The Wake Island Rodent Eradication: Part Success, Part Failure, but Wholly Instructive

Richard Griffiths, **Alex Wegmann**, **Chad Hanson**, **Brad Keitt**, and **Gregg Howald**
Island Conservation, Santa Cruz, California
Derek Brown
Blenheim, New Zealand
Bernie Tershy
University of California-Santa Cruz, Santa Cruz, California
William Pitt
USDA APHIS National Wildlife Research Center, Hawaii Field Station, Hilo, Hawaii
Matthew Moran
U.S. Air Force, AFCEC/CZO, Alaska IST, JBER, Alaska
Kristen Rex
U.S. Air Force, 611th CES/CEAN - AFCEC/CFPD, JBPH-Hickam, Hawaii
Susan White and **Beth Flint**
U.S. Fish & Wildlife Service, Pacific Reefs National Wildlife Refuge Complex, Honolulu, Hawaii
Nick Torr
Te Anau, New Zealand

ABSTRACT: Rodent eradications undertaken on tropical islands have had a lower success rate than those attempted in temperate regions. A recent project undertaken to eradicate *Rattus tanezumi* and *R. exulans* from the 3 islands comprising Wake Atoll is illustrative. *R. tanezumi* was successfully removed from all 3 islands. *R. exulans* was permanently eradicated on Peale Island (95 ha) and temporarily on Wilkes Island (76 ha). *R. exulans* eradication on Wake Island (525 ha) was unsuccessful and the species has since repopulated Wake Island and recolonized Wilkes Island. We completed a detailed review of the project in an attempt to isolate potential causes of eradication failure. Based on the evidence available, we were not able to positively identify a single factor to explain why *R. exulans* survived on Wake Island. However, monitoring after the operation points to a sequence of events that comprised delayed mortality amongst a subset of breeding females and the emergence of young rats after bait was no longer readily available. Such an event was likely influenced by an abundance of natural food resources throughout the treatment area, a high density of rats, interspecific competition for toxic bait, and rapid disappearance of bait because of consumption by non-target consumers (land crabs). These factors are common to many tropical islands. We provide recommendations for addressing these factors in a future attempt to remove rats from Wake Atoll.

KEY WORDS: Asian house rat, commensal, eradication, invasive species, Polynesian rat, rats, *Rattus exulans*, *Rattus tanezumi*, restoration, rodent control, tropical, Wake Island

Proc. 26th Vertebr. Pest Conf. (R. M. Timm and J. M. O'Brien, Eds.)
Published at Univ. of Calif., Davis. 2014. Pp. 101-111.

INTRODUCTION

At the time of writing, invasive rodents have been permanently removed from 444 islands worldwide (DIISE 2014) resulting in considerable benefits to native species, ecosystems, and human livelihoods (Lorvelec and Pascal 2005, Benayas et al. 2009, Bellingham et al. 2010). However, rodent eradications are challenging and a great deal of resources, thought, and effort has been invested to achieve this level of success (Phillips 2010). Tropical islands have created additional headaches for eradication practitioners and success rates within this region have been lower (Holmes et al. 2015). A recent project undertaken to remove 2 species of rat [Polynesian rat (*Rattus exulans*) and Asian house rat (*R. tanezumi*)], on Wake Atoll had to contend with the challenges associated with tropical islands as well as others and is illustrative of the greater risk these factors pose to operational success.

The eradication attempt on Wake Atoll was undertaken in May 2012 by the U.S. Air Force's 15th Airlift Wing, Pacific Air Forces, the U.S. Fish and Wildlife Service, and Island Conservation. Rodent bait containing the second-generation anticoagulant brodifacoum at 25 ppm was applied by hand and by helicopter across the atoll. In addition, bait stations were established inside and outside occupied buildings and bait placed into 607 unoccupied structures across the island. The use of multiple methods to apply bait increased operational complexity as did the island's commensal environment, an extensive and largely unmapped infrastructure, vegetated intertidal habitats, and operating on an active base.

However, in spite of these challenges, *R. tanezumi* was successfully removed from all 3 islands and *R. exulans* was eliminated on Peale Island (95 ha) and, as evidenced by monitoring, on Wilkes Island (76 ha). However, *R. exulans* survived on Wake Island (525 ha) and has since repopulated Wake and Wilkes Islands, which are interconnected by a narrow causeway. Peale Island, which is separated from Wake by a 50-m channel of water, remains rat-free.

In this paper, we review the Wake project in an attempt to identify the most likely reasons for the out-

comes observed. An independent review of the Wake project was undertaken in 2013, which examined the design of the operation and the quality of planning and implementation in an attempt to distil lessons that could be applied to a future eradication attempt (Brown et al. 2013). We draw heavily on the findings of this review, but focus more closely on the circumstances created by the eradication operation and the conditions present on the island at the time of implementation, in an attempt to determine the most likely reasons for the project's outcome.

SITE

Encompassing 3 islands, Peale, Wake, and Wilkes, Wake is a tropical coral atoll in the Pacific Ocean located just west of the international date line at 19°17' North 166°38' East (Figure 1). Wake Atoll is an unorganized, unincorporated territory of the United States and is managed by the U.S. Air Force. The only personnel routinely permitted to be present on Wake Atoll are military personnel and contractors, and the majority of human activity on Wake is limited to Wake Island and part of Wilkes Island.

The V-shaped atoll encompasses 696 ha of emergent land with a maximum elevation of 6.5 m amsl. The island receives approximately 900 mm of rainfall annually with the wettest months being July to October, and temperatures range from 23-29º C. The atoll's native plant and animal communities were extensively modified during World War II but have since staged a partial recovery. Native vegetation typical of many Pacific islands now covers a considerable proportion of the island and several of the 56 bird species recorded from the atoll, such as sooty terns (*Sterna fuscata*), can be found at high densities in some parts of the atoll (Rauzon et al. 2008a).

Rauzon et al. (2008b) describe 4 native vegetation communities of scrub, grass, and wetlands: 1) *Tournefortia argentia* scrub including some *Scaevola taccada*, *Cordia subcordata*, and *Pisonia grandis*; 2) *Pemphis acidula* scrub that extends into intertidal areas of the lagoon; 3) grasslands with *Dactyloctenium aegyptium* and *Tribulus cistoides*; and 4) *Sesuvium portulacastrum* wetlands. Introduced vegetation communities include almost mono-cultural *Casuarina equisetifolia* forest and ruderal areas that support predominantly introduced or weedy plant species such as *Cynodon dactylon* and *Leucaena leucocephala* (Fosberg and Sachet 1969). Approximately 13% of the atoll is developed and is largely devoid of vegetation.

Several species of land crabs are present on Wake Atoll, although just the hermit crab (*Coenobita perlatus*) is common. As seen elsewhere, *C. perlatus* is patchily distributed across the atoll; average densities of between 0 and 600 crabs/ha were recorded in a study completed in 2009 (Wegmann et al. 2009). Several species of introduced ants are also present (Wegmann et al. 2009).

METHODS

We identified the following 5 hypotheses that could explain the failed eradication of *R. exulans* on Wake Island:

1) *R. exulans* reinvaded Wake Atoll from elsewhere;
2) Some individuals within the island's *R. exulans* population were tolerant or resistant to brodifacoum;
3) Some or all of the bait contained an insufficient quantity of brodifacoum;
4) All individuals within the island's *R. exulans* population had access to bait but some would not consume a sufficient amount to ingest a lethal dose, and;
5) Some individuals within the island's *R. exulans* population could not eat a lethal dose of bait.

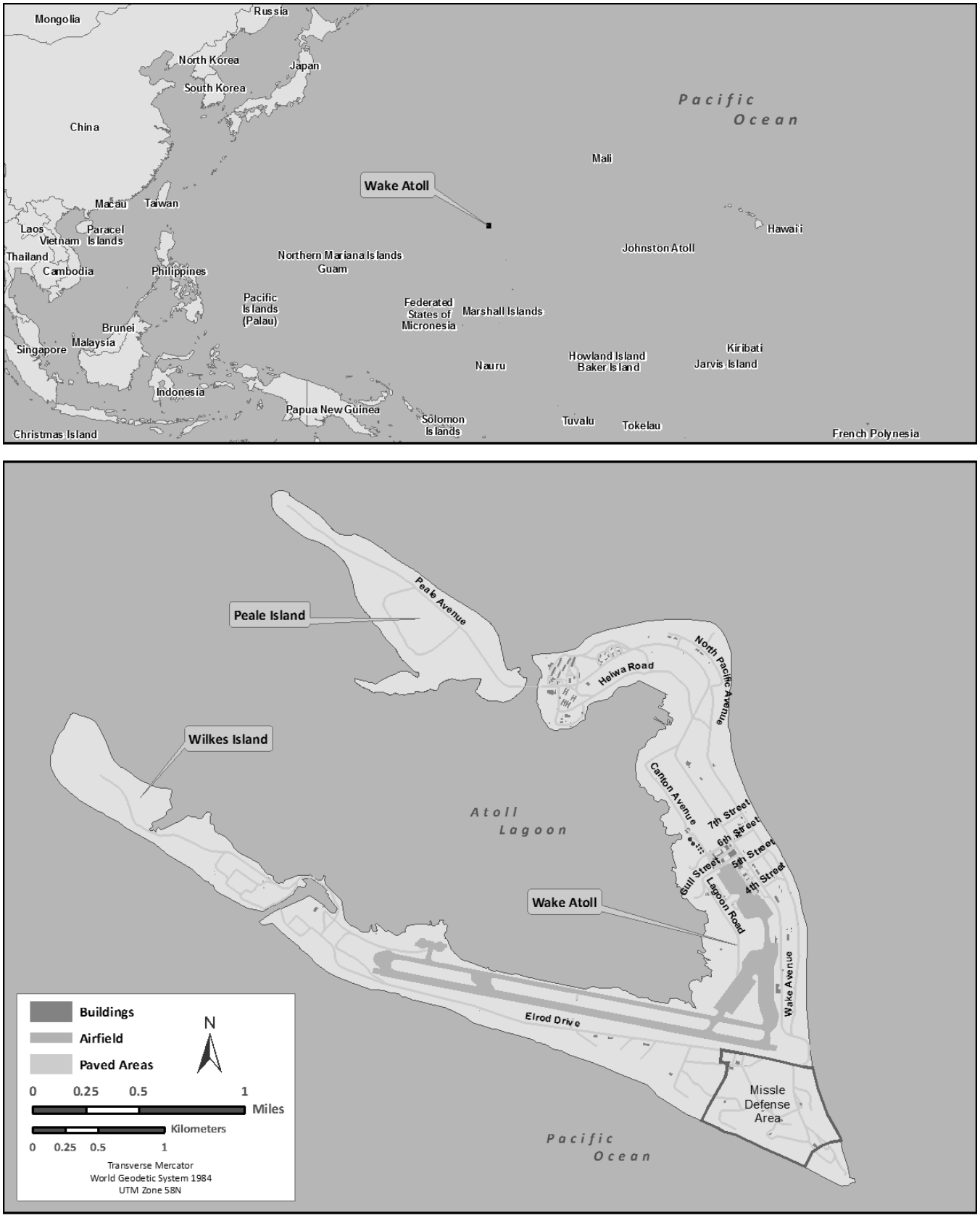
We then looked for evidence to support or refute these hypotheses. We present the conclusions of the 2013 review and offer more recent insights and further information on the relative importance of these hypotheses. To support the conclusions, we reviewed research completed to inform project planning and assessed information available on the conditions present on Wake at the time of project implementation. We spoke to project team members about project execution and the monitoring associated with implementation and reviewed all reports completed on the project. Evidence for and against each hypothesis was weighed to derive its relative influence on project's outcome.

RESULTS

Project Summary

The Wake rodent eradication was undertaken in May 2012. To target both rat species, rodent bait containing the second-generation anticoagulant brodifacoum was applied by helicopter across most parts of the island (Figure 2). Most flight lines were completed using a spreader bucket calibrated to produce a 70-m, 360º swath, but a deflector bucket with a 35-m, 180º swath was used to apply bait along the atoll's coastline. A trickle bucket with a swath width of less than 10 m was used to treat terrestrial areas of *Pemphis* habitat and fill gaps where a risk of bait drift into areas excluded from aerial application was identified. With the exception of areas sown using the trickle bucket, helicopter flight lines were spaced so that a 50% overlap between adjacent baiting swaths was achieved.

In step with the aerial operation, bait was hand spread across areas excluded from aerial application such as the residential area. Bait was also placed within the 607 unoccupied structures that had been located shortly prior to project implementation. These ranged in size from 0.5 m^2 (e.g., an electrical box) to 500 m^2 (the abandoned hospital). No blueprints of the atoll's complex and unoccupied infrastructure were available, and 39 unoccupied structures were not treated during the first application. Bait stations were placed inside and along the perimeter of occupied buildings. No bait was applied on the hard impermeable surfaces of the island's runway and bunded fuel storage areas. A second application of bait that mirrored the first in all aspects, except that all structures were treated, was undertaken 9 days later. The first bait application took 3 days to complete whereas the second was concluded within 2 days.



Source of Base Data: 15 AW June 2007

Figure 1. Location of Wake Atoll in the Pacific Ocean and layout of the atoll.

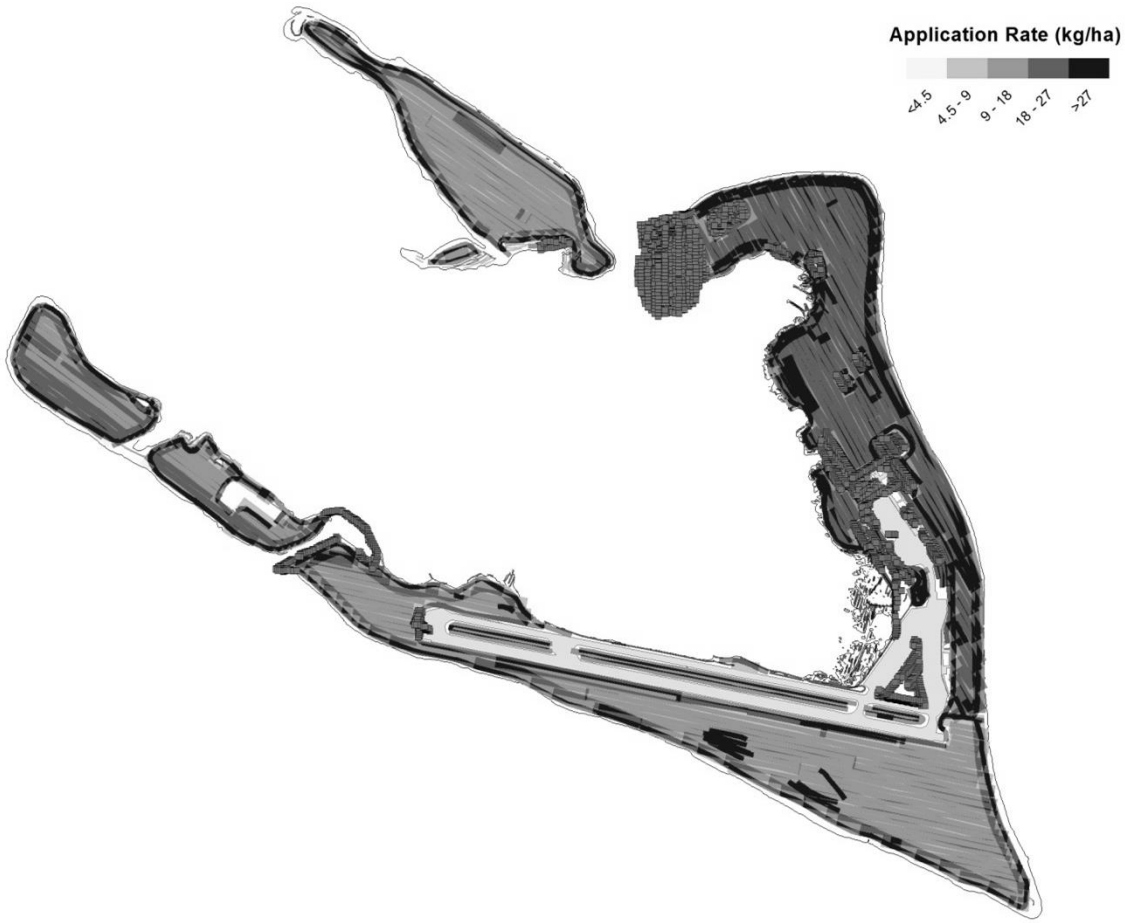


Figure 2. Map of the 1st application of rodent bait on Wake Atoll showing relative densities of bait achieved in kg/ha. Points represent hand baiting points where bait was applied at an average of 18.3 kg/ha.

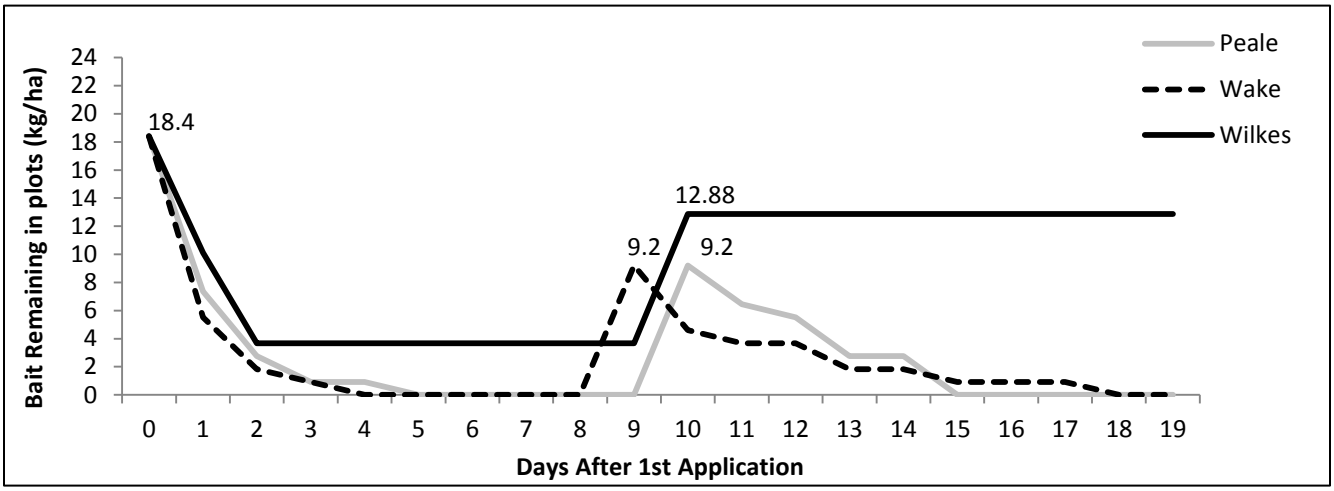


Figure 3. Minimum amount of bait remaining in transects after bait application on Peale Wilkes and Wake islands. Data points show the representative application rate on the ground after the first and second bait application, respectively.

After the first bait application, monitoring of bait availability was undertaken in 18 transects distributed across all 3 islands. Bait take was rapid, and bait had disappeared entirely from some transects within 4 days of the 1st and within 6 days of the 2nd application. Bait persisted for longer in transects located on Wilkes Island, whereas transects on Peale and Wake showed a similar trend (Figure 3).

As listed in Table 1, a juvenile rat was discovered inside a bait station 18 days after bait was applied, and 47

Table 1. Diary of key events associated with the Wake Rat Eradication Project.

Date	Days after the first aerial bait application on Wake	Event
2012		
May 12	-2	Rodent bait placed within external bait stations
May 13	-1	1st aerial application of bait on Wilkes and Peale Islands and hand baiting of areas excluded from aerial application
May 14	1	1st aerial application completed on Wake Island, hand baiting continued, internal bait stations filled and structure baiting initiated.
May 15	1	Hand broadcast application completed
May 16	2	Structure baiting completed and bait stations refilled
May 23	9	2nd aerial application, hand baiting, loading of bait stations
May 24	10	Hand broadcast completed
May 25	11	Structure baiting completed
Jun 1	18	Young *R. exulans* captured and killed within bait station near golf course. Appeared to be unwell.
Jun 25	42	Reliable report of a rat observed near roadway by golf course
Jun 27	44	Response to rat sighting implemented. Glue boards, traps, and bait stations placed within a 6 ha area immediately surrounding June 25 sighting.
Jun 29	46	180 rodent detection chew blocks set up across the atoll, no indications of rodent presence
Jun 30	47	Young *R. exulans* captured near industrial area, appeared sick, later confirmed to have ingested brodifacoum.
Jul 13–17	60-64	Spotlight surveys completed occur across all three islands and rodent detection chew blocks surveyed 2-3 times with no evidence of rodents recorded. Additional detection block grid placed at June 30 detection site with no detections made.
Jul 21	68	Bait hand broadcast over 4 ha in the vicinity of the June 30 detection site.
Sep 25	134	Dead rat collected on roadway.
Sep 26	135	10 hectare detection grid of snap traps and glue boards established across site of September 25 detection; no detections made
Oct 5	144	Rat sighted at marina; Snap traps set up with 2 additional captures (all *R. exulans*)
Nov 4	174	Rodent detection chew blocks surveyed, 60 additional chew blocks in 3 new areas deployed, 62 detection stations (Protecta bait stations with baited snap trap) deployed; no indications of rodent presence
Nov 4-9	174-179	Spotlight surveys occur across each island; no detections made
Nov 9-25	179-195	Hand broadcast of bait around the marina (11.5 ha), the site of the young rat reported on October 5, and at the site where the dead rat was recovered on September 25 (4 ha).
Dec 19	219	Three recently weaned juvenile rats caught in golf course area
Dec 30 - present	>230	More than 130 rodents examined by island pest manager with all specimens identified as *R. exulans*
2014		
Sep 19	858	*R. exulans* detected on Wilkes Island for the first time Rauzon (Gilardi and Rauzon 2014).

days after bait application another juvenile was found. Both rats were euthanized. Because of where it was found, it is presumed that the first juvenile had consumed bait, and an assay of the second juvenile showed that it had been exposed to brodifacoum. One other rat sighting was made over this period. The first mature rat to be observed after the eradication operation (134 days after bait application) was found dead and appeared to have been run over by a vehicle. Three sexually mature rats were caught over a 1-month period near the island's marina between 151 and 178 days after bait application. These captures were accompanied by additional sightings at the marine and elsewhere on Wake Island. The first documented evidence of breeding was confirmed at the island's golf course, when 3 recently weaned rats were found in the same location in December 18, 218 days after bait application.

As of the November 2014, all rats trapped subsequent to the eradication operation (>100) have been identified as *R. exulans* based on morphometric measurements. No rats have yet been detected on Peale Island. The first evidence of rats being present on Wilkes Island was found on September 19, 2014, months after the operation.

Reinvasion

Aside from the persistence of rats on Wake Island, we could find no evidence to support a reinvasion event (e.g., a rat arriving from Hawaii or elsewhere) being the cause of the project's outcome. Instead, evidence against an incursion having occurred is convincing. First, a comparative analysis between DNA samples taken from *R. exulans* captured on Wake prior to the operation and 5 *R. exulans* caught subsequent to project implementation detected no unique alleles, strongly suggesting that rats caught after the operation were survivors. Second, a biosecurity plan that aimed to minimize the risk of rodent

reinvasion was implemented shortly before the operation took place. Third, if an incursion had taken place, it is more likely that it would have been a rat species other than *R. exulans*, given the origins of most shipments to the atoll. *R. exulans* is not present in Seattle, where barge shipments originate, and does not occur in Japan or Alaska where most aircraft depart (Roberts 1991). *R. exulans* is present in Hawaii along with 3 other commensal rodent species, *R. rattus*, *R. norvegicus*, and *Mus musculus*. However, *R. exulans* is less likely to predominate at locations such as the airfield in Honolulu, where fortnightly flights to Wake originate, and the port where barge shipments pass through (Tobin 1994).

Bait Toxicity

An assay of a sample of the rodent bait applied on Wake completed by Bell Laboratories, Inc. found the bait contained brodifacoum at 28.3 ppm, confirming that it was sufficiently toxic. Assuming the 2 species present on Wake were similarly susceptible to brodifacoum, the successful removal of *R. tanezumi* (a larger-bodied species) also rules out the possibility that some of the bait was insufficiently toxic.

Resistance

'Practical' resistance is defined by Greaves (1994) as the "major loss of efficacy in practical conditions where the anticoagulant has been applied correctly, the loss in efficacy being due to the presence of a strain of rodent with a heritable and commensurately reduced sensitivity to the anticoagulant." 'Technical' resistance is defined by Buckle and Prescott (2012) as "Low-level resistance, which may be detected by resistance testing methods such as laboratory feeding tests and blood clotting response (BCR) tests, but which has no obvious practical effect on the outcome of rodenticide applications." 'Pharmacodynamic' resistance, likely a prime mechanism behind anticoagulant resistance in rats, is associated with altered structures of the VKOR enzyme normally responsible in vertebrates for clotting blood (Buckle and Prescott 2012).

Brodifacoum and other anticoagulants have been used extensively on Wake for many years prior to the operation for hygiene and sanitary reasons but also to protect valuable infrastructure (Mosher et al. 2008). This history of use of anticoagulants created the conditions necessary for pharmacodynamic resistance to have arisen within the island's rat populations. However, no reports of reduced effectiveness of control efforts were reported by operators on Wake Atoll.

As part of a study that aimed to assess the feasibility of the project, a 2-choice test comparing the relative palatability of rodent bait containing brodifacoum or diphacinone with laboratory chow was undertaken on Wake in 2007 (Mosher et al. 2008). Mosher et al. (2008) reported that all rats observed to consume rodent bait died and on this basis concluded that the presence of resistance was unlikely. Certainly, the successful removal of *R. tanezumi* from the atoll removes any doubts about resistance for this species. Similarly, the failure to detect *R. exulans* for a period of 3 months between June and the end of September despite 2 10-day periods of intensive monitoring contrasts strongly with the observations of survivorship seen at sites where practical resistance has been documented (Buckle 2006).

Bait Palatability

No conclusive evidence exists to prove or disprove the existence of behavioral aversion or the possibility that some rats found rodent bait unpalatable. Monitoring of commensal areas during the operation found no evidence of human food waste that could have supported rats during the operation. However, some natural foods were abundant. For example, *C. equisetifolia* was seeding at the time of the operation, and rats were observed foraging on these seeds as well as the roots of an unknown plant species within ruderal habitat in the first few days after rodent bait was applied. Anecdotal reports of rats being at high density at the time of the operation on Wake are also indicative that an abundance of natural food was available.

The fact that 19 of 58 rats did not consume either of the 2 rodent baits provided over the course of the 17-day 2-choice trial described above raises concerns about bait palatability. These were partially offset by an *in situ* bait acceptance trial undertaken at the same time in which the same bait types were observed to be readily taken by rats (Mosher et al. 2008). Mosher et al. (2008) unfortunately did not report the fate of rats incorporated in trial by gender, species, or age group, and these data appear to have been lost.

As a further test of bait acceptance by rats, a trial was undertaken in 2009 in 2 10-ha plots, one on Peale Island and the other on Wake Island. The same bait application strategy and bait type as used in the eradication operation were applied although the bait contained pyranine (Wegmann et al. 2009). All 24 rats (both *R. tanezumi* and *R. exulans*) caught subsequent to bait application within the Peale Island plot showed signs of exposure to pyranine, indicating 100% bait acceptance there. However, 3 individuals, all *R. exulans*, from a total of 33 caught within the residential area on Wake Island, showed no sign of having eaten rodent bait. The possibility that these individuals had recently moved into the core area where they were trapped was not supported by radio telemetry (n = 11) that showed limited movement into baited areas. Wegmann et al. (2009) suggested these individuals may not have consumed bait because they had ready access to fruit and vegetables in nearby gardens and other commensal food sources. On this basis, a commensal plan outlining conditions for minimizing alternative food resources to rats was developed and implemented for the eradication.

Set against the evidence supporting bait aversion is the successful removal of *R. exulans* from Peale and possibly Wilkes Islands and the marked reduction of the Wake Island population to potentially just a few surviving individuals. Despite greater human activity, no rats were also detected in commensal areas until at least 8 months after the operation, well after many other detections had been made. Although no formal monitoring of rodent behavior during the operation was undertaken, project team members, moving about the atoll during the day and night, observed no instances of rats actively avoiding bait.

Inadequate Bait Availability

As concluded by Brown et al. (2013), the complexity of the Wake eradication operation incorporating exclusion zones, aerial broadcast, hand spreading, and bait stations created a high chance of gaps in bait spread (Figure 2, Table 2). The *Pemphis* habitat, described by Rauzon et al. (2008b), is intertidal so bait application in this habitat is complicated by regulations requiring that bait does not enter the marine environment. Application of bait within *Pemphis* habitat, the use of inexperienced staff for hand spreading, and the unavailability of blueprints pinpointing the location of all abandoned infrastructure increased this risk further (Brown et al. 2013). A camera mounted on the spreader bucket recorded some instances when the pilot failed to immediately identify when the supply of bait within the bucket had run out and continued logging bait spread as though bait was still being sown. Coupled with the documented pilot error, the complexities associated with bait application increased the likelihood that in some areas bait was applied at a reduced density or no bait was applied at all.

Table 2. Relative size of zones receiving different treatments during the Wake rat eradication as illustrated in Figure 2.

Zone	Size (ha)
Aerial application – full swath spreader bucket (70m swath)	429.6
Aerial application – coastal deflector bucket (35m swath)	155.3
Aerial application – overlap between coastal swath and inland flight lines (70m swath)	212.0
Aerial application – trickle bucket (<10m swath) e.g. *Pemphis* habitat	1.0
Hand broadcast within areas excluded from aerial bait application e.g. residential area	45.7
Areas treated using bait stations	33.1
Areas excluded from bait application e.g. runway	59.5
Total	**936.2**[a]

[a] Total area is greater than the area of the island because of overlap between methods.

The impact of rats and non-target consumers (land crabs) on bait availability had been assessed in a trial completed in 2009, and trial results factored into decisions on the application rates to be used for the operation. However, operational application rates were based on averages and not the highest rates of bait disappearance observed, a strategy that Brown et al. (2013) suggested was insufficiently cautious. Certainly during the operation, bait disappeared rapidly from some of the transects monitored (Figure 3). The 9-day interval between applications extended the period over which bait was available, but as evidenced by monitoring, bait was still only available in some parts of the atoll for a maximum of 15 days. Bait stations extended the period that bait was available around occupied buildings.

Interactions between *R. exulans* and *R. tanezumi* were not researched on Wake, but investigations at other locations show that *R. exulans* is displaced from habitats and food resources by *R. rattus* and *R. norvegicus* (Harper et al. 2005, Shiels 2010). Based on the interspecific competition observed in these studies, it is likely that access to bait by *R. exulans* on Wake was affected to some degree by the presence of *R. tanezumi*, and this may have magnified the consequences of spatial and temporal gaps in bait distribution.

The successful removal of *R. tanezumi* from all 3 islands challenges concerns about irregular bait distribution. This species was formerly widespread across the atoll, suggesting that despite the project's complexities, broad coverage across all habitats was achieved. Relative differences in foraging range between the 2 rat species on Wake and how these varied seasonally are unknown. However, no discernible difference could be found between the 2 species for the 80%, 90%, and 100% minimum convex polygons generated from a radio-telemetry study completed on Wake (Mosher et al. 2008). Based on the ranges recorded by Mosher et al. (2008) (the smallest being 1,441 m^2) and the fact that the bait application strategy encompassed 2 applications, each with a 50% overlap in the swath produced by the helicopter and spreader bucket, we consider it likely that all individual *R. exulans* foraging at the time of the operation would have encountered bait after at least one of the 2 applications.

Not all rats on Wake, however, were foraging at the time bait was applied. Rats were breeding at the time of the operation, as documented by necropsy and the detection of juveniles after the operation, and it is likely that rats were at various stages of reproduction. Juveniles in the nest would have been largely isolated from the toxicant for much of the period of time they were dependent on the lactating female (Figure 4). Weaning times reported for *R. exulans* range from 3 to 4 weeks (Wirtz 1972, Tobin 1994). The juvenile found 18 days after bait application emerged after bait had disappeared from 22% of transects, and if monitoring had continued beyond this point, it is likely that few transects would have contained bait at the time the second juvenile was found, 47 days after bait was applied. Rat populations on Wake were at extremely high density, so it is likely that such instances were replicated across the atoll. Juveniles emerging from nests after bait had disappeared from some parts of the atoll could have survived to repopulate the island (Figure 4).

DISCUSSION

Like Brown et al. (2013), we could not isolate a single reason to explain why *R. tanezumi* was successfully removed but *R. exulans* survived the eradication attempt. However, we consider there is sufficient evidence to rule out 3 of the hypotheses put forward. The possibility of reinvasion can be dismissed because of the low likelihood that *R. exulans* reinvaded Wake Atoll and the fact that the DNA of survivors matched that of the original population. Similarly, bait toxicity can be discounted based on the testing conducted and the successful removal of *R. tanezumi*, a larger-bodied rodent species.

Evidence for and against resistance as a factor was less conclusive, but available information undermines

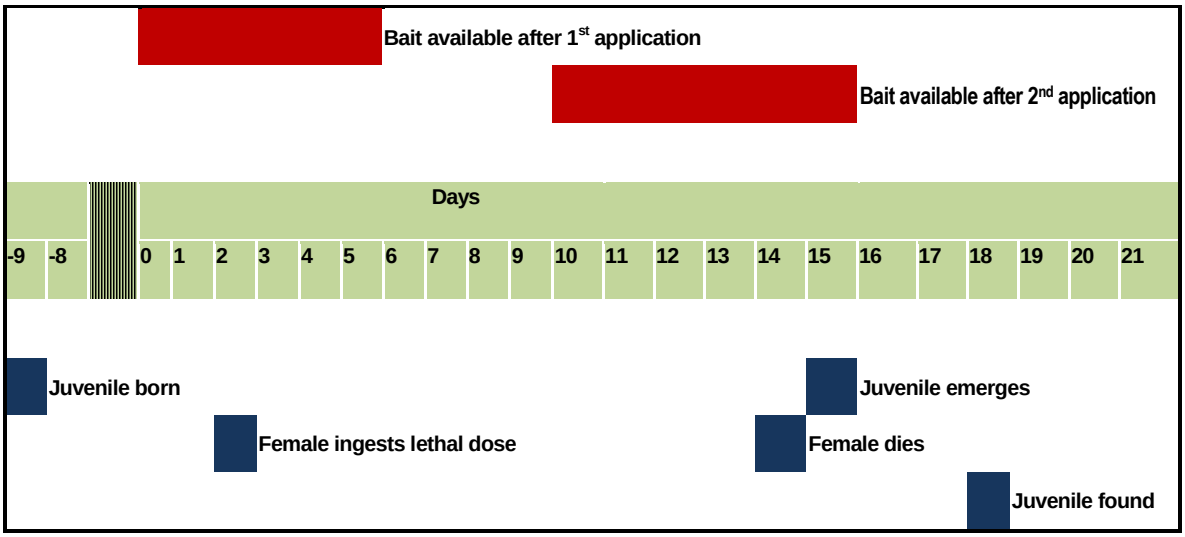


Figure 4. Possible timing of key events resulting in the discovery of a juvenile *R. exulans* in a bait station 18 days after the application of rodent bait on Wake Atoll.

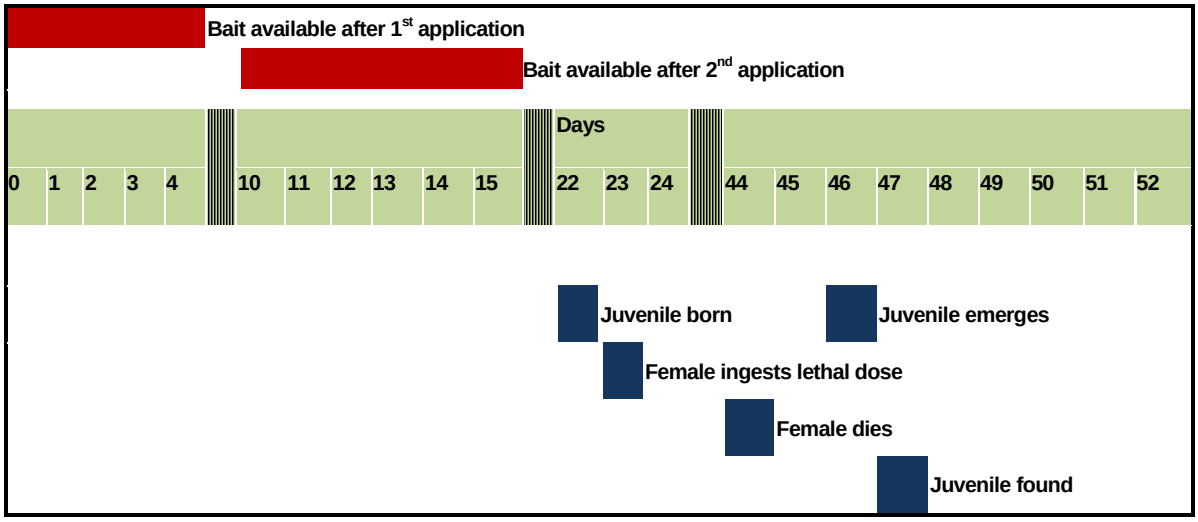


Figure 5. Possible timing of key events resulting in the discovery of a malnourished but recently weaned juvenile *R. exulans* 47 days after the application of rodent bait on Wake Atoll.

support for this hypothesis. The successful eradication of *R. tanezumi* from all 3 islands and of *R. exulans* from Peale and Wilkes Islands, and the control of *R. exulans* to undetectable levels for a period of 3 months on Wake, is at odds with the levels of survivorship reported for rodent populations for which practical resistance has been documented (e.g., Drummond and Rennison 1973, Greaves et al. 1982). It is important to note that while technical resistance to brodifacoum has been documented for some rat populations, pharmocodynamic resistance, which might have caused the Wake rodent eradication to fail, has never been detected (Buckle and Prescott 2012).

Having rejected these 3 hypotheses, we are left with just 2 possible scenarios that might explain why *R. exulans* persisted on Wake Island. One, a proportion of the *R. exulans* population on Wake Island did not have access to bait, and 2, some individuals chose not to eat it. In teasing out the relative importance of these 2 causal factors, we point to the juvenile rats discovered after bait application as particularly informative. The first juvenile *R. exulans* found 18 days after bait was first applied highlights that a proportion of the Wake rat population was isolated from the toxicant. For as long as they remained in the nest and dependent on the lactating female, juveniles were comparatively isolated from the eradication method (Figure 4). Evidence suggests that brodifacoum is not passed on in sufficient amounts via lactation to cause mortality (Milne et al. 2001, Gabriel et al. 2012) and although juvenile rats test and sometimes consume solid food prior to weaning, this pathway may also be insufficient to lead to ingestion of a lethal dose.

As evidenced by monitoring, bait was no longer available in some parts of the atoll after 15 days. Recently-weaned juveniles emerging after this time had a reduced chance of encountering bait, and with natural food abundant on Wake, these individuals could have

survived to repopulate the island. Other examples of juveniles being found after bait application have been observed. The majority of rats trapped 9 days after bait application on Bird Island were juveniles (Merton et al. 2002). During the successful removal of *R. rattus* from Palmyra, a juvenile rat was sighted and captured 28 days after the first bait application (unpubl.). The Palmyra juvenile also appeared to have suffered from malnutrition and was likely prematurely weaned as a result of early maternal death (unpubl.).

The juvenile found on Wake Island 47 days after bait was first applied is in many ways even more interesting. The presence of this individual confirms that a female rat survived for much longer than expected. Rats have survived for up to 21 days after ingestion of a lethal dose in laboratory trials (Pitt 2004), but time to death is generally much shorter (Littin et al. 2000). How and why did this female survive for so long? Did she not have access to bait for a period of time? This is possible on Wake, given the increased risk of gaps in bait spread, the short time bait remained in some parts of the atoll (Figure 3), and the impact of inter-specific competition that likely exacerbated spatial or temporal gaps in bait availability (Figure 5). This individual did eventually die, as evidenced by the malnourished state of the recently weaned juvenile.

Feasibility trials pointed to the possibility of bait aversion, but the possibility the female rat actively avoided bait for a period of time appears less likely, given her death prior to weaning her young. The reduction of *R. exulans* to undetectable levels for a period of 3 months does not match reports from locations where behavioural resistance has been documented (Humphries et al. 2000), weighing further against bait aversion having played a role on Wake. Palatability of the bait used on Wake was demonstrated on Palmyra, where natural food resources were also readily available to the resident *R. rattus* population (Wegmann et al. 2012).

Given the high density of rat populations on Wake at the time of the operation, it is highly likely that the events represented by the 2 juveniles found were replicated elsewhere on the atoll. Based on data from captivity (Tobin and Fall 2005), juveniles that did survive could have reached sexual maturity by August and weaned their first litters by November. This theoretical timeline is consistent with the first report of rats breeding on Wake made in late December (Table 1).

Why such a scenario did not play out on Peale and Wilkes Islands, where rats were also likely breeding, is unknown. However, bait persisted for a much longer period on Wilkes, and as Brown et al. (2013) suggested, both Peale and Wilkes were simpler propositions for bait application; thus, the chance of gaps in bait spread is likely to have been significantly less. It is also possible that the different outcome observed on Peale and Wilkes was the result of a 'numbers game.' More individuals on Wake increased the likelihood that some breeding females survived for long enough to wean juveniles after bait was no longer readily available. Insufficient evidence is available to confirm or refute this hypothesis.

In any case, the Wake rodent eradication had not been planned to account for female rats surviving for a longer period of time nor juveniles emerging so late after bait application. A future attempt to remove rats from Wake, designed with these insights taken into account, should have a much higher chance of success. Based on our analysis, we highlight the following set of recommendations for a future attempt to remove *R. exulans* from Wake Atoll.

RECOMMENDATIONS

A second attempt to remove *R. exulans* from Wake Atoll should be in accordance with recently developed best practice guidelines for topical island rat eradication (Keitt et al. 2015). Specifically, 2 equally comprehensive bait applications should be undertaken with the same bait application rate and swath overlap. If any breeding is occurring, then a proportion of the population may not be exposed to the initial application of bait, and the second application will necessarily be targeting survivors. A longer interval should also be left between bait applications. An interval of at least 24 days is proposed, as this would account for the maximum period of time (25 days) documented for young rats between birth and emergence from the nest (Innes 1990), and the maximum interval of 21 days documented for mortality of a wild-caught rat after ingestion of a lethal dose of brodifacoum (Pitt 2004).

On arrival at the island and prior to bait application, a rapid assessment should be made to assess rat body condition and reproductive status. If rats are in good condition and the population is expanding, then delaying the eradication should be considered. Monitoring for surviving rats in the months after the operation should be considered. The use of rodent dogs and other detection methods could be used to locate survivors on Wake, and additional bait or other methods used to target these individuals. A larger amount of contingency bait should be ordered and transported for the operation. More contingency bait would allow the rates used for the second application to be adjusted upwards if the level of bait take observed is higher than anticipated.

To reduce the risk of gaps in bait spread, a simplified bait application strategy should be adopted with fewer areas excluded from aerial bait application. Another search for disused infrastructure should be undertaken to ensure all potential rat habitat is treated. A system should also be established to ensure that false sowing does not occur during bait application. This may be as simple as checking the bucket each time it is returned to the loading zone to ensure that at least 10 kg of bait remains. Any flight lines where false sowing may have occurred should be re-flown.

In preparation for a future eradication attempt, we also recommend the following be researched:

- Ranging behavior of radio-tagged rats in *Pemphis* habitat.
- Rat access to and consumption of bait in *Pemphis* habitat.
- Genetic diversity of the residual population to assess relatedness.
- Assay of the first rats captured after the 2012 implementation to determine exposure levels.
- Biomarker and ranging behavior focused on lactating females and emerging young.

- Seasonal changes in rodent abundance, breeding status, and population demography, and natural food abundance in key differentiated habitats.

ACKNOWLEDGEMENTS

Special thanks to the organizations involved in the implementation of the Wake rat eradication project. These include the U.S. Air Force's 15th Airlift Wing, Pacific Air Forces, the U.S. Fish and Wildlife Service, Island Conservation, and Chugach Federal Solutions, Inc. We are very grateful to members of the project team and the Wake Atoll based staff who assisted in compiling the evidence on which this paper is based. Thanks to Nick Holmes and several anonymous reviewers who provided constructive criticism on this manuscript.

LITERATURE CITED

Bellingham, P. J., D. R. Towns, E. K. Cameron, J. J. Davis, D. A. Wardle, J. M. Wilmshurst, and C. P. H. Mulder. 2010. New Zealand island restoration: Seabirds, predators, and the importance of history. NZ J. Ecol. 34:115-136.

Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: A meta-analysis. Science 325: 1121-1124.

Brown, D., B. R. Tershy, and W. C. Pitt. 2013. A review of the Wake Island Rat Eradication Project. U.S. Fish & Wildlife Service, Honolulu, HI.

Buckle, A. 2006. The current status of anticoagulant resistance, resistance monitoring and management strategies. *In*: International Forum for Sustainable Management of Disease Vectors, Beijing, China.

Buckle, A., and C. Prescott. 2012. The current status of anticoagulant resistance in rats and mice in the UK. Report from the Rodenticide Resistance Action Group of the United Kingdom to the Health and Safety Executive. Vertebrate Pests Unit, The University of Reading, UK.

DIISE. 2014. The Database of Island Invasive Species Eradications, developed by Island Conservation, Coastal Conservation Action Laboratory UCSC, IUCN SSC Invasive Species Specialist Group, University of Auckland and Landcare Research New Zealand.

Drummond, D., and B. D. Rennison. 1973. The detection of rodent resistance to anticoagulants. Bull. World Health Org. 48:239.

Fosberg, F. R., and M.-H. Sachet. 1969. Wake Island vegetation and flora, 1961-1963. Atoll Res. Bull. 123:1-15.

Gabriel, M. W., L. W. Woods, R. Poppenga, R. A. Sweitzer, C. Thompson, S. M. Matthews, J. M. Higley, S. M. Keller, K. Purcell, R. H. Barrett, G. M. Wengert, B. N. Sacks, and D. L. Clifford. 2012. Anticoagulant rodenticides on our public and community lands: Spatial distribution of exposure and poisoning of a rare forest carnivore. PLoS ONE 7:e40163.

Gilardi, J., and M. J. Rauzon. 2014. Wake Island Seabird Population Survey. Chugach Federal Solutions, Inc., Honolulu, HI.

Greaves, J., D. Shepherd, and J. Gill. 1982. An investigation of difenacoum resistance in Norway rat populations in Hampshire. Ann. Appl. Biol. 100:581-587.

Greaves, J. H. 1994. Resistance to anticoagulant rodenticides. Pp. 197-217 *in*: A. P. Buckle and R. Smith (Eds.), Rodent Pests and their Control. CAB International, Wallingford, Oxon, UK.

Harper, G. A., K. J. Dickinson, and P. J. Seddon. 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/ Rakiura, New Zealand. NZ J. Ecol. 29:251-260.

Holmes, N. D., R. Griffiths, M. Pott, A. Alifano, D. Will, A. S. Wegmann, and J. C. Russell. 2015. Factors associated with rodent eradication failure. Biol. Conserv. 185:8-16.

Humphries, R., R. Sibly, and A. Meehan. 2000. Cereal aversion in behaviourally resistant house mice in Birmingham, UK. Appl. Anim. Behav. Sci. 66:323-333.

Innes, J. 1990. Ship rat. Pp. 206-225 *in*: C. M. King (Ed.), The Handbook of New Zealand Mammals. Oxford University Press, Auckland, NZ.

Keitt, B., R. Griffiths, S. Boudjelas, K. Broome, S. Cranwell, J. Millett, W. Pitt, and A. Samaniego-Herrera. 2015. Best practice guidelines for rat eradication on tropical islands. Biol. Conserv. 185:17-26.

Littin, K. E., C. E. O'Connor, and C. T. Eason. 2000. Comparative effects of brodifacoum on rats and possums. NZ Plant Protect. 53:310-315.

Lorvelec, O., and M. Pascal. 2005. French attempts to eradicate non-indigenous mammals and their consequences for native biota. Biol. Invas. 7:135-140.

Merton, D., G. Climo, V. Laboudallon, S. Robert, and C. Mander. 2002. Alien mammal eradication and quarantine on inhabited islands in the Seychelles. Pp. 182-198 *in*: C. R. Veitch and M. N. Clout (Eds.) Turning the tide: The eradication of invasive species. Proceedings of the International Conference on Eradication of Island Invasives. Occ. Paper of the IUCN Species Survival Commission, No. 27. IUCN, Gland, Switzerland and Cambridge, UK.

Milne, L., G. Wright, C. Eason, and C. O'Connor. 2001. Human exposure to poisons through contaminated food. Pp. 141-145 *in*: Proceedings, 12th Australasian Vertebr. Pest Conf.

Mosher, S., A. Hebshi, K. Swift, P. Dunlevy, D. Vice, A. Wegmann, B. Jacobs, B. Thomas, and J. Gilardi. 2008. Rat eradication feasibility study: 29 September - 27 October 2007. Dept. of Defense, Hickam AFB.

Phillips, R. A. 2010. Eradications of invasive mammals from islands: Why, where, how and what next. Emu 110:i-vii.

Pitt, W. 2004. Appendix 2. Brodifacoum Resistance Study. Pp. 47-56 *in*: G. Howald, A. Samaniego, S. Buckelew, P. McClelland, B. Keitt, A. Wegmann, W. C. Pitt, D. S. Vice, E. Campbell, K. Swift, and S. Barclay, (Eds.), Palmyra Atoll rat eradication assessment trip report, August 2004. Island Conservation, Santa Cruz, CA.

Rauzon, M. J., D. Boyle, W. T. Everett, and J. Gilardi. 2008a. The status of the birds of Wake Atoll. Atoll Res. Bull. 561: 1-41.

Rauzon, M. J., W. T. Everett, D. Boyle, L. Bell, and J. Gilardi. 2008b . Eradication of feral cats at Wake Atoll. Atoll Res. Bull. 560:1-21.

Roberts, M. 1991. Origin, dispersal routes, and geographic distribution of *Rattus exulans*, with special reference to New Zealand. Pacific Sci. 45:123-130.

Shiels, A. B. 2010. Ecology and impacts of introduced rodents (*Rattus* spp. and *Mus musculus*) in the Hawaiian Islands. Ph.D. dissert., University of Hawaii, Honolulu, HI.

Tobin, M. E. 1994. Polynesian rats. Pp. B121-124 *in*: S. E. Hygnstrom, R. M. Timm, and G. E. Larson (Eds.), Prevention and Control of Wildlife Damage. Cooperative Extension Service, Univ. of Nebraska, Lincoln, NE.

Tobin, M., and M. Fall. 2005. Pest Control: Rodents. Agricultural Sciences, Encyclopedia of Life Support Systems (EOLSS) Vol. II. EOLSS Publishers, under the auspices of United Nations Educational, Scientific, and Cultural Organization, Oxford, UK.

Wegmann, A., J. Helm, N. Torr, C. Golding, and G. Howald. 2009. Wake Atoll rat eradcation strategic plan: Biomarker study trip report (27 February to 27 March, 2009). Island Conservation, Kelowna, Canada.

Wegmann, A., E. Flint, S. White, M. Fox, G. Howald, P. McClelland, A. Alifano, and R. Griffiths. 2012. Pushing the envelope in Paradise: A novel approach to rat eradication at Palmyra Atoll. Proc. Vertebr. Pest Conf. 25:48-53.

Wirtz, W. O. I. 1972. Population ecology of the Polynesian rat, *Rattus exulans*, on Kure Atoll, Hawaii. Pacific Sci. 26:433-461.