

Assessing the critical role that land crabs play in tropical island rodent eradications and ecological restoration

A. Samaniego-Herrera^{1,2}, S. Boudjelas^{2,3}, G.A. Harper⁴ and J.C. Russell¹

¹*School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand. <ara.samaniego.mx@gmail.com>*. ²*Pacific Invasives Initiative, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand.* ³*Centre for Biodiversity and Biosecurity, University of Auckland, Private Bag 92019, Auckland 1142, New Zealand.* ⁴*Biodiversity Restoration Specialists, PO Box 65, Murchison, New Zealand.*

Abstract Invasive rodent eradications are one of the most effective conservation interventions to restore island ecosystems. However, achievements in the tropics are lagging behind those in temperate regions. Land crab interference in bait uptake has been identified as one of the main causes of rodent eradication failure on tropical islands, but the issue of effective mitigation of bait loss due to land crab consumption is poorly understood. For example, there are over 100 species of land crab and each may behave differently. We reviewed the available literature to answer: (1) which crab species are the most problematic? (2) what mitigation measures have been effective? and (3) how do invasive rodents impact land crab communities? We analysed a systematic dataset from six tropical islands to test two hypotheses: (a) bait uptake is highest when burrowing (*Brachyura*) land crabs are present; and (b) small land crabs (including juveniles of the larger species) are highly vulnerable to rodent predation. We found that large species (e.g. genera *Cardisoma*, *Johngarthia* and *Birgus*) are the most problematic during rodent eradications. Effective mitigation measures to prevent bait loss include using higher bait application rates and conducting eradications during the driest months. Land crab communities tend to go through significant changes after rodent removal. From our analyses, we confirmed pre-eradication data are valuable for eradication planning, as seasonality and type of crab can influence outcomes. Post-eradication data confirmed small crab species (<60 mm) are highly vulnerable to rodent predation. More effort should be invested into monitoring land crabs in tropical latitudes, particularly to determine any biogeographic or taxon trends in land crab interference. Land crabs are key for the restoration of the islands, as they shape ecosystems through their role as ecosystem engineers, hence they are excellent indicators of ecosystem recovery. Our results will contribute to the better planning of future rodent eradications on tropical islands where land crabs are significant bait competitors.

Keywords: *Birgus*, *Cardisoma*, *Coenobita*, *Gecarcinus*, impacts, monitoring, *Mus*, *Rattus*

INTRODUCTION

Islands are some of the most important repositories for biodiversity, with 15–20% of terrestrial biodiversity held on only 5.3% of the world's land area (Weigelt, et al., 2013). Tropical islands are particularly important due to their high levels of endemism (Myers, et al., 2000). Island species are also highly vulnerable to anthropogenic impacts, of which invasive alien species (IAS) introductions are often the most severe (Russell, et al., 2017), causing 86% of island endemic species extinctions (Bellard, et al., 2016). Moreover, IAS also interrupt ecosystem functioning through predation of, and competition with, other biotic components (Athens, et al., 2002; Towns, et al., 2006; Hilton & Cuthbert, 2010).

Over the past 50 years, eradication of IAS has been increasing (Towns, et al., 2013; Jones, et al., 2016), with the removal of invasive rodents proving highly effective in targeted species recovery and island ecosystem restoration (Le Corre, et al., 2015; Croll, et al., 2016). Over 90% of rat eradication attempts have been successful, with increasingly larger islands being effectively targeted (Holmes, et al., 2015). However, the rate of eradication failure on tropical islands has been 2–2.5 times higher than on temperate islands (Russell & Holmes, 2015). This discrepancy is due to several contributing factors (Holmes, et al., 2015). Probably the most significant are the benign climate facilitating rodent reproduction (Harper & Bunbury, 2015), and bait competition from abundant land crabs (Wegmann, 2008; Griffiths, et al., 2011).

Land crabs comprise over a hundred species in three broad groups, burrowing crabs, hermit crabs and coconut crabs, although the latter single species (*Birgus latro*) is technically a hermit crab. As the largest invertebrates on islands, particularly coral atolls, land crabs are often the apex land predator (Burggren & McMahan, 1988), and can attain high population densities and occupy the niches of vertebrates on small oceanic islands. As such, they act as

allogenic ecosystem engineers (Green, et al., 2008; Paulay & Starmer, 2011) through their significant influence on forest structure, plant species composition, soil formation and nutrient transfer and cycling (Green, et al., 1999; Sherman, 2002; Gutiérrez & Jones, 2006; Gutiérrez, et al., 2006; Sherman, 2006; Green, et al., 2008; Lindquist, et al., 2009). As keystone consumers (Paine, 1966), the removal of or reduction in crab abundance through the introduction of IAS can trigger a trophic cascade of effects, leading to 'meltdown' in island ecosystems in the worst cases (O'Dowd, et al., 2003; Pitman, et al., 2005; Nigro, et al., 2017). Moreover, as smaller crab species in particular are vulnerable to predation by rodents (St Clair, 2011; Samaniego-Herrera & Bedolla-Guzmán, 2012) and invasive rodents are found on >80% of island groups (Atkinson, 1985), an improved understanding of the interaction between rodents and land crabs is urgently required. However, land crabs have rarely been monitored before and after rodent eradications (but see Nigro, et al., 2017), and basic tools such as inventories are lacking for most tropical islands where rodent eradications are being planned.

The Pacific Invasives Initiative (PII) commissioned the first review on land crab interference in rodent eradications about 10 years ago (Wegmann, 2008) and many lessons have been learnt since. To improve the justification and implementation of rodent eradications on tropical islands, we conducted literature reviews on two main topics: the role of land crabs in invasive rodent eradications and the vulnerability of land crabs to rodent invasion. A case study from six tropical islands is presented, demonstrating the utility of monitoring land crabs both pre- and post-rodent eradications. Based on our previous observations of land crabs across islands, we expected (a) bait uptake to be highest on the islands where large burrowing species were abundant, and (b) population abundance of small burrowing species to increase over time after rodent eradications.

METHODS

Land crabs and rodent eradications

Following Burggren & McMahon (1988), we consider land crabs to be crabs that show significant behavioural, morphological, physiological, or biochemical adaptations permitting extended activity out of water. This includes a few families of the diverse infraorders Anomura (hermit crabs) and Brachyura (burrowing crabs), yet there are over a hundred species that can be considered land crabs. Land crab distribution ranges from tropical to subtropical areas, hence the scope of this paper focuses on islands located between $\sim 25^\circ$ north and south of the equator. We also focus on the two most common rodent eradication methods: aerial and hand broadcast of bait directly onto the ground (Howald, et al., 2007; DIISE, 2016).

The islands included in the review are a subset from the Database of Island Invasive Species Eradications (DIISE, 2016). These were selected based on the following criteria: 1) location: between latitudes $\sim 25^\circ$ north and south of the equator, 2) target IAS taxa: Muridae, 3) whole island eradications, 4) toxicant used: 2nd generation anticoagulant, 5) main bait delivery method: hand or aerial broadcast, 6) quality of data: good or satisfactory, the latter were updated to good, and 7) eradication status: known or 'to be confirmed', the latter were updated to failed or successful. Islands without land crabs such as the Galapagos Islands and Western Australia islands were excluded.

For each island, we collated the following additional data: bait rates used during the rodent eradications, island type (savanna, tropical seasonal forest or tropical rainforest), presence/absence status and abundance for each land crab group (hermit, coconut, burrowing), land crab group identified as the main bait competitor and timing of the eradication (dry or wet season). This information was collated through review of project documents (i.e. feasibility studies, operational plans, post-operation reports and scientific papers). We also sought inputs from project managers when we required further clarification/confirmation or information was missing from the documents available. Given the scarcity of scholarly information on land crabs, and the lack of a single source with the basic biology and current taxonomy for all land crabs (as most crab species are marine), we conducted an additional literature review to compile such information.

A 2-way ANOVA test for unbalanced designs was used to evaluate the variations in bait rates in relation to island type and main bait competitors. Data were log-transformed to achieve normality. All analyses were performed in R 3.4.

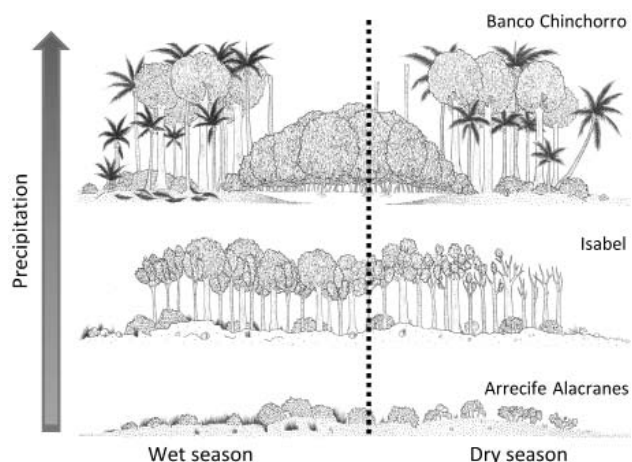


Fig. 1 Dominant vegetation on the islands where the case study took place.

Rodent impacts on land crabs

Some of the information on the impacts of rodents on land crabs was collated from the project documents mentioned above. In addition, we also searched the Web of Science, Scopus and Google Scholar for published literature using keywords: [island OR atoll OR cay OR archipelago] AND [rodent OR rat OR rattus OR mus] AND ["land crab" OR invertebrate]. We collated information on impacts through review of the resulting publications and relevant references listed in these.

Case study: Mexican tropical islands

Study sites

As part of a wider restoration programme led by Grupo de Ecología y Conservación de Islas (GECI) (Samaniego-Herrera, et al., 2011), bait uptake and land crab monitoring was conducted on six Mexican tropical islands. The islands, three in the Gulf of Mexico, one in the Mexican Pacific, and two in the Caribbean Sea fall into the three categories of tropical island ecosystems described by Russell and Holmes (2015): savanna, tropical seasonal forest and tropical rainforest, respectively (Table 1; Fig. 1). The aims of the monitoring were to inform the specific rodent eradication plans by assessing the potential interference of each land crab community, and to compare such communities before and after the removal of the invasive rodents. Invasive rodents (Table 1) were successfully eradicated from all islands either by hand or aerial broadcast of bait (Samaniego-Herrera, et al., 2014; Samaniego-Herrera, et al., 2018), following international best practices (Keitt, et al., 2015).

Bait uptake

Two types of bait were used: placebo bait for pre-eradication assessments and toxic bait for the actual rodent eradications. The toxic bait consisted of 2 g cereal bait pellets containing 25 ppm brodifacoum (second generation anticoagulant), manufactured by Bell Labs. The placebo bait, also from Bell Labs, was identical but non-toxic. Total bait uptake (i.e. by the target and non-target species) was measured before and during each eradication operation. Pre-eradication, bait uptake was monitored to help decide application rates for the eradication. During eradications, the monitoring took place to (a) validate the intended bait rate, by estimating bait density on the ground immediately after the bait drops, (b) assess the daily uptake rate, by repeating measurements every 24 hours, and (c) investigate the relationship of bait uptake rate, rodent abundance, and land crab diversity and abundance, by combining results from different islands.

In all cases, bait uptake was measured daily for 6–10 consecutive days in a systematic way, starting on the same day of bait broadcast. For all pre-eradication studies bait was broadcast by hand, whereas for the eradications either aerial or hand broadcast was used (Table 1). Bait uptake was measured in fixed circular plots as described by Pott, et al. (2015). A subset of the resulting dataset was included in the meta-analysis by Pott, et al. (2015), which showed the utility of bait availability studies. However, there are three major differences with the present study. Firstly, Pott and colleagues only used a subset of the Mexican dataset due to the limited data available for the other islands (e.g. data from only two of the 6–10 days available were analysed). Secondly, the results presented here derived from standardised monitoring methodologies. Lastly, our focus is to investigate the role of land crabs in the overall bait uptake in more detail, distinguishing for crab type (hermit and burrowing).

Table 1 General description of the six Mexican islands where land crabs were monitored before and after the successful rodent eradications.

Archipelago Island	Area (ha)	Ecosystem type	Dominant vegetation ¹	Species eradicated (year) ²	Eradication method and bait rate (total kg/ha)	Main bait competitors (seasonal fluctuation)
Arrecife Alacranes						
Pájaros	3	Savanna	Shrubs and grasses	<i>Mus musculus</i> (2011)	Hand broadcast 17 kg/ha	Hermit crabs (low fluctuation)
Pérez	13	Savanna	Shrubs	<i>Rattus rattus</i> (2011)	Hand broadcast 17 kg/ha	Hermit crabs (low fluctuation)
Muertos	15	Savanna	Shrubs	<i>Mus musculus</i> (2011)	Hand broadcast 17 kg/ha	Small burrowing crabs (low fluctuation)
Isabel	82	Tropical seasonal forest	Deciduous forest	<i>Rattus rattus</i> (2009)	Aerial broadcast 20 kg/ha	Large burrowing crabs ³ (high fluctuation)
Banco Chinchorro						
Cayo Norte Mayor	30	Tropical rainforest	Mangroves & evergreen forest	<i>Rattus rattus</i> (2012)	Aerial broadcast 42 kg/ha	Large burrowing crabs (moderate fluctuation)
Cayo Centro	539	Tropical rainforest	Mangroves & evergreen forest	<i>Rattus rattus</i> (2015)	Aerial broadcast 60 kg/ha	Large burrowing crabs (moderate fluctuation)

¹See Fig. 1.

²Always end of dry season.

³There was virtually no crab interference during the rat eradication; bait lasted for weeks.

Sources: Samaniego-Herrera, et al., 2013; Samaniego-Herrera, et al., 2014; Samaniego-Herrera, et al., 2018.

Land crab recovery

On all islands, land crab activity was monitored twice a year, at the end of each dry and wet season, both before (2–3 years) and after (1–5 years) each rodent eradication. Every season, several (6–18) fixed plots (25 m × 2 m) were used to estimate crab density; the exception was on Isabel Island, where two 300 m × 6 m plots were used. Plots were walked for 3–5 consecutive nights. One person with a headlamp walked in the middle of the plot, starting one hour after sunset. In order to walk all plots within 90 minutes (i.e. the peak activity period), several observers participated each night on some islands. The number of land crabs, by species, was recorded. Minimum training is required to carry out this task given the morphological differences of the species present.

Data analysis

Bait uptake trends (always measured in the dry season) were investigated using a linear mixed model (R software package nlme) for bait availability, where the density of bait (kg/ha), using the difference of target density minus measured density as the response variable (i.e. comparing rates of decline rather than actual densities), was dependent on time (days) and interactions of time with fixed effect covariates (i.e. covariates which would affect bait availability). These fixed effects included whether the study was conducted prior to or during the eradication (distinguishing between first and second bait application), whether rats or mice were the target species and how abundant they were (according to local mark-recapture studies by Samaniego-Herrera (2014)), and the abundance of both types of land crabs: hermit and burrowing (low – high, based on the monitoring in this study, therefore standardised). Although each island used different bait application rates, we were specifically interested in the rates of decline in bait availability. Inter-island differences

were accounted for by including island as a random effect in our model. Diagnostic plots were visually checked for violations of model assumptions.

For land crab activity, an index of density was estimated as the number of nocturnal surface-active crabs per hectare. First, we used 2-way ANOVA to test the difference in density between seasons (dry and wet) and islands only for the pre-eradication periods (i.e. avoiding potential confounding effects caused by the eradications), as obvious fluctuations were occurring at least on some islands. In order to compare trends during favourable periods (hence closer to real density, as inactive crabs typically bury themselves), and given that the lower land crab activity during the dry season was confirmed for some islands, further analysis comparing pre- and post-eradication density used data from wet seasons only. Differences in density among island types (savanna, seasonal, rainforest) and periods (pre- and post-eradication) were tested with linear models. Data were log-transformed to achieve normality. All analyses were performed in R 3.4.

RESULTS

Land crabs and rodent eradications

The resulting database contains 108 eradication attempts spread over 101 tropical islands (Appendix 1; detailed spreadsheet: www.pacificinvasivesinitiative.org/). On some islands, there were two eradication attempts targeting a single rodent species or there were two rodent species being targeted by a single eradication attempt. Island sizes range from 0.1 ha to 4,310 ha (median = 10 ha). Most attempts (86.1%) targeted only rats (*Rattus exulans*, *R. norvegicus*, *R. rattus* or *R. tanezumi*), 2.8% only mice (*Mus musculus*) and 11.1% targeted both rats and mice.

Eighty-nine (82.4%) of the eradication attempts were successful and 19 (17.6%) failed (Table 2). Land crab interference was reported as important in 56.2% of the successful attempts and in 100% of the failed ones. However, for the latter, in addition to land crab interference other potential factors that may have contributed to the failure were also reported. Examples of such factors are gaps in bait coverage, which in turn can increase in area as land crabs take bait at the edges.

Over 82% of the eradication attempts used higher bait rates ($\bar{x} = 25.7$ kg/ha, range: 3–163 kg/ha) compared to those typically used on temperate islands (12 kg/ha; Broome, et al., 2014). In all cases, the justification for using higher bait rates was high rodent abundances (either estimated or assumed) and land crab presence, although abundance of either was rarely quantified. On some islands, additional factors such as high abundance of small invertebrates (e.g. ants and cockroaches, also bait consumers) were also mentioned.

Land crab abundances were reported as having been estimated either through measurements (21.5%) or observations (55.9%) during the planning phase; the rest (22.6%) of the cases did not try to estimate land crab abundance. On most islands, land crabs have been identified to the genus level. Through our research on current taxonomy, we identified 165 species of land crabs in 52 genera and 15 families, of which seven genera have been reported as important bait consumers (Table 3). For most islands (90.7%), only three or fewer land crab species were reported to be present.

Considering all islands, the 2-way ANOVA test revealed significant differences in total bait rates used depending on which type of land crab was the main source of interference ($F = 11.33, p < 0.001$) and on the interaction between crab type and island type ($F = 3.65, p < 0.001$), whereas island type was marginally significant ($F = 3.02, p = 0.05$). Higher bait rates (17–163 kg/ha) were used when burrowing crabs were the main bait competitors ($n = 8$), followed by hermit crabs (3–83.3 kg/ha; $n = 55$) and cases with ‘no interference’ (8–33.2 kg/ha; $n = 39$), i.e. low crab abundance (Fig. 2). When considering only successful attempts, the patterns remained the same.

Rodents impacts on land crabs

Accounts of insular land crab populations being negatively impacted by invasive rodents included 15 populations of ten species across nine countries and overseas territories (Table 4). These impacts are mainly in the form of population suppression and ecological

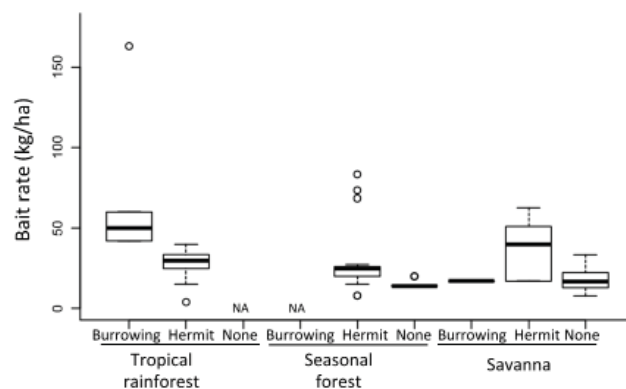


Fig. 2 Total bait used (median, IQR, range and outliers) in successful rodent eradications on tropical islands with land crabs, by type of dominant land crab and type of island. None = land crabs were present at low densities therefore interference was minimum.

Table 2 Success rate of hand and aerial rodent eradication projects, per target species, on tropical islands with land crabs.

Target species	Failed		Successful	
	%	n	%	n
<i>Mus musculus</i>	28.6	2	71.4	5
<i>Rattus exulans</i>	17.4	12	82.6	57
<i>Rattus norvegicus</i>	0	0	100	3
<i>Rattus rattus</i>	18.5	5	81.5	22
<i>Rattus tanezumi</i>	0	0	100	2
TOTAL	17.6	19	82.4	89

extirpation. Pascal, et al. (2004) first suggested possible rat predation on *Gecarcinus ruricola* on Hardy Islet, after they found numerous crab carapaces in rat middens and the index of crab abundance increased after the rat eradication. Samaniego-Herrera & Bedolla-Guzmán (2012) and Samaniego-Herrera (2014) confirmed invasive rats can indeed cause ecological extirpations of land crabs; they documented how *G. quadratus*, a small burrowing crab, shifted from being extremely rare before the *R. rattus* eradication to being the most abundant species four years post-eradication. Evidence of rodent predation on land crabs as well as the dramatic recovery responses following rat eradication is growing (Harper & Bunbury, 2015; Samaniego-Herrera, et al., 2017). For example, Nigro, et al. (2017) showed that the recovery of two carnivorous species (*Geograpsus* spp.), the smallest of the Palmyra atoll crabs, led to a dramatic widening of the crab trophic niche following the rat eradication on Palmyra atoll, which is altering the ecology of the atoll presumably towards a more natural state. Likewise, Russell, et al. (2015) showed land crab trophic position differed depending on what invasive rat species is present.

Case study: Mexican tropical islands

Bait uptake

Linear mixed models were constructed, including period (trials or during eradication), rodent species (*R. rattus* or *M. musculus*), rodent abundance (high or low) and land crab abundance (high or low) per crab type (hermit or burrowing) as covariates. The model with the greatest support (49.8%) revealed a complex relationship between the difference in bait density from target density (response variable) and all variables tested and some interactions (Table 5). Essentially, the rate of decline of bait density depends on (a) days since broadcast, declining over time, (b) the type of crab, declining faster with burrowing crabs, (c) the density of burrowing crabs, declining with high density, (d) the density of hermit crabs, declining with high density, (e) study type, declining faster during trials, (f) the broadcast, declining faster after first broadcast, (g) the density of rats, declining faster with high density, and (h) the density of mice, declining with high density. Fig. 3 illustrates the variability in bait density among plots and islands after the rodent eradications, although in all cases (trials and eradications) bait was still readily available after the recommended four nights (Keitt, et al., 2015). The faster decline in available bait when burrowing crabs are abundant is a novel result.

Land crab recovery

For the pre-eradication period, the 2-way ANOVA revealed significant differences in land crab density depending on island type (highest on rainforest islands)

Table 3 Current taxonomy of the 52 genera and 165 species of land crabs with island records.

Infraorder	Family	Genus ¹	No. species ¹	Documented bait consumer? ²	Documented rodent vulnerability? ³		
Anomura	Coenobitidae	<i>Birgus</i>	1	Yes	Yes		
		<i>Coenobita</i>	17	Yes			
Brachyura	Diogenidae	<i>Clibanarius</i>	4				
		<i>Calcinus</i>	1				
	Porcellanidae	<i>Petrolisthes</i>	1				
	Eriphiidae	<i>Eriphia</i>	2				
		<i>Barytelphusa</i>	1				
		Parathelphusidae	<i>Adeleana</i>	1			
			<i>Austrothelphusa</i>	1			
			<i>Geelvinkia</i>	1			
			<i>Holthuisana</i>	2			
			<i>Rouxana</i>	3			
			<i>Terrathelphusa</i>	1			
			<i>Thelphusula</i>	2			
			Gecarcinidae	<i>Cardisoma</i>	4	Yes	
				<i>Discoplax</i>	7	Yes	
				<i>Epigrapsus</i>	3		
		<i>Gecarcinus</i>		4	Yes	Yes	
		Gecarcinidae	<i>Gecarcoidea</i>	3	Yes		
	<i>Johngarthia</i>		5	Yes	Yes		
	Grapsidae		<i>Geograpsus</i>	5	Yes	Yes	
			Sesarmidae	<i>Aratus</i>	1		
	<i>Armases</i>			5			
	<i>Chiromantes</i>			4			
	<i>Episesarma</i>			1			
	<i>Geosesarma</i>			24			
	<i>Karstama</i>			3			
	<i>Labuanium</i>			2			
	<i>Metasesarma</i>	1					
<i>Metopaulinas</i>	1						
<i>Neosarmatium</i>	1						
<i>Parasesarma</i>	1						
<i>Sesarma</i>	8						
<i>Sesarmoides</i>	1						
<i>Sesarmops</i>	1						
Mictyridae	<i>Mictyris</i>	1					
Ocypodidae	<i>Afruca</i>	1					
	<i>Austruca</i>	1					
	<i>Cranuca</i>	1					
	<i>Gelasimus</i>	2					
	<i>Leptuca</i>	12					
	<i>Minuca</i>	6					
	<i>Ocypode</i>	6	Yes	Yes			
	<i>Tabuca</i>	1					
	<i>Uca</i>	1		Yes			
	<i>Ucides</i>	2					
	Geryonidae	<i>Carcinus</i>	1				
	Potamidae	<i>Cerberusa</i>	1				
		<i>Potamon</i>	2				
Potamonautidae	<i>Madagapotamon</i>	1					
	<i>Malagasya</i>	1					
Pseudothelphusidae	<i>Guinotia</i>	2					

¹According to Ng, et al. (2008), McLaughlin, et al. (2010) and Shih, et al. (2016).²According to this review.³See Table 4.

Table 4 Documented land crab species negatively impacted by invasive rodents on tropical islands.

Species	Mean size (mm)	Invasive rodent	Rodent impact	Island/archipelago	Reference
<i>Birgus latro</i>	640	<i>Rattus rattus</i>	Population suppression	Tetiaroa Atoll, Society Islands, French Polynesia	Genet & Gaspar, pers. comm. 2017
<i>Gecarcinus lateralis</i>	37.7	<i>Rattus rattus</i>	Ecological extirpation	Pérez Island, Arrecife Alacranes, Mexico	Samaniego-Herrera, et al., 2017
		<i>Rattus rattus</i>	Ecological extirpation	Banco Chinchorro, Mexico	This study
		<i>Rattus rattus</i>	Ecological extirpation	Half Moon Caye, Belize	Samaniego-Herrera, et al., 2015
<i>Gecarcinus quadratus</i>	38.5	<i>Rattus rattus</i>	Ecological extirpation	Isabel Island, Mexico	Samaniego-Herrera & Bedolla-Guzmán, 2012
<i>Gecarcinus ruricola</i>	69	<i>Rattus rattus</i>	Population suppression	Hardy Island, Martinique	Lorvelec & Pascal, 2005
<i>Geograpsus crinipes</i>	46.4	<i>Rattus rattus</i>	Ecological extirpation	Palmyra Atoll, Tropical Pacific	Nigro, et al., 2017
		<i>Rattus</i> sp.	Ecological extirpation	Mañagaha Island, Northern Mariana Is	Paulay & Starmer, 2011
<i>Geograpsus grayi</i>	55.3	<i>Rattus norvegicus</i> , <i>R. exulans</i>	Ecological extirpation	Raoul Island, New Zealand	Bellingham, et al., 2010
		<i>Rattus rattus</i>	Ecological extirpation	Palmyra Atoll, Tropical Pacific	Nigro, et al., 2017
		<i>Rattus</i> sp.	Ecological extirpation	Mañagaha Island, Northern Mariana Is	Paulay & Starmer, 2011
<i>Johngarthia planata</i> ¹	92.5	<i>Rattus rattus</i>	Population suppression	Clipperton Island, eastern Pacific	Pitman, et al., 2005
<i>Ocypode kuhlii</i>	50	<i>Rattus norvegicus</i> , <i>R. exulans</i>	Ecological extirpation	Raoul Island, New Zealand	Bellingham, et al., 2010
<i>Ocypode quadrata</i>	45	<i>Mus musculus</i> , <i>Rattus rattus</i>	Population suppression	Alacranes Islands, Mexico	This study
<i>Uca</i> spp.	25–40	<i>Rattus exulans</i> , <i>R. tanezumi</i>	Population suppression	Wake Atoll, Tropical Pacific	Carlton & Hodder, 2003

¹Referred to as *Gecarcinus planatus* before 2008.

($F = 28.01$, $p < 0.001$) and season (higher in wet season) ($F = 15.05$, $p < 0.001$). However, Tukey comparisons confirmed that the increase during wet seasons was significant only on two islands (Isabel and Muertos).

Given the differences between seasons on some islands, trends in land crab abundance between pre and post eradication periods was evaluated only for wet seasons. The linear model confirmed that land crab densities (pooling species) are significantly higher ($R^2 = 0.19$, $F = 30.27$, $p < 0.001$) post-eradication (1–5 years later) on all islands, except on Cayo Norte and Pérez where the increase was not significant. On Isabel Island, the smallest burrowing crab (*G. quadratus*) showed a substantial trend of increase over a period of five years after the rat eradication (Fig. 4).

DISCUSSION

Land crabs and rodent eradications

Interference by land crabs remains poorly understood, documented and managed, despite its significant impact on rodent eradication operations on tropical islands. It appears that inconsistent application of recommended practices

(Wegmann, 2008; PII, 2011; Keitt, et al., 2015) continues across projects (Broome, 2011), e.g. a lack of estimating land crab densities and undertaking consumption trials to inform baiting rates. Without determining how significant the land crab problem is on an island and how it fluctuates with seasons, managers tend to automatically apply a mitigation strategy of high bait application rates.

However, the use of high bait rates increases the cost of operations, adds logistical complexity and, if unnecessarily high, potentially increases the risk to non-target vertebrates (Pitt, et al., 2015) (as invertebrates are not susceptible to anticoagulants (Broome, et al., 2012)). The highest total bait rate used in a rodent eradication to date was 186 kg/ha on Palmyra Atoll (Wegmann, et al., 2012). This high bait rate (spread over two applications) was determined and approved on the basis of sound field studies (Wegmann, et al., 2008; Wegmann, et al., 2011) as it had been demonstrated that the diverse and abundant land crab community represented a significant bait ‘sink’, warranting drastic mitigation measures. Importantly, Palmyra has an exceptionally wet climate and this eradication case is an outlier, as the second highest bait rate used to date is 94.2 kg/ha for the eradication of *R. exulans* on two Gambier

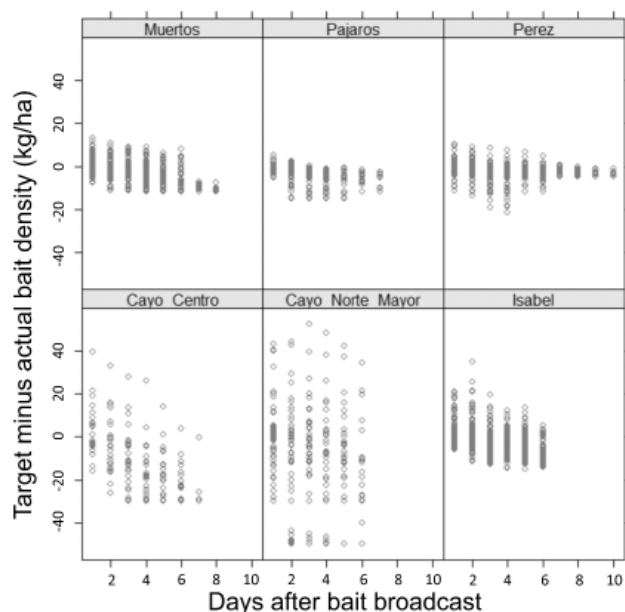


Fig. 3 Bait availability days after hand or aerial broadcast during six rodent eradications on Mexican islands.

islets (Kamaka and Makaroa)(Appendix 1). In addition, the largest rat eradication on a rainforest island (539 ha Cayo Centro, Banco Chinchorro), where large land crabs are abundant, was successful using 60 kg/ha over two applications (Samaniego-Herrera, et al., 2018). Moreover, there have been several instances where managers reported that the bait rates used were higher than required based on their observations of bait availability 5–15 days post bait application, which also coincided with ‘fewer land crabs than expected’ (Steve Cranwell, Araceli Samaniego, Elenoa Seniloli, pers. comm.). Studies (Samaniego-Herrera, et al., 2014; Samaniego-Herrera, et al., 2018) have shown that temporal land crab interference can vary substantially even on rainforest islands, the lowest peaks of activity being over the driest months. Thus, timing the eradication operation to coincide with the driest conditions of the year is recommended, particularly on islands with high abundance of burrowing crabs. Unquestionably, land crab activity is only one of the many factors that must be taken into account while planning an eradication (PII, 2011), so this has to be done in tandem with the other components, for example, minimising operational risks and the potential lethality to non-target species. Land crab interference with bait stations was outside the scope of this paper, but it is certainly a problem (Wegmann, 2008).

In addition to land crab abundance, land crab species composition also affects bait uptake. Burrowing land crabs, in particular large species (e.g. genera *Cardisoma*, *Johngarthia* and *Discoplax*), are generally the most problematic, although coconut crabs (*B. latro*) can be as troublesome even though they are usually in low to medium abundances. This has been reflected in the tendency to use higher bait rates on islands with abundant burrowing crabs, and confirmed by our case study where bait availability was quantified. Hermit crabs appear to be more widespread globally, so they may cause less interference on individual islands but affect more islands overall. Note that burrowing crabs, although larger, are more elusive than hermits due to their propensity to burrow or seek shelter under rocks or leaf litter during the day (Bliss, et al., 1978). Species richness of land crabs per island is likely to be generally underestimated. On the few islands for which comprehensive inventories exist (e.g. Christmas Island, Seychelles or French Polynesia), a list of 5–12 species of land crabs is common (Orchard, 2012), which is

higher when compared to the three or fewer species usually recorded by eradication managers.

At present, bait uptake trials (e.g. Pott, et al., 2015) are the best way to predict bait rates required for rodent eradication. However, if climatic conditions are not very similar during implementation, the ‘land crab scenario’ could be very different and significantly affect the bait consumption rate. In order to better predict the potential variability of bait uptake in the presence of certain land crab communities, future monitoring of climatic conditions and land crab communities on a suite of islands is required. Note that carnivorous and intertidal crabs may also consume bait (confirmed for ghost crabs, A. Barnaud pers. comm.), but due to their generally low abundance (probably due to vulnerability to rats) and/or limited distribution (coastal), they tend to be neglected. The implications for failed eradication attempts are important. Estimations of bait uptake rates may no longer be true if a second eradication attempt occurs within a few years of the first one, i.e. when crab populations are more abundant because rats haven’t had the time to fully recover and therefore haven’t again suppressed the land crabs.

Behaviours as well as consumption capabilities vary widely among groups and species, hence the importance of identifying species or at least type of crab (hermit, coconut, burrowing; Fig. 5). Hermit crabs are small and slow eaters and walkers compared to the average burrowing crab. They can take only one piece of bait at a time and they do not cache food. In contrast, most burrowing crabs are able to take up to three pieces of bait at a time (depending on crab size/species) and walk quickly to their burrow where they cache the bait (G. Harper & A. Samaniego pers. obs.). How much bait they can accumulate, how fast, and how long it takes for it to be eaten has not been determined.

Land crab activity is regulated by a combination of air and soil surface temperature, relative humidity, the intensity of insolation (solar radiation) and the availability of protective cover, be it leaf litter, suitable cavities, or soil for burrowing, which is further influenced by the soil compaction (Bliss, et al., 1978; Green, 1997; Brook, et al., 2009). The optimum temperature for land crab activity appears to be about 30°C, with virtually no activity below 18°C (Bliss, et al., 1978). Hence, in order to mitigate the desiccating effects of the high temperatures that crabs require to be active, their activity is largely restricted to periods and locations with high humidity. To reduce interference by land crabs, on ‘wet’ subtropical islands cooler months should be targeted for eradications.

The thermoregulatory abilities of hermit crabs (*Coenobita* spp.) are low, which is less of a problem where there is little temperature variation, as often occurs on wet tropical islands, but on arid islands they are essentially nocturnal (Achituv & Ziskind, 1985). Wind strength will also affect activity through increasing desiccation (Barnes, 1997). For burrowing crabs (e.g. *Gecarcinus* spp.) on seasonally arid islands, activity is dictated by relative humidity, with little or no activity below 77% RH, through to high activity above 95% RH (Bliss, et al., 1978; Green, 1997; Capistrán-Barradas, et al., 2003). Burrowing crabs probably occupy burrows to reduce their water loss. Often, unseasonal rain or even showers will initiate short periods of activity, but if conditions are very dry land crabs can remain underground for several months (Bliss, et al., 1978).

The effects of humidity and insolation on land crab activity strongly suggest nocturnal land crab monitoring will detect the highest crab activity and species diversity, particularly if all habitats are sampled and the season is taken into account. Land crabs are long-lived species, so monitoring tends to indicate how many land crabs are active at that time, not how many are actually present.

Table 5 Significant parameters in relation to bait availability after rodent eradications, according to linear mixed models for six rodent eradications on Mexican tropical islands.

	Value	Std Error	DF	t-value	p-value
Day	-1.456	0.275	2768	-5.287	> 0.001
Period	4.204	1.014	2768	4.142	> 0.001
Bait application	-4.658	1.056	2768	-4.407	> 0.001
Day × Burrowing	-2.343	0.262	2768	-8.914	> 0.001
Day × Hermit	-1.135	0.338	2768	-3.357	> 0.001
Day × Period	-0.896	0.254	2768	-3.521	> 0.001
Day × Bait application	1.115	0.275	2768	4.050	> 0.001
Hermit × Bait application	6.912	1.610	2768	4.291	> 0.001
Day × Rodent	-0.019	0.005	2768	-3.725	> 0.001
Day × Burrowing × Bait application	1.672	0.431	2768	3.875	> 0.001

Rodent impacts on land crabs

Except for New Zealand, little has been documented regarding impacts of invasive rodents on island invertebrates in general (St Clair, 2011). Furthermore, few land crab accounts exist, due to the limited research conducted in the tropics (Brook, et al., 2009) and the low proportion of rodent eradications carried out in this region (Howald, et al., 2007; Holmes, et al., 2015). Our list of land crab species impacted by rodents is most likely to be severely under-reported as Rodentia comprise over a quarter of terrestrial mammal species known to forage on intertidal food sources. Burrowing crabs make up a substantial proportion of this and the number of species is highly likely to be an underestimation (Carlton & Hodder, 2003).

Adding to the impacts of invasive rodent predation on a wide range of plants and animals (Carlton & Hodder, 2003; St Clair, 2011; Sunde, 2012; Harper & Bunbury, 2015), the suppression of native ecosystem engineers, such as land crabs, by rats and other invasive species such as ants, cats and dogs, could have significant and enduring consequences on relatively simple island ecosystems (Carlton & Hodder, 2003; O'Dowd, et al., 2003). Land crabs are often the largest invertebrates on tropical islands, and particularly atolls, and will occupy the niches of vertebrates on small oceanic islands (Burggren & McMahon, 1988). They are highly integrated in the ecosystem energetics of tropical islands, as they control recruitment and species composition of

seedlings on the forest floor (Green, et al., 1999; Lindquist & Carroll, 2004). They also regulate nutrient dynamics through substantial leaf litter consumption (Kellman & Delfosse, 1993; Capistrán-Barradas, et al., 2003; Gutiérrez & Jones, 2006; Gutiérrez, et al., 2006). Hence, they may govern the growth and productivity of tropical forests (Lindquist, et al., 2009) and sustain diversity at large scales (Young, et al., 2013; Nigro, et al., 2017). Moreover, plant composition will be influenced by soil structure, which is affected by land crab activity through inland transfer of marine debris and shells, removal of algae from rock surfaces subsequently deposited as faeces, and by increasing leaf litter breakdown through deposition underground in burrows. Given the critical role land crabs play in island ecosystems, it is recommended that these are included as outcome indicators and monitored post-eradication.

CONCLUSION

Land crabs are a diverse group. For management purposes, it is useful to distinguish three groups: hermit crabs, coconut crabs and burrowing crabs, noting the latter vary widely in size. The ecology and climatic tolerances of each group is different, as is their capacity as bait consumers. Assessing species richness and abundance of land crabs should be a priority in the planning phase of rodent eradication projects in the tropics, so that their interference can be efficiently managed during eradications. Similarly, changes to the land crab community should be measured

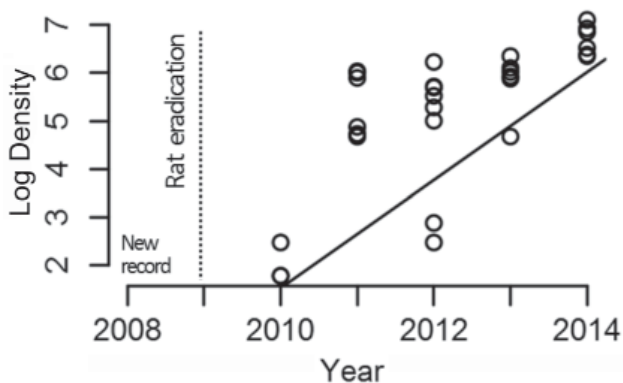


Fig. 4 Population increase of *Gecarcinus quadratus* on Isabel Island, Mexico after the ship rat eradication in 2009. The single record in 2008 was a new record for the island.

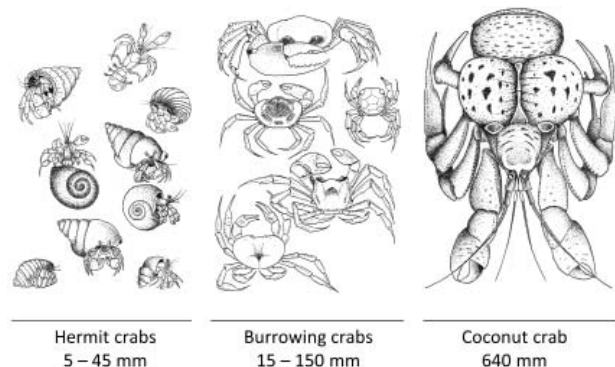


Fig. 5 Types of land crabs in relation to potential interference with rodent eradications on tropical islands. Sizes refer to the range of mean size across species.

post-eradication as indicators of ecosystem recovery. Once enough data are gathered regarding bait consumption in a standardised manner, we will improve our ability to predict appropriate bait rates for the eradication of invasive rodents on different types of tropical islands, as is currently done for temperate islands. Where compatible with other factors (e.g. non-target species and human activities), rodent eradications on tropical islands should be timed for the driest conditions or alternatively on 'wet' subtropical islands, the coolest months.

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REFERENCES

- Achituv, Y. and Ziskind, M. (1985). 'Adaptation of *Coenobita scaevola* (Forskål, 1775) (Crustacea, Anomura) to terrestrial life in desert-bordered shore line'. *Marine Ecology Progress Series* 25: 189–197.
- Athens, J.S., Tuggle, H.D., Welch, D.J. and Ward, J.V. (2002). 'Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawaii'. *Archaeology in Oceania* 37(2): 57.
- Atkinson, I.A.E. (1985). 'The spread of commensal species of *Rattus* to oceanic islands and their effect on island avifaunas'. In: P.J. Moors (ed.) *Conservation of Island Birds*. pp. 35–81. Cambridge: International Council for Bird Preservation.
- Barnes, D.K. (1997). 'Ecology of tropical hermit crabs at Quirimba Island, Mozambique: Distribution, abundance and activity'. *Marine Ecology Progress Series* 154: 133–142.
- Bellard, C., Cassey, P. and Blackburn, T.M. (2016). 'Alien species as a driver of recent extinctions'. *Biology Letters* 12(2): 20150623.
- Bliss, D.E., Van Montfrans, J., Van Montfrans, M. and Boyer, J.R. (1978). 'Behavior and growth of the land crab *Gecarcinus lateralis* (Fremerville) in southern Florida'. *Bulletin of the American Museum of Natural History* 160(11): 111–152.
- Brook, S., Grant, A. and Bell, D. (2009). 'Can land crabs be used as a rapid ecosystem evaluation tool? A test using distribution and abundance of several genera from the Seychelles'. *Acta Oecologica* 35(5): 711–719.
- Broome, K. (2011). 'Transferring rodent eradication success from temperate regions into the tropical Pacific – What do we need to learn?'. *PII News*. Auckland: Pacific Invasives Initiative.
- Broome, K.G., Fairweather, A.A.C. and Fisher, P. (2012). *Brodifacoum Pesticide Information Review. Version 2012/1*. Hamilton, New Zealand: New Zealand Department of Conservation.
- Broome, K.G., Cox, A., Golding, C., Cromarty, P., Bell, P. and McClelland, P. (2014). *Rat Eradication Using Aerial Baiting: Current Agreed Best Practice Used in New Zealand (Version 3.0)*. Wellington, New Zealand: New Zealand Department of Conservation.
- Burggren, W.W. and McMahon, B.R. (1988). *Biology of the Land Crabs*. Cambridge, Cambridge University Press.
- Capistrán-Barradas, A., Defeo, O. and Moreno-Casasola, P. (2003). 'Density and population structure of the red land crab *Gecarcinus lateralis* in a tropical semi-deciduous forest in Veracruz, Mexico'. *Interciencia* 28(6): 323–327.
- Carlton, J.T. and Hodder, J. (2003). 'Maritime mammals: Terrestrial mammals as consumers in marine intertidal communities'. *Marine Ecology Progress Series* 256: 271–286.
- Croll, D.A., Newton, K.M., McKown, M., Holmes, N., Williams, J.C., Young, H.S., Buckelew, S., Wolf, C.A., Howald, G., Bock, M.F., Curl, J.A. and Tershy, B.R. (2016). 'Passive recovery of an island bird community after rodent eradication'. *Biological Invasions* 18(3): 703–715.
- DIISE (2016). *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. <<http://diise.islandconservation.org>>.
- Green, P.T. (1997). 'Red crabs in rain forest on Christmas Island, Indian Ocean: Activity patterns, density and biomass'. *Journal of Tropical Ecology* 13(1): 17–38.
- Green, P.T., Lake, P.S. and O'Dowd, D.J. (1999). 'Monopolization of litter processing by a dominant land crab on a tropical oceanic island'. *Oecologia* 119(3): 435–444.
- Green, P.T., O'Dowd, D.J. and Lake, P.S. (2008). 'Recruitment dynamics in a rainforest seedling community: Context-independent impact of a keystone consumer'. *Oecologia* 156(2): 373–385.
- Griffiths, R., Miller, A. and Climo, G. (2011). 'Addressing the impact of litter processing by a dominant land crab on a tropical oceanic island'. *Biology* 17(4): 347–353.
- Gutiérrez, J.L. and Jones, C.G. (2006). 'Physical ecosystem engineers as agents of biogeochemical heterogeneity'. *Bioscience* 56(3): 227–236.
- Gutiérrez, J.L., Jones, C.G., Groffman, P.M., Findlay, S.E.G., Iribarne, O.O., Ribeiro, P.D. and Bruschetti, C.M. (2006). 'The contribution of crab burrow excavation to carbon availability in surficial salt-marsh sediments'. *Ecosystems* 9(4): 647–658.
- Harper, G.A. and Bunbury, N. (2015). 'Invasive rats on tropical islands: Their population biology and impacts on native species'. *Global Ecology and Conservation* 3: 607–627.
- Hilton, G.M. and Cuthbert, R.J. (2010). 'The catastrophic impact of invasive mammalian predators on birds of the UK Overseas Territories: A review and synthesis'. *Ibis* 152(3): 443–458.
- Holmes, N.D., Griffiths, R., Pott, M., Alifano, A., Will, D., Wegmann, A.S. and Russell, J.C. (2015). 'Factors associated with rodent eradication failure'. *Biological Conservation* 185: 8–16.
- Howald, G., Donlan, C.J., Galván, J.P., Russell, J.C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pascal, M., Saunders, A. and Tershy, B. (2007). 'Invasive rodent eradication on islands'. *Conservation Biology* 21(5): 1258–1268.
- Jones, H.P., Holmes, N.D., Butchart, S.H.M., Tershy, B.R., Kappes, P.J., Corkery, I., Aguirre-Muñoz, A., Armstrong, D.P., Bonnaud, E., Burbidge, A.A., Campbell, K., Courchamp, F., Cowan, P.E., Cuthbert, R.J., Ebbert, S., Genovesi, P., Howald, G.R., Keitt, B.S., Kress, S.W., Miskelly, C.M., Opper, S., Poncet, S., Rauzon, M.J., Rocamora, G., Russell, J.C., Samaniego-Herrera, A., Seddon, P.J., Spatz, D.R., Towns, D.R. and Croll, D.A. (2016). 'Invasive mammal eradication on islands results in substantial conservation gains'. *Proceedings of the National Academy of Sciences* 113(15): 4033–4038.
- Keitt, B., Griffiths, R., Boudjelas, S., Broome, K., Cranwell, S., Millett, J., Pitt, W. and Samaniego-Herrera, A. (2015). 'Best practice guidelines for rat eradication on tropical islands'. *Biological Conservation* 185: 17–26.
- Kellman, M. and Delfosse, B. (1993). 'Effect of the red land crab (*Gecarcinus lateralis*) on leaf litter in a tropical dry forest in Veracruz, Mexico'. *Journal of Tropical Ecology* 9(1): 55–65.
- Le Corre, M., Danckwerts, D.K., Ringler, D., Bastien, M., Orłowski, S., Morey Rubio, C., Pinaud, D. and Micol, T. (2015). 'Seabird recovery and vegetation dynamics after Norway rat eradication at Tromelin Island, western Indian Ocean'. *Biological Conservation* 185: 85–94.
- Lindquist, E.S. and Carroll, C.R. (2004). 'Differential seed and seedling predation by crabs: Impacts on tropical coastal forest composition'. *Oecologia* 141(4): 661–671.
- Lindquist, E.S., Krauss, K.W., Green, P.T., O'Dowd, D.J., Sherman, P.M. and Smith, T.J. (2009). 'Land crabs as key drivers in tropical coastal forest recruitment'. *Biological Reviews* 84(2): 203–223.
- McLaughlin, P.A., Komai, T., Lemaitre, R. and Rahayu, D.L. (2010). 'Annotated checklist of anomuran decapod crustaceans of the world (exclusive of the Kiwaoidea and families Chirostylidae and Galatheidae of the Galatheoidea) Part I – Lithodoidea, Lomisoidea and Paguroidea'. *The Raffles Bulletin of Zoology* 23(1): 131–137.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A.B. and Kent, J. (2000). 'Biodiversity hotspots for conservation priorities'. *Nature* 403(6772): 853–858.
- Ng, P.K.L., Guinot, D. and Davie, P.J.F. (2008). 'Systema Brachyurorum: Part 1. An annotated checklist of extant brachyuran crabs of the world'. *The Raffles Bulletin of Zoology* 17: 1–286.
- Nigro, K.M., Hathaway, S.A., Wegmann, A.S., Miller-ter Kuile, A., Fisher, R.N. and Young, H.S. (2017). 'Stable isotope analysis as an early monitoring tool for community-scale effects of rat eradication'. *Restoration Ecology* 10.1111/rec.12511.

- O'Dowd, D.J., Green, P.T. and Lake, P.S. (2003). 'Invasional 'meltdown' on an oceanic island'. *Ecology Letters* 6(9): 812–817.
- Orchard, M. (2012). *Crabs of Christmas Island*, Christmas Island Natural History Association.
- Paine, R.T. (1966). 'Food web complexity and species diversity'. *American Naturalist* 100(910): 65–75.
- Pascal, M., Brithmer, R., Lorgele, O. and Vennart, N. (2004). 'Conséquences sur l'avifaune nicheuse de la réserve naturelle des Îlets De Sainte-Anne (Martinique) de la récente invasion du rat noir (*Rattus rattus*), établies à l'issue d'une tentative d'éradication'. *Revue d'écologie* 59(1–2): 309–318.
- Paulay, G. and Starmer, J. (2011). 'Evolution, insular restriction, and extinction of oceanic land crabs, exemplified by the loss of an endemic *Geograpsus* in the Hawaiian Islands'. *PLOS ONE* 6(5): e19916.
- PII. (2011). *Resource Kit for Rodent and Cat Eradication*. Pacific Invasives Initiative. <<http://pacificinvasivesinitiative.org/rce/index.html>>. [Accessed January 2017].
- Pitman, R.L., Ballance, L.T. and Bost, C. (2005). 'Clipperton Island: Pig sty, rat hole and booby prize'. *Marine Ornithology* 33: 193–194.
- Pitt, W.C., Berentsen, A.R., Shiels, A.B., Volker, S.F., Eisemann, J.D., Wegmann, A.S. and Howald, G.R. (2015). 'Non-target species mortality and the measurement of brodifacoum rodenticide residues after a rat (*Rattus rattus*) eradication on Palmyra Atoll, tropical Pacific'. *Biological Conservation* 185: 36–46.
- Pott, M., Wegmann, A.S., Griffiths, R., Samaniego-Herrera, A., Cuthbert, R.J., Brooke, M.d.L., Pitt, W.C., Berentsen, A.R., Holmes, N.D., Howald, G.R., Ramos-Rendón, K. and Russell, J.C. (2015). 'Improving the odds: Assessing bait availability before rodent eradications to aid in selecting bait application rates'. *Biological Conservation* 185: 27–35.
- Russell, J.C., Caut, S., Anderson, S.H. and Lee, M. (2015). 'Invasive rat interactions and over-invasion on a coral atoll'. *Biological Conservation* 185: 59–65.
- Russell, J.C. and Holmes, N.D. (2015). 'Tropical island conservation: Rat eradication for species recovery'. *Biological Conservation* 185: 1–7.
- Russell, J.C., Meyer, J.-Y., Holmes, N.D. and Pagad, S. (2017). 'Invasive alien species on islands: Impacts, distribution, interactions and management'. *Environmental Conservation* 10.1017/S0376892917000297.
- Samaniego-Herrera, A. (2014). 'Ecology and Impacts of Invasive Rodents on Tropical Islands, in Relation to Eradication Operations'. PhD thesis. Auckland: The University of Auckland.
- Samaniego-Herrera, A., Aguirre-Muñoz, A., Rodríguez-Malagón, M., González-Gómez, R., Torres-García, F., Méndez-Sánchez, F., Félix-Lizárraga, M. and Latofski-Robles, M. (2011). 'Rodent eradications on Mexican islands: Advances and challenges'. In: C.R. Veitch, M.N. Clout and D.R. Towns (eds.) *Island invasives: eradication and management*, pp. 350–355. Occasional Paper SSC no. 42. Gland, Switzerland: IUCN and Auckland, New Zealand: CBB.
- Samaniego-Herrera, A. and Bedolla-Guzmán, Y. (2012). 'Land crabs (Decapoda, Brachyura, Gecarcinidae) on Isabel Island, Mexico, including a new record, and its relation to the removal of invasive rats'. *Crustaceana* 85(8): 1007–1011.
- Samaniego-Herrera, A., Anderson, D.P., Parkes, J.P. and Aguirre-Muñoz, A. (2013). 'Rapid assessment of rat eradication after aerial baiting'. *Journal of Applied Ecology* 50(6): 1415–1421.
- Samaniego-Herrera, A., Russell, J.C., Choquenot, D., Aguirre-Muñoz, A. and Clout, M. (2014). 'Invasive rodents on tropical islands: eradication recommendations from Mexico'. In: R.M. Timm and J.M. O'Brien (eds.) *Proceedings of the 26th Vertebrate Pest Conference*, pp. 43–50. Davis: University of California.
- Samaniego-Herrera, A., Clout, M.N., Aguirre-Muñoz, A. and Russell, J.C. (2017). 'Rodent eradications as ecosystem experiments: A case study from the Mexican tropics'. *Biological Invasions* 19(6): 1761–1779.
- Samaniego-Herrera, A., Aguirre-Muñoz, A., Bedolla-Guzmán, Y., Cárdenas-Tapia, A., Félix-Lizárraga, M., Méndez-Sánchez, F., Reina-Ponce, O., Rojas-Mayoral, E. and Torres-García, F. (2018). 'Eradicating invasive rodents from wet and dry tropical islands in Mexico'. *Oryx* 52: 559–570.
- Sherman, P.M. (2002). 'Effects of land crabs on seedling densities and distributions in a mainland neotropical rain forest'. *Journal of Tropical Ecology* 18(1): 67–89.
- Sherman, P.M. (2006). 'Influence of land crabs *Gecarcinus quadratus* (Gecarcinidae) on distributions of organic carbon and roots in a Costa Rican rain forest'. *Revista de Biología Tropical* 54(1): 149–161.
- Shih, H.-T., Ng, P.K., Davie, P.J., Schubart, C.D., Türkay, M., Naderloo, R., Jones, D. and Liu, M.-Y. (2016). 'Systematics of the family Ocypodidae Rafinesque, 1815 (Crustacea: Brachyura), based on phylogenetic relationships, with a reorganization of subfamily rankings and a review of the taxonomic status of *Uca* Leach, 1814, sensu lato and its subgenera'. *The Raffles Bulletin of Zoology* 64: 139–175.
- St Clair, J.J.H. (2011). 'The impacts of invasive rodents on island invertebrates'. *Biological Conservation* 144(1): 68–81.
- Sunde, F.G. (2012). 'The Effects of Rats on Rocky Intertidal Ecosystems in Northeastern New Zealand'. MSc thesis. Auckland: University of Auckland.
- Towns, D.R., Atkinson, I.A.E. and Daugherty, C.H. (2006). 'Have the harmful effects of introduced rats on islands been exaggerated?'. *Biological Invasions* 8(4): 863–891.
- Towns, D.R., West, C.J. and Broome, K.G. (2013). 'Purposes, outcomes and challenges of eradicating invasive mammals from New Zealand islands: An historical perspective'. *Wildlife Research* 40(2): 94–107.
- Wegmann, A.S. (2008). *Land Crab Interference with Eradication Projects: Phase I – Compendium of Available Information*. Auckland: Pacific Invasives Initiative.
- Wegmann, A.S., Helm, J., Jacobs, B., Samaniego, A., Smith, W., Drake, D., Fisher, R., Hathaway, S., Henry, A., Smith, J. and McKown, M. (2008). *Palmyra Atoll Rat Eradication: Biomarker Validation of an Effective Bait Application Rate*. Technical Field Report. Santa Cruz, California: Island Conservation.
- Wegmann, A.S., Buckelew, S., Howald, G., Helm, J. and Swinerton, K. (2011). 'Rat eradication campaigns on tropical islands: Novel challenges and possible solutions'. In: C.R. Veitch, M.N. Clout and D.R. Towns (eds.) *Island invasives: eradication and management*, pp. 239–243. Occasional Paper SSC no. 42. Gland, Switzerland: IUCN and Auckland, New Zealand: CBB.
- Wegmann, A.S., Flint, E., White, S., Fox, M., Howald, G., McClelland, P., Alifano, A. and Griffiths, R. (2012). 'Pushing the envelope in paradise: A novel approach to rat eradication at Palmyra Atoll'. In: R.M. Timm (ed.) *25th Vertebrate Pest Conference*, pp. 48–53. Davis: University of California.
- Weigelt, P., Jetz, W. and Kreft, H. (2013). 'Bioclimatic and physical characterization of the world's islands'. *Proceedings of the National Academy of Sciences* 110(38): 15307–15312.
- Young, H.S., McCauley, D.J., Guevara, R. and Dirzo, R. (2013). 'Consumer preference for seeds and seedlings of rare species impacts tree diversity at multiple scales'. *Oecologia* 172(3): 857–867.

Appendix 1. Details of rodent eradications on tropical islands with land crabs, up to 2015, conducted either by aerial broadcast (Aerial) or hand broadcast (Hand); Hand* = bait piles on the ground on a grid) of bait. Target species: Mm = *Mus musculus*, Re = *Rattus exulans*, Rn = *Rattus norvegicus*, Rt = *Rattus tanezumii*; Eradication result: F = failure, S = success; Bait type: 20R = Pestoff 20R, 25D = Bell-25D, 25W = Bell-25W; Crab genera: Bi = *Birgus*, Ca = *Cardisoma*, Co = *Coenobita*, Ge = *Gecarcinus*, Gd = *Gecarcoidea*, Gg = *Geograpsus*, Jo = *Johnngartia*, Oc = *Ocypode*. ¹During the eradication; ²Observed by project managers throughout the project.

Country/ territory	Island	Area (ha)	Target species	Erad. year	Erad. season	Erad. result	Erad. method	Total bait rate (kg/ ha)	Bait type	Island type	Main interference	Burrowing crab density ¹	Hermit crab density ¹	Coconut crab density ¹	Land crab genera ²
Bahamas	Allen Cay	6.9	Mm	2012	Dry	S	Hand	40	25D	Savanna	Hermit	Low	Low	None	Ca, Co, Ge
Cook Islands	Anchorage	12.8	Re	2012	Wet	S	Hand	20	20R	Seasonal	Hermit	Medium	Medium	Medium	Bi, Ca, Co, Oc
Cook Islands	Motu Kena	1.2	Re	2012	Wet	S	Hand	20	20R	Seasonal	Hermit	Medium	Medium	Low	Bi, Ca, Co, Oc
Cook Islands	Motu Kena-iti	0.7	Re	2012	Wet	S	Hand	20	20R	Seasonal	Hermit	Low	Medium	Medium	Bi, Ca, Co, Oc
Cook Islands	Motu Tou	14.7	Re	2012	Wet	F	Hand	20	20R	Seasonal	Hermit	Medium	Medium	High	Bi, Ca, Co, Oc
Fiji	Mabualau	3.2	Re	2008	Dry	S	Hand	26	20R	Seasonal	Hermit	High	High	None	Ca, Co
Fiji	Nukubasaga	18.0	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	Low	Bi, Co
Fiji	Nukupureti	3.0	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	None	Co
Fiji	Nukusemanu	1.6	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	None	Co
Fiji	Qelelevu	147.0	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	High	Bi, Co
Fiji	Tauraria	49.3	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	Low	Bi, Co
Fiji	Tumbeka	2.9	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	Low	Bi, Co
Fiji	Vátu-i-Ra	2.0	Re	2006	Dry	S	Hand	26	20R	Seasonal	Hermit	Low	Medium	None	Co
Fiji	Vetaua	35.0	Re	2008	Dry	S	Aerial	25	20R	Seasonal	Hermit	Low	Medium	High	Bi, Co
French Polynesia	Hiuveru	3.2	Rr	2008	Wet	F	Hand	15	20R	Seasonal	Hermit	Low	Low	None	Co
French Polynesia	Hiveu	4.7	Rr	2008	Wet	F	Hand	15	20R	Seasonal	Hermit	Low	Low	None	Co
French Polynesia	Kamaka	47.6	Re	2015	Dry	F	Aerial	94.2	25W	Rainforest	Hermit	Low	Medium	None	Co, Gg
French Polynesia	Makapu	11.2	Re	2003	Dry	S	Hand	4	20R	Rainforest	Hermit	Low	Medium	None	Co
French Polynesia	Makaroo	16.4	Re	2015	Dry	S	Aerial	94.2	25W	Rainforest	Hermit	Low	Medium	None	Co, Gg
French Polynesia	Mekiro	11.5	Re	2003	Dry	F	Hand	4	20R	Rainforest	Hermit	Low	Medium	None	Co
French Polynesia	Motu-o-ari	4.5	Re	2003	Dry	F	Hand	3	20R	Rainforest	Hermit	Low	High	None	Co
French Polynesia	Teauaone	8.8	Re	2003	Dry	F	Hand	3	20R	Rainforest	Hermit	Low	High	None	Co
French Polynesia	Temoe	430.8	Re	2015	Dry	S	Aerial	87.6	25W	Seasonal	Hermit	None	High	None	Co
French Polynesia	Tenarunga	424.0	Re	2015	NA	S	Aerial	72.6	25W	Seasonal	Hermit	None	Medium	None	Co
French Polynesia	Tenarunga	424.0	Rr	2015	NA	S	Aerial	72.6	25W	Seasonal	Hermit	None	Medium	None	Co
French Polynesia	Tepapuri	26.0	Re	2003	Dry	F	Hand	3	20R	Rainforest	Hermit	Low	High	None	Co
French Polynesia	Tiarao	4.2	Rr	2008	Wet	F	Hand	15	20R	Seasonal	Hermit	Low	Low	None	Co, Ge

Appendix 1 (continued) Details of rodent eradications on tropical islands with land crabs, up to 2015, conducted either by aerial broadcast (Aerial) or hand broadcast (Hand; Hand* = bait piles on the ground on a grid) of bait. Target species: Mm = *Mus musculus*, Fe = *Rattus exulans*, Rn = *Rattus norvegicus*, Rr = *Rattus rattus*, Rt = *Rattus tanezumi*; Eradication result: F = failure, S = success; Bait type: 20R = Pestoff 20R, 25D = Bell-25D, 25W = Bell-25W; Crab genera: Bi = *Birgus*, Ca = *Cardisoma*, Co = *Coenobita*, Ge = *Gecarcinus*, Gd = *Gecarcoidea*, Gg = *Geograpsus*, Jo = *Johngartia*, Oc = *Ocypode*. ¹During the eradication; ²Observed by project managers throughout the project.

Country/ territory	Island	Area (ha)	Target species	Erad. year	Erad. season	Erad. result	Erad. method	Total bait rate (kg/ ha)	Bait type	Island type	Main interference	Burrowing crab density ¹	Hermit crab density ¹	Coconut crab density ¹	Land crab genera ²
French Polynesia	Toreauta	5.3	Rr	2011	Dry	S	Hand	27.3	25W	Seasonal	Hermit	Low	Low	Low	Bi, Co, Gg
French Polynesia	Vahanga	380.0	Re	2015	NA	S	Aerial	72.4	25W	Seasonal	Hermit	Low	Medium	Low	Co, Ca?
Kiribati	Big Ambo	1.4	Re	2009	Dry	S	Hand	14.3	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Big Fred/Tonga	3.5	Re	2009	Dry	S	Hand	22.8	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Big Nimroona	6.5	Re	2009	Dry	S	Hand	19.2	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Big Tibo	3.8	Re	2012	Dry	S	Hand	12.5	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Bimie	49.4	Re	2011	Dry	S	Aerial	51	20R	Savanna	Hermit	Low	High	None	Ca, Co
Kiribati	Drum	6.1	Re	2009	Dry	S	Hand	22.15	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	E isle	0.8	Re	2009	Dry	S	Hand	13.3	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	East Drum	1.0	Re	2009	Dry	S	Hand	15	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Enderbury	608.0	Re	2011	Dry	F	Aerial	38.4	20R	Savanna	Hermit	Low	High	None	Bi, Ca, Co, Gg
Kiribati	Isles Lagoon 13	1.2	Re	2009	Dry	S	Hand	16.6	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 16	4.1	Re	2009	Dry	S	Hand	13.9	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 2	1.4	Re	2009	Dry	S	Hand	17.1	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 21	1.2	Re	2009	Dry	S	Hand	16.6	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 22	1.5	Re	2009	Dry	S	Hand	14.6	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 23	0.1	Re	2009	Dry	S	Hand	10	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 3	0.5	Re	2009	Dry	S	Hand	20	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 4	1.4	Re	2009	Dry	S	Hand	10	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	Isles Lagoon 5	0.3	Re	2009	Dry	S	Hand	20	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	McKean	27.0	Rt	2008	Dry	S	Hand	62.8	20R	Savanna	Hermit	Low	High	None	Ca, Co
Kiribati	North Drum	2.5	Re	2009	Dry	S	Hand	24	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	NW Fred/Tonga	1.3	Re	2009	Dry	S	Hand	26.9	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	NW Nimroona	0.6	Re	2009	Dry	S	Hand	33.2	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	NW Tibo	0.8	Re	2009	Dry	S	Hand	12.5	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	SE Fred/Tonga	0.8	Re	2009	Dry	S	Hand	22.5	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	SW Islet Koil	0.1	Re	2009	Dry	S	Hand	8	20R	Savanna	None	Low	None	None	Ca?, Oc?
Kiribati	SW motu Koil	3.0	Re	2009	Dry	S	Hand	10	20R	Savanna	None	Low	None	None	Ca?, Oc?

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Country/ territory	Island	Area (ha)	Target species	Erad. year	Erad. season	Erad. result	Erad. method	Total bait rate (kg/ ha)	Bait type	Island type	Main interference	Burrowing crab density ¹	Hermit crab density ¹	Coconut crab density ¹	Land crab genera ²
Kiribati	SW Nimroona	3.9	Re	2009	Dry	S	Hand	22.6	20R	Savanna	None	Low	None	None	Ca?, Oc?
Mauritius	Flat	249.6	Rr	1998	Dry	S	Hand	15	20R	Seasonal	Hermit	Low	High	None	Ca, Co
Mauritius	Flat	249.6	Mm	1998	Dry	S	Hand	15	20R	Seasonal	Hermit	Low	High	None	Ca, Co
Mauritius	Gabriel	40.5	Rr	1995	Dry	S	Hand	20	20R	Seasonal	Hermit	High	High	None	Ca, Co
Mauritius	Gunner's Quoin	65.0	Rn	1995	Dry	S	Hand	15	20R	Seasonal	Hermit	Low	Low	None	Ca, Co
Mexico	Cayo Centro	539.0	Rr	2015	Dry	S	Aerial	60	25W	Rainforest	Burrowing	Medium	Low	None	Ca, Co, Ge
Mexico	Cayo Norte Mayor	29.0	Rr	2012	Dry	S	Aerial	42	25W	Rainforest	Burrowing	Medium	Low	None	Ca, Co, Ge
Mexico	Cayo Norte Menor	15.0	Rr	2012	Dry	S	Aerial	42	25W	Rainforest	Burrowing	Medium	Low	None	Ca, Co, Ge
Mexico	Isabel	82.0	Rr	2009	Dry	S	Aerial	20	25D	Seasonal	Hermit	Low	Low	None	Co, Ge, Jo
Mexico	Muertos	15.0	Mm	2011	Dry	S	Hand	17	25D	Savanna	Burrowing	Medium	Low	None	Co, Ge
Mexico	Pájaros	3.0	Mm	2011	Dry	S	Hand	17	25D	Savanna	Hermit	Low	High	None	Co, Ge
Mexico	Pérez	14.0	Rr	2011	Dry	S	Hand	17	25D	Savanna	Hermit	Low	High	None	Co, Ge
Micronesia	Dekehtik	2.6	Re	2007	Dry	S	Hand	50	25W	Rainforest	Burrowing	High	High	Low	Bi, Ca, Co
Micronesia	Pein Mal	2.2	Rr	2007	Dry	S	Hand	50	25W	Rainforest	Burrowing	High	High	Low	Bi, Ca, Co
New Caledonia	Double	6.0	Re	2008	Dry	S	Hand	20	20R	Seasonal	None	None	Low	None	Co
New Caledonia	G'I	5.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Laregnere	0.5	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Mato	5.0	Rr	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Ndo	17.2	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Nge	7.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Redika	7.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Signal	6.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Table	11.5	Rr	2008	Dry	S	Hand	20	20R	Seasonal	None	None	Low	None	Co
New Caledonia	Tiam'bouene	17.0	Re	2008	Dry	S	Hand	20	20R	Seasonal	None	None	Low	None	Co
New Caledonia	Uatembé	1.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Uatio	5.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Uje	2.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
New Caledonia	Uo	3.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?

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Country/ territory	Island	Area (ha)	Target species	Erad. year	Erad. season	Erad. result	Erad. method	Total bait rate (kg/ ha)	Bait type	Island type	Main interference	Burrowing crab density [†]	Hermit crab density [†]	Coconut crab density [†]	Land crab genera [‡]
New Caledonia	Via	5.0	Re	1998	Dry	S	Hand*	14	20R	Seasonal	None	Low	Low	None	Co, Ge?
Palau	Fanna	35.0	Re	2009	Dry	F	Hand	50	20R	Rainforest	Burrowing	High	Low	Low	Bi, Co, Gd
Palau	Kayangel	112.0	Re	2011	Wet	F	Hand	25	20R	Rainforest	Hermit	Low	Low	None	Bi, Ca, Co
Pitcairn	Ducie	75.0	Re	1997	Dry	S	Hand	8	20R	Seasonal	Hermit	Low	High	None	Co
Pitcairn	Henderson	4,310.0	Re	2011	Dry	F	Aerial	16	20R	Seasonal	Hermit	Low	Medium	Low	Bi, Co
Pitcairn	Oeno	66.0	Re	1997	Dry	S	Hand	8	20R	Seasonal	Hermit	Low	High	Low	Co
Pitcairn	Pitcairn	476.1	Re	1998	Dry	F	Hand	8	20R	Seasonal	Hermit	Low	Low	Low	Co
Puerto Rico	Desecheo	116.0	Rr	2012	Dry	F	Aerial	26	25D	Savanna	Hermit	Low	High	None	Co, Ge
Seychelles	Conception	69.0	Rn	2007	Dry	S	Aerial	26.7	20R	Rainforest	Hermit	Low	Low	None	Co
Seychelles	Curieuse	289.0	Rr	2000	Dry	S	Aerial	23	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Curieuse	289.0	Mm	2000	Dry	F	Aerial	23	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Denis	133.0	Rr	2000	Dry	F	Aerial	23.6	20R	Rainforest	Hermit	Low	High	None	Co, Jo?
Seychelles	Denis	133.0	Mm	2000	Dry	F	Aerial	23.6	20R	Rainforest	Hermit	Low	High	None	Co, Jo?
Seychelles	Fregate	219.0	Mm	2000	Dry	S	Aerial	35	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Fregate	219.0	Rn	2000	Dry	S	Aerial	35	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Grande Ile	143.0	Rr	2007	Dry	S	Aerial	29.7	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Grande Polyte	21.0	Rr	2007	Dry	S	Aerial	29.7	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Grande Soeur	105.2	Rr	2010	Dry	S	Aerial	35.9	20R	Rainforest	Hermit	Low	Low	None	Co, Jo?
Seychelles	Ile aux Rats	1.0	Rr	2005	Wet	S	Hand	15	20R	Rainforest	Hermit	Low	Low	None	Co, Jo?
Seychelles	North	201.0	Rr	2003	Dry	S	Aerial	31	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	North	201.0	Rr	2005	Dry	S	Aerial	39.9	20R	Rainforest	Hermit	Low	Low	None	Co, Jo?
Seychelles	Petit Polyte	1.0	Rr	2007	Dry	S	Aerial	29.7	20R	Rainforest	Hermit	Low	Medium	None	Co, Jo?
Seychelles	Petite Soeur	48.0	Rr	2010	Dry	S	Aerial	32.1	20R	Rainforest	Hermit	Low	Low	None	Co, Jo?
US Islands	Palmyra	234.9	Rr	2011	Dry	S	Aerial	163	25D	Rainforest	Burrowing	High	High	Medium	Bi, Ca, Co
US Islands	Wake	696.0	Re	2012	Dry	F	Aerial	36	25D	Seasonal	Hermit	Low	Low	None	Ca, Co
US Islands	Wake	696.0	Rt	2012	Dry	S	Aerial	36	25D	Seasonal	Hermit	Low	Low	None	Ca, Co