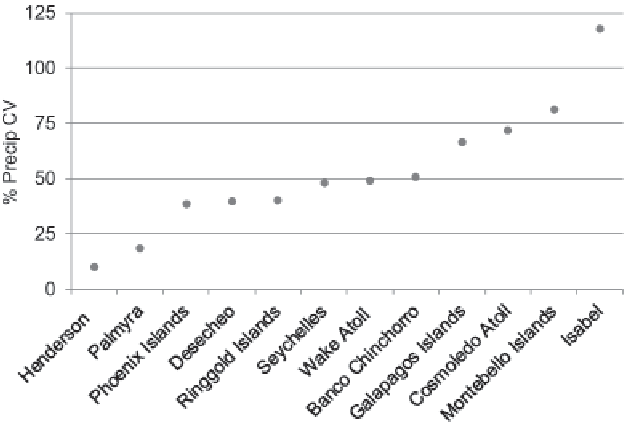

Fig. 1 Monthly Precipitation Coefficient of Variance (CV) for tropical islands where rodent eradications have been attempted using rodent bait containing a 2nd generation anticoagulant applied by helicopter.

Of the 17 discrete projects completed on tropical islands that applied rodent bait containing a second generation anticoagulant by helicopter, eight were selected for analysis. Six were completed on islands located in the tropical Pacific; Henderson (part of the United Kingdom Overseas Territory of Pitcairn), Wake (an unincorporated territory of the United States north of the Marshall Islands), Palmyra (an unincorporated territory of the United States in the Northern Line Islands), Enderbury and Birnie (part of the Phoenix Islands Group of the Republic of Kiribati) and the Ringgolds (part of Fiji). Two projects were located outside of the Pacific Region; Desecheo (Puerto Rico Archipelago) located in the Caribbean and Frégate (Seychelles) in the Indian Ocean.

Island size varied from 49 to 4,310 ha (Table 1) and all islands experienced relatively similar temperature ranges and annual rainfall (Table 1). Except for the Wake project that targeted Pacific rat (*R. exulans*) and Asian house rat (*R. tanezumi*), the eradication operations targeted the removal of just one species. *R. exulans* was targeted in four operations, ship rat (*R. rattus*) in two and Norway rat (*R. norvegicus*) in one (Table 1). Holmes, et al. (Holmes, et al., 2015) found no significant difference in eradication success between rat species for projects that applied bait aerially. Four of the islands were inhabited; Wake, Frégate, Palmyra and the Ringgolds (Table 1).

Determining success and failure

In line with best practice guidelines produced by the New Zealand Department of Conservation (Broome, et al., 2011), we considered an eradication project to be successful where the absence of rats was determined after a minimum of two breeding seasons (at least one year) after the completion of the operation, as rat populations may remain low and undetected for shorter periods. Rats were first reported as being present five months after the operation on Wake Island; eight months after on Henderson Island; 13 months after on Desecheo; and two years after on Enderbury. At the time of writing 14, six, four and three years have passed for the Frégate, Ringgolds, Birnie and Palmyra projects, respectively, and all four islands remain rat free. A failed attempt to eradicate rats from Palmyra Atoll in 2001 was hampered by both technical and implementation constraints and was not evaluated (USFWS, 2011).

Identifying potential factors that influenced success and failure.

While there are other alternate or contributing hypotheses (Table 2; Holmes, et al., 2015), the most proximate reason for the reduced rate of success for tropical rodent eradications is likely to be that not all rats consumed a lethal dose of brodifacoum, the rodenticide used in most rat eradications (Howald, et al., 2007) either because they did not have access to sufficient bait or because they did not consume bait that was available (Holmes, et al., 2015). We used the framework outlined in Keitt, et al. (2015) to review the four unsuccessful projects. To determine if some individuals within the rat population *could not* eat a lethal dose of bait, we reviewed operational design, operational procedures, GIS maps of bait coverage, baiting density,

Table 1 Characteristics of the islands where the eight projects were undertaken.

	Henderson	**Wake**	**Desecheo**	**Enderbury**	**Birnie**	**Palmyra**	**Ringgolds**	**Frégate**
Project outcome	Failed	Failed[a]	Failed	Failed	Succeeded	Succeeded	Succeeded	Succeeded
Latitude	24°21’S	19°18’N	18°23’N	3°8’S	3°35’S	5°53’S	16°30’S	4°35’S
Area (area of largest sub-unit of land) (ha)	4,310	696 (602)	116	608	49	235 (98)	266 (147)	219
Mean annual precipitation (mm)	1,623	1,780	750–1,039	750–1,300	750–1,301	4,422	2,467	2,182
Coefficient of variance for monthly precipitation (%)	10	49	40	40	38	19	39	49
Temperature Range (°C)	24–30	24–28	24–32	24–30	24–30	24–27	22–28	24–32
Maximum elevation (m)	33.5	6.4	213	6.7	4	1.8	12	125
Principal landform	Raised coral atoll	Coral atoll	Small mountainous island of volcanic origin	Coral atoll	Coral atoll	Coral atoll	Coral atoll	Granite island with two coastal plateaux
Principal vegetation types	Tangled, scrub and scrub-forest	Grass, low growing scrub, and *Casuarina* forest.	Grass and dry tropical *Bursera* forest	Grass and low growing scrub	Grass and low growing scrub	*Pisonia* and *Cocos* forest	Low scrub and *Cocos* forest	Modified forest
Target species for eradication	*R. exulans*	*R. exulans* and *R. tanezumi*	*R. rattus*	*R. exulans*	*R. exulans*	*R. rattus*	*R. exulans*	*R. norvegicus*
Permanent human population	0	100–200	0	0	0	12	2	20–30

[a] The Wake project successfully removed *Rattus tanezumi* but not *R. exulans* from Wake Atoll and successfully removed both species from part of the atoll, Peale Island (95 ha).

Table 2 Hypotheses to explain increased failure of rat eradications on tropical islands.

Proximate cause	Underlying cause	Possible response to increase success rates
Some individuals within the island's rat population could not eat a lethal dose of bait		
	Land crabs or other species consume bait	Higher bait application rates Additional bait applications Bait at a time when competitors are at lower density or less active
	Rats have small home ranges	Higher bait application rates Flexible scheduling to apply bait when food supply low
	Bait decomposes rapidly	More preservatives in bait Additional bait applications
	Lactating females or young in nest when bait available	Bait available longer (more bait, additional applications) Flexible scheduling to drop bait when breeding is reduced or non-existent.
	Rats don't leave human dwellings	Comprehensively bait entire island including within commensal areas
Some individuals within the island's rat population would not consume a lethal dose of bait		
	Bait biodegrades rapidly	More wax or preservatives in bait Additional bait applications
	Abundant natural food	Multiple bait formulations Bait available longer (more bait, additional applications) Flexible scheduling to drop bait when food supply low
	Individual foraging preferences	Multiple bait formulations Bait available longer (more bait, additional applications)
	Lactating females very neophobic	Bait available longer (more bait, additional applications)
	Different dietary preferences of lactating females	Multiple bait formulations Bait available longer (more bait, additional applications) Flexible scheduling to drop bait when food supply low
Poor quality planning and implementation		
	Lack of capability	More training & collaboration Appointment of experienced staff Adequate resourcing Peer review during the planning process
	Lax regulatory requirements	Plan & implement using internationally recognised standards
	Insufficient resourcing	Source more funding Increase collaboration
Higher rate of reinvasion		
	Warm water allows increased swimming distances	Select more isolated islands
	Human use characteristics	Better biosecurity Incorporate human use into island selection criteria

bait availability over time, timing between applications, and any operational difficulties noted. The statistical approach of Holmes, et al. (2015) could not address all of these issues because of the scarcity of well documented projects such as those we investigated. We also assessed bait toxicity and the chance that rats were resistant or tolerant to anticoagulants. Insufficient information was available to evaluate the impact of any spatial variation in land crab density across each of the islands.

To evaluate if some individuals within the rat population *would not* eat a lethal dose of bait, we looked at the operational design, the bait type, data from trials completed, the environmental conditions present at the time of the eradication and any observations made during implementation. Evidence for and against each factor was evaluated and used to form an opinion on its relative importance to the project's outcome. Evidence for the existence of a similar or different set of conditions for the successful projects was used to inform this analysis.

Not all projects monitored bait availability over time and for those projects that did, different methods were used, making it difficult to compare how long bait remained available to rats after its application. To compare between projects we used both the minimum period of time that bait was available in all plots or transects sampled and, where data were available, the lower limit of 99% CI of the T-Statistic for bait availability four days after its application as recommended by Pott, et al. (2015). For those islands where no monitoring was undertaken we used anecdotal reports to provide an estimate of the minimum period of bait availability.

Comparison among projects

We undertook a qualitative comparative review because the number of projects that formed the basis of our assessment was small, there was inconsistency between projects in the data collected and the methods by which data were obtained. A qualitative comparative review allows for generalisations to be made among cases and we considered it the best option for this study. Akin to Abrahamsson, et al. (2003), we cross-examined all projects to identify factors common to successful or unsuccessful projects. To inform this cross examination we drew from Holmes, et al. (2015) and our cumulative experience to identify a set of environmental variables and components of operational design we considered to be important to the success of rat eradication operations. These variables are listed in Tables 1–3. Information on each project was obtained from documentation prepared prior to and after project implementation and from personal communications with project team members.

RESULTS

Identifying causes of operational failure

Some individuals within the island's rat population could not eat a lethal dose of bait

The design of each of the four unsuccessful eradications, encompassing aerial application, overlapping aerial bait swaths, application rates comparatively higher than those applied in temperate regions and a minimum of two applications (Table 4), should have ensured comprehensive coverage of the islands with rodent bait. During the first bait application on Desecheo, some technical difficulties resulted in several small areas of the island (the largest being ~0.8 ha in size) receiving bait at less than the planned application rate. These issues were remedied for the second application when a more even spread of bait was achieved and, between both applications, comprehensive coverage of the island was achieved. Similarly, with the exception of areas deliberately excluded from bait application such as the sealed runway on Wake, we could not discern any biologically significant gaps in bait distribution from a review of the GIS data accumulated for any of the four unsuccessful projects. A biological gap was defined for our analysis as a gap greater than 0.015 ha in area. This was the smallest home range size reported in the literature for any of the four rat species targeted (Wirtz, 1972; King, 1990; Shiels, 2010; Low, et al. 2013).

On this basis we conclude that the operational strategy employed on Henderson, Desecheo and Enderbury likely ensured that all foraging rats encountered rodent bait. Although not identified from GIS maps of bait spread, it was more difficult to reach the same conclusion for Wake because of the more complex operational strategy (multiple methods of bait application) employed there (Griffiths, et al., 2014). The existence of interspecific competition, not a factor for the other islands, also likely limited access to bait for some individual rats. However, the successful eradication of *R. tanezumi,* formerly widespread across the atoll (Griffiths, et al., 2014), demonstrated that broad coverage across all habitats was achieved.

All four projects had factored bait consumption by non-target species such as land crabs into operational decisions on application rates (Table 4). However, bait disappeared more rapidly than anticipated from some transects monitored on Wake and Desecheo (Brown, et al., 2013; Brown & Tershy, 2013) (Table 4). Bait persisted in all transects monitored on Henderson until close to the end of the 30-day monitoring period (Brooke, et al., 2011). However, as described by Pott, et al. (2015), a different monitoring method was used and, because of the inaccessible nature of the island, monitoring was confined to a small part of the island. No monitoring of bait availability was undertaken on Enderbury but ad hoc observations suggest that rodent bait was broadly available for at least the first five days after its initial application (Pierce & Kerr, 2013).

Rat pups yet to emerge from the nest may not have had immediate access to bait. Evidence of rat breeding activity was documented on all four islands at the time of implementation (Brooke, et al., 2011; Brown, et al., 2013; Brown & Tershy, 2013; Pierce & Kerr, 2013). A rat of indeterminate age was sighted and captured on Desecheo, 23 days after the first bait application. On Wake, a juvenile *R. exulans* was found inside a bait station 18 days after bait was first applied and a second juvenile *R. exulans* was caught alive at the base of a coconut (*Cocos nucifera*) palm after 47 days. A low body weight and large head relative to body size indicated the latter individual had suffered from malnutrition likely because of having been weaned prematurely. As evidenced by liver assay, it had been exposed to brodifacoum (Griffiths, et al., 2014). No live rats were seen by project team members monitoring Henderson rails (*Porzana atra*) at the north-east end of Henderson beyond five days after the initial bait application, despite being on the island for more than three months after the operation. However, two very small, freshly dead, likely juvenile, rats were discovered 11 and 14 days after bait was applied suggesting these animals had survived for 10–13 days after the initial bait application.

Operational procedures were in some instances modified during project implementation due to environmental and physical factors encountered during the operation and/or the detection of a small number of rats after bait application. Lack of accurate geographical data led to an underestimate of island size for Henderson during project planning. As a consequence, the application rate for the second application across the island's plateau had to be reduced from 7 kg/ha to 6 kg/ha (Torr & Brown, 2012). Methods for applying bait to vegetated intertidal habitats were modified during implementation on Wake (Griffiths, et al., 2014). Bait stations were also deployed and bait was hand spread at several sites on Wake to target rats detected within five months of bait application, although such efforts were eventually abandoned after increasing numbers of rats sighted confirmed the eradication had been unsuccessful for *R. exulans* (Griffiths, et al., 2014). We do not consider the operational changes made for these three projects to have reduced the availability of bait to rats. No significant changes to the operational strategy were reported for the Enderbury project and bait application, as described by team members, followed the prescription outlined within the project's operational plan.

Based on the evidence available, we conclude that some individuals within the island's rat populations could not eat a lethal dose of bait. Unweaned rats present at the time of bait application did not have immediate access to bait and, as evidenced by individuals surviving for so long after bait application on Wake, this is also likely for some breeding female rats. However, we cannot conclude that this factor was the only cause of failure for the four failed projects.

Bait toxicity

Assays of samples of the rodent bait applied on Henderson (mean brodifacoum concentrations of 16.4 ppm), Wake (28.3 ppm) and Desecheo (29.3 ppm) confirmed that bait toxicity was within normal tolerances (Brown, et al., 2013; Brown & Tershy, 2013; RSPB, unpublished data). Inadequate bait toxicity is unlikely to have been a factor on Enderbury because the bait used there was produced at the same time as the bait used for the successful Birnie operation. Mortality associated with the operation and a rapid decline in rat numbers was also observed at all sites. All three bait types used are produced via an industrial production process with quality assurance checks in place to ensure appropriate rodenticide concentrations prior to shipping and all have been used successfully on both temperate and tropical islands. Based on the evidence available we conclude that inadequate bait toxicity was not a factor in the failure of the four unsuccessful projects reviewed.

Resistance

There were no indications to suggest rats on Henderson, Wake, Enderbury and Desecheo were resistant or tolerant to anticoagulants. Rats on Henderson, Enderbury and Desecheo had no prior exposure to anticoagulants so there was no selection pressure for pharmacodynamic resistance involving mutations in the Vkorc1 gene. For Henderson, subsequent testing of rats from the surviving population confirmed the lack of any genetic basis for resistance to brodifacoum (RSPB, unpubl. data). Although anticoagulants were used on Wake prior to the eradication (Mosher, et al., 2008) available evidence, as discussed in Griffiths, et al. (2014), did not support resistance as a factor in the project's outcome. Most importantly, although increased tolerance to brodifacoum has been documented for some rat populations, 'practical' resistance, as defined by Buckle & Prescott (2012), that might have caused the Wake project to fail, has never been encountered, even at sites where anticoagulants have been used repeatedly for long periods of time (Lund, 1984; Bailey, et al., 2005). It is unknown if any plant species present on Henderson, Wake, Desecheo and Enderbury contained elevated levels of vitamin K, but dietary-based resistance is not considered a major mechanism of resistance elsewhere (Buckle & Prescott, 2012). Based on the lack of evidence for resistance or increased tolerance to anticoagulants we conclude that this mechanism was not a factor in the recorded failures.

Some individuals within the island's rat population would not consume a lethal dose of bait

All four of the unsuccessful projects used proven bait types (Table 4) that have achieved rat eradication on other tropical islands. In addition, palatability of two of the bait types was proven by bait exposure trials undertaken on Henderson and Desecheo that showed, through use of a biomarker, 100% acceptance by trapped rats (Swinnerton & McKown, 2009; Brooke, et al., 2010). On Wake, concerns about behavioural resistance were generated after some rats in a two-choice laboratory trial undertaken on the island (Mosher, et al., 2008) were documented not eating rodent bait. Three *R. exulans* also avoided exposure during an *in situ* biomarker trial (Wegmann, et al., 2009). However, as outlined by Griffiths et al. (2014), the successful elimination of *R. tanezumi* from the atoll, the complete removal of *R. exulans* from a discrete part of the atoll (Peale Island), and the marked reduction of *R. exulans* for a period of time, are not consistent with a bait shy rat population. No pre-eradication trials to assess bait palatability were undertaken on Enderbury.

Some evidence for neophobia or rats preferring alternative foods over rodent bait was seen at the time of bait application for Enderbury and Wake. On the first night after the initial application of bait on Enderbury, rats were observed walking past rodent bait, despite it being readily available, to forage on the flowers and fruits of *Tribulus cistoides* on the island (Pierce & Kerr, 2013). Observations of rats foraging on natural foods in the presence of bait were also made on Wake (Griffiths, et al., 2014). However, it is unknown if such observations are unusual or should be considered the norm for rodent eradications, because of a lack of information.

Relative to previous site visits, signs of elevated resource availability were observed on Henderson and Enderbury islands (Cuthbert, 2012; Pierce & Kerr, 2013) at the time of project implementation. Rainfall leading up to the operations is presumed to have led to this increase (Cuthbert, 2012; Pierce & Kerr, 2013). On Henderson, three plant species, *Cyclophyllum barbatum, Myrsine hosakae* and *Eugenia reinwardtiana* were observed with more fruit than seen in previous years and the presence of a large number of recently fledged fruit doves (*Ptilinopus insularis*) indicated that a large fruiting event had occurred shortly prior to the operation (Cuthbert, 2012). On Enderbury, 10 of the 11 common plant species present were recorded as either flowering or fruiting at the time of the operation including the four dominant plants *T. cistoides, Portulaca lutea, Boerhavia albiflora* and *Sida fallax*. Higher than average rainfall prior to the unsuccessful Desecheo eradication (as evidenced by mainland weather records) may have also generated increased food availability there (Brown & Tershy, 2013). It is unknown if resources on Wake were elevated at the time of the operation, but abundant seed observed on *Casuarina* trees growing across the island at the time of the operation and high numbers of rats observed at the time of the operation correspond with this possibility.

Based on available evidence we cannot reach a definite conclusion on the role of this factor in the outcome observed in the four unsuccessful projects. However, the elevated availability of alternative resources may have compounded other factors such as rat breeding to influence project outcome.

Comparison among all eight projects

We could not separate unsuccessful projects from successful projects based on geographic location, habitat or standard climatic variables (Table 1). However, three of the unsuccessful projects were undertaken on islands significantly larger than those that were successful. Rats were also successfully removed from the smaller of the two disconnected land masses that comprise the Wake Atoll complex (Griffiths, et al., 2014). Commensal issues associated with the presence of a resident human population, a known risk factor for rodent eradications (Oppel, et al., 2011), were a significant component of the Wake project but were also present, albeit on a smaller scale, on three of the islands where rats were successfully removed suggesting these issues were not insurmountable.

Similarly, more parallels than differences were evident between successful and unsuccessful projects for the environmental variables identified by Holmes, et al. (2015) and ourselves as important to eradication success (Table 3). Elevated rainfall preceding the eradication operation differentiated three of the unsuccessful projects, Desecheo, Henderson and Enderbury. However, abundant natural food resources, as observed on Henderson, Enderbury, Desecheo and Wake at the time of project implementation, were also observed on Palmyra, the Ringgolds and Frégate where rats were successfully removed. Fruiting *Pandanus tectorius*, coconut and nesting sooty terns (*Onychoprion fuscatus*) on Palmyra, *Terminalia littoralis* fruit and coconut on the Ringgolds and coconut, multiple fruiting tree species, breeding seabirds, kitchen refuse, cultivated crops and food for livestock on Frégate all offered plentiful resources to rats. However, the level of natural food availability during project implementation relative to other times of the year for these islands is unknown. An abundance of natural resources was not documented on Birnie, where rats were successfully removed. Little flowering or fruiting by the four common plant species that are present was noted on this island at the time of the implementation (Pierce & Kerr, 2013).

Land crabs were an influential factor on all eight islands. Bait availability data provided some indication of their relative impact on each of the operations but, in the absence of crab survey data for each island, an independent assessment of relative crab population density among islands was not possible. Such data would have provided a clearer picture of the relative impact of land crabs on project success. Anecdotal observations suggest that rat numbers were high on all eight islands at the time of project implementation, but relative population densities were once again unknown. Reproduction was not investigated on the Ringgolds, but evidence indicates that rats were breeding at the time of the eradication at the other sites. On Palmyra, where rats were successfully removed, a juvenile rat was sighted and captured 28 days after the initial bait application within the island's commensal area where bait stations were being maintained. This individual was near death and an assay of its liver confirmed exposure to brodifacoum. Like the second of the two juveniles discovered on Wake after bait application, this rat also appeared malnourished. It is possible, based on observations of elevated rainfall and increased resource availability, that the intensity of rat breeding was higher on Henderson, Enderbury and possibly Desecheo than on the islands where rats were successfully removed but in the absence of data this cannot be confirmed. Two of the successful projects targeted rat populations that had previously been exposed to anticoagulants (Table 3). Rats on Palmyra, where anticoagulants had been used previously, were thought to be tolerant to brodifacoum because some individuals survived for longer than anticipated during a toxicity trial (Howald, et al., 2004), yet this project was successful.

Details for each of the eight eradication operations are presented in Table 4. All projects used a helicopter and bait spreading bucket as the principal method for bait application, utilised proven rodent bait types and applied bait with a similar swath overlap. The main difference between operations was in the amount of bait applied, which ranged between 10 and 84 kg/ha for the first application and between 6 and 79 kg/ha for the second. Difference in application rate was largely a function of decisions made by respective project teams based on an assessment of relative bait competition by land crabs for each island. While this difference was evident, there was no clear relationship between application rate and success or failure for the eight projects (Table 4). Relative to the three unsuccessful projects where monitoring of bait availability was undertaken, bait on Palmyra also disappeared rapidly but remained at higher densities beyond the seven-day observation period in coconut canopy (Berentsen, et al., 2013), a preferred habitat for rats (Wegmann, 2008). Bait persisted in all plots monitored on Frégate for 10 days after its application and bait availability would have been extended by the third application (Merton, et al., 2002) but this was not monitored. No monitoring of bait was undertaken on Birnie or the Ringgolds, but bait was reported to be widely available on both islands for the six days between the first and second applications of bait.

As with two of the failed projects, operational procedures were also modified during project implementation for two successful projects. For instance, an unplanned third application of bait was completed following the sighting of

Table 3 Environmental variables present at the time of project implementation that could have influenced the project's outcome.

	Henderson	Wake	Desecheo	Enderbury	Birnie	Palmyra	Ringgolds	Frégate
Project outcome	Failed	Failed	Failed	Failed	Succeeded	Succeeded	Succeeded	Succeeded
Hermit crabs present	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Other land crab species present	No	No	Yes	No	No	Yes	Yes	Yes
Ant species present	Yes	Yes	Yes	No	No	Yes	Yes	Yes
Permanent human population present	No	Yes	No	No	No	Yes	Yes	Yes
Rat population had been previously exposed to anticoagulants	No	Yes	No	No	No	Yes	No	Yes
Higher than anticipated rainfall preceded operation	Yes	No	Yes	Yes[a]	Unknown	No	No	No
Observations of high natural food availability immediately prior to or during project implementation	Yes	Yes	Yes	Yes	No	Yes	Yes	Yes
Seabirds nesting at time of implementation	Yes	No	No	Yes	Yes	Yes	Yes	Yes
Rat population breeding at time of project implementation	Yes	Yes	Yes	Yes	Yes	Yes	Unknown	Yes

[a]Inferred from observations of flowering and fruiting during project implementation.

a surviving rat on Frégate Island (P. Garden, pers. comm.). On Palmyra, bait was hand broadcast across a 10 ha area on Cooper Island following the discovery of the juvenile rat mentioned above (Wegmann, et al., 2012). No changes to the operational strategy were reported for the Ringgolds and Birnie projects and, as with the Enderbury project, bait application proceeded according to plan.

From our qualitative comparative analysis, we could not reach a conclusion on the role of geographic, habitat, climatic and environmental variables or operational parameters on the relative outcome of the eight projects reviewed. The two variables that best differentiated unsuccessful from successful projects were elevated rainfall preceding the operation and island size.

DISCUSSION

Reasons for project failure

Based on the robust design of the eradication operations reviewed and GIS maps of bait coverage, we conclude that bait was made available to all rats actively foraging at the time of the operation for the Henderson, Enderbury and Desecheo projects. We cannot be as confident of this for Wake, despite one rat species being successfully eradicated, because the more complex operational strategy employed there coupled with competitive exclusion may have led to functional gaps in bait availability (Griffiths, et al., 2014). Notwithstanding the greater risk on Wake, some individuals within the rat population were not actively foraging at the time of bait application on all four islands

Table 4 Key elements of operational design for the eight projects.

	Henderson	**Wake**	**Desecheo**	**Enderbury**	**Birnie**	**Palmyra**	**Ringgolds**	**Frégate**
Project outcome	Failed	Failed	Failed	Failed	Succeeded	Succeeded	Succeeded	Succeeded
Bait type[a]	20R	25W	25D	20R	20R	25W	20R	20R
Application rate 1st /2nd/3rd bait applications (kg/ha)[b]	10/6[c]	18/9	19/10	22/17	25/25	84/79	16/11	14/9/12
Mean total bait application rate (kg/ha)	17.4	27.7	29	38.4	50	165	27	35
Percentage swath overlap per application	50/25	50/50	50/50	50/25	50/25	50/50	50/50	50/50/50
Area of plot/transect used to sample bait availability	~270 m^2	25 m^2	25 m^2	NA	NA	2.49 m^2	NA	10 m^2
Number of days that bait remained available in all sampled plots/transects after 1st application	25+	3	2	6[d]	6[d]	1[e]	10[d]	10[f]
Number of days that bait remained available in all sampled plots/transects after 2nd application	20+	5	1	Unknown	Unknown	1[d]	Unknown	5[e]
Number of days between applications	5	9	10	5	6	6	10	5/24
Lower 99% CI of the T-statistic for bait available four days after the 1st application (kg/ha)	1.93	6.33	0.25	Unknown	Unknown	19.16	Unknown	-3.32
Areas excluded from aerial bait application	No	Yes	No	No	No	Yes	No	Yes

[a] Bait pellet types listed are 20R – Pestoff 20R rodent bait produced by Animal Control Products, Wanganui, New Zealand; 25W – Brodifacoum-25W Conservation manufactured by Bell Laboratories, Wisconsin, USA; 25D – Brodifacoum-25D Conservation manufactured by Bell Laboratories, Wisconsin, USA.

[b] Areas subject to hand broadcast were applied at the same rates as for aerial application.

[c] Rates listed here were used across the island's plateau which amounted to 95% of the island's area. Higher bait application rates were applied in the vicinity of the island's beaches where hermit crabs were most numerous.

[d] No monitoring of bait availability was undertaken and figures are inferred from ad hoc observations. The project team left the islands after the number of days listed.

[e] The figure reported is for terrestrial plots: bait persisted longer in coconut palm canopy.

[f] No monitoring was undertaken after the 3rd application which would have extended the number of days that bait was available.

where rats survived. Rats were breeding on Henderson, Wake, Desecheo and Enderbury at the time of project implementation and evidence suggests that brodifacoum is not passed on in sufficient amounts via lactation to cause mortality (Milne, et al., 2001; Gabriel, et al., 2012). Pups in the nest at the time of bait application were therefore effectively isolated for the period they were dependent on the lactating female.

Such a scenario has been previously considered by eradication practitioners as a theoretical possibility (e.g. Broome, et al., 2011), but the discovery of juvenile rats on both Palmyra and Wake after bait application validates it as a very real concern for tropical island rodent eradications, where breeding cycles cannot be predicted with certainty. Weaning times reported for *R. exulans* (Wirtz, 1972; Tobin, 1994), *R. rattus* (Cowan, 1981; Yom-Tov, 1985) and *R. norvegicus* (King, 1990) range from 21 to 28 days, much longer than the period over which bait is typically available for tropical rat eradication projects including a number of the projects reviewed here.

It has generally been accepted that breeding females, like other individuals within a rat population, would access and ingest a lethal dose of bait and die within a few days of bait application. However, there are reasons to be sceptical that this will always occur. Home ranges for female rats (e.g. *R. rattus*) can be significantly smaller than those of males (Pryde, et al., 2005) and, as has been documented for house mice (*Mus musculus*) (Krebs, et al., 1995), lactating female rats may have constricted foraging ranges. Changes in dietary requirements by rats can also occur during lactation (Leshner, et al., 1972) potentially affecting bait palatability. The maximum period of time documented for mortality following the ingestion of a lethal dose of brodifacoum is 21 days, from a trial conducted with captive *R. rattus* on Palmyra (Howald, et al., 2004). Any of these traits could increase the chance of juveniles emerging after bait is no longer readily available on an island and, with natural food abundant on many tropical islands, these individuals have an enhanced probability of survival.

The fact that bait remained available in all transects monitored on Henderson for more than 25 days challenges the premise of juvenile survival as a potential cause of failure for this project. However, as described by Pott, et al. (2015), a different method of monitoring bait availability was used for this project and monitoring was confined to one small corner of the island (Brooke, et al., 2011) so comparison with other projects is difficult. It is also possible that bait disappeared more rapidly in unmonitored parts of the island. Bait was applied at a lower rate on Henderson than in the other projects reviewed and this, coupled with the island's complicated 'makatea' or uplifted coral substrate, may have reduced the rate at which breeding female rats encountered bait.

Rats were confirmed as breeding during project implementation on Birnie, Palmyra and Frégate where rats were successfully removed. Why did these projects succeed? Some explanations can be tendered but, without additional evidence, cannot be verified. For example, the high bait application rate used on Palmyra likely ensured that breeding female rats rapidly encountered bait plus bait in the coconut palm canopy, a known nesting habitat for female rats, was accessible for a longer period. On Frégate, a third bait application extended the period of bait availability out beyond 24 days and less competition by hermit crabs and lower rat densities on Birnie may have increased bait availability there. It is also plausible that in the absence of the supplementary interventions made on Palmyra and Frégate, these projects could also have failed. Insufficient information is available to form similar conclusions for the Ringgolds project.

We were able to rule out inadequate bait toxicity and resistance as factors for the survival of rats on Henderson, Enderbury and Desecheo and the persistence of *R. exulans* on Wake. Neither has been documented for any of the 490 attempted higher latitude rat eradications and we know of no viable hypothesis that would predict a greater incidence of resistance in rats or insufficient bait toxicity for tropical rat eradication projects. For the unsuccessful projects we reviewed we reject bait toxicity as a factor based on: factory test results demonstrating that the bait used on Henderson, Wake and Desecheo contained a sufficient concentration of brodifacoum; the marked reduction in rat numbers on all three islands; and the fact that *R. tanezumi* was successfully removed from Wake. The bait applied on Enderbury was produced as part of the same consignment as that was used successfully to remove rats from Birnie.

Similarly, we found no evidence to support anticoagulant resistance as a factor in the unsuccessful outcome seen on Henderson, Wake, Desecheo and Enderbury. Rat populations on Henderson, Enderbury and Desecheo had no prior exposure to anticoagulants and the successful eradication of *R. tanezumi* from Wake, the removal of *R. exulans* from part of the atoll, and the reduction of *R. exulans* to undetectable levels elsewhere is at odds with the levels of survivorship reported for rodent populations in which practical resistance has been documented (e.g. Drummond & Rennison, 1973; Greaves, et al., 1982). Most importantly, 'practical' resistance to brodifacoum that might have caused the failure of these projects, has never been encountered, even at sites where anticoagulants have been used repeatedly for long periods of time (Buckle & Prescott, 2012). Increased tolerance to brodifacoum has been detected in some locations (Buckle & Prescott, 2012) and may have been present on the three islands where anticoagulants had been used previously. However, rats were successfully removed from two of these islands including Palmyra where a bait toxicity trial had suggested the possibility of anticoagulant tolerance.

Conflicting evidence meant we could not rule out the possibility that some rats avoided rodent bait in preference for natural foods. Certainly, for all four unsuccessful projects, natural food was readily available to rats at the time of project implementation. Observations of rats foraging on natural foods after bait application on Enderbury and Wake lend weight to this hypothesis. However, this may simply have been a function of neophobia, as described by Barnett (1956), and not necessarily active bait avoidance. We are unaware of similar observations from other projects, but this is likely a result of insufficient observational effort. The discovery of recently weaned juvenile rats on Palmyra and Wake, more than four weeks after bait application, suggests that some individuals, in this case lactating female rats, may have avoided bait for a period. Rats detected on Desecheo and Fregate after bait application also point to this possibility. Set against this evidence is the fact that natural food was also available on the islands where rats were successfully removed, and signs of malnutrition and early weaning of the juveniles found on Palmyra and Wake suggest that the females producing these pups died because they consumed bait. A necropsy verified bait consumption for the Desecheo rat and the Frégate project was ultimately successful, confirming all individuals there were eventually exposed. The successful removal of the more dominant rat species on Wake also perhaps points to bait availability rather than bait palatability as the more important influence.

In summary, it is unknown if the elevated availability of natural resources on Henderson, Enderbury, Wake and Desecheo led to bait avoidance, but the possibility cannot be discounted. Increased natural food availability may have also compounded other factors influencing project success such as the intensity of rat breeding. Given the unpredictability of resource availability within many tropical island ecosystems this will need to be an important consideration for future rat eradication projects.

Comparative analysis

We could not separate unsuccessful projects from successful projects based on habitat or standard climatic variables. However, three of the unsuccessful projects were undertaken on islands significantly larger than those that were successful and both rat species present on Wake were removed from Peale Island, one of the two land units that make up the Wake Atoll complex. This is consistent with the trend identified by Holmes, et al. (2015) of an increasing failure rate for larger islands. It is therefore possible that the outcomes observed on Henderson, Wake and Enderbury were simply a consequence of biogeographic theory. Larger populations on the bigger islands increased the chance that some individuals would avoid bait or that some breeding females would survive for long enough to wean juveniles when bait was no longer readily available. No threshold for island size has yet been identified for rodent eradications undertaken using the methodology reviewed in this paper. However, the threshold may be smaller for tropical islands because of increased availability of natural resources, higher rat population densities and the likelihood that a proportion of the population will be breeding during project implementation.

Rainfall is closely linked to ecosystem productivity on tropical islands (Murphy & Lugo, 1986) and elevated rainfall levels preceding the eradication were associated with three of the unsuccessful projects reviewed. Variability in rainfall was also found by Holmes, et al. (2015) to be correlated with failure for tropical rat eradications. However, as discussed above, we could not fully resolve whether rainfall contributed to an increased risk of failure for these projects because palatability of rodent bait was reduced in the presence of increased natural food availability or greater reproductive activity within the targeted rat populations led to juveniles surviving the eradication attempt.

In summary, although our review of eight tropical rodent eradications could not discern the relative importance of bait availability or bait palatability in the outcome of the four unsuccessful projects, it suggests that both are important to consider in the planning of future rodent eradications on tropical islands. In the absence of a more palatable bait type, we recommend greater emphasis is placed on operational design for future tropical island rodent eradications. As recommended by Keitt, et al. (2015), projects should aim to ensure that bait is readily available within all rat territories for a period of time that allows all individuals within the population to encounter bait. Even though the projects we reviewed were well documented, our analysis was limited by a lack of consistency in data collection. Until more is known about the mechanisms that promote survival during a rat eradication attempt, future monitoring of eradication projects undertaken on tropical islands should aim to document as many of the variables discussed in this paper as possible to determine the relative importance of these factors in the project's fate. Standardisation of monitoring protocols, as promoted by Keitt, et al. (2015) and Pott, et al. (2015), should also be instigated.

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