



Review paper

Invasive rats on tropical islands: Their population biology and impacts on native species

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ABSTRACT

The three most invasive rat species, black or ship rat *Rattus rattus*, brown or Norway rats, *R. norvegicus* and Pacific rat, *R. exulans* have been incrementally introduced to islands as humans have explored the world's oceans. They have caused serious deleterious effects through predation and competition, and extinction of many species on tropical islands, many of which are biodiversity hotspots. All three rat species are found in virtually all habitat types, including mangrove and arid shrub land. Black rats tend to dominate the literature but despite this the population biology of invasive rats, particularly Norway rats, is poorly researched on tropical islands. Pacific rats can often exceed population densities of well over 100 rats ha⁻¹ and black rats can attain densities of 119 rats ha⁻¹, which is much higher than recorded on most temperate islands. High densities are possibly due to high recruitment of young although the data to support this are limited. The generally aseasonally warm climate can lead to year-round breeding but can be restricted by either density-dependent effects interacting with resource constraints often due to aridity. Apparent adverse impacts on birds have been well recorded and almost all tropical seabirds and land birds can be affected by rats. On the Pacific islands, black rats have added to declines and extinctions of land birds caused initially by Pacific rats. Rats have likely caused unrecorded extinctions of native species on tropical islands. Further research required on invasive rats on tropical islands includes the drivers of population growth and carrying capacities that result in high densities and how these differ to temperate islands, habitat use of rats in tropical vegetation types and interactions with other tropical species, particularly the reptiles and invertebrates, including crustaceans.

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1. Introduction

Invasive rats, the archetypal tramp species, have spread across the globe alongside humans. The black or ship rat *Rattus rattus*, and Norway or brown rat *R. norvegicus*, are now found throughout the world from their source populations in SE Asia and China respectively (Barnett, 2001; Aplin et al., 2011). The Pacific rat *R. exulans*, originated in southern Indonesia and has now spread throughout the Pacific (Matisoo-Smith and Robins, 2004).

Introductions of rats to islands have invariably caused breakdowns in linkages within ecosystems. Island species that have evolved in the absence of mammalian predators are particularly susceptible. Extinction, or severe reduction in numbers of native species in the wake of rat invasions, has been catalogued from the sub-Arctic and sub-Antarctic islands to the tropics (Atkinson, 1985; Jones et al., 2008; Kurle et al., 2008). Rats disrupt ecosystem function through predation of animals and plants, which causes direct or indirect cascades of collapse, through interruption of pollination, nutrient pathways, and seed predation, in some cases leading to forest collapse (Townes et al., 2006; Athens, 2009; Kaiser-Bunbury et al., 2009; Townes, 2009; Hilton and Cuthbert, 2010). Moreover, the impact of invasive rats on tropical islands is proportionally worse than at higher latitudes as virtually all tropical islands are biodiversity hotspots with high levels of endemism (Meyers et al., 2000).

Most research on the island biology and impacts of invasive rats has been conducted in temperate islands, principally New Zealand (*inter alia* Harper et al., 2005; Russell et al., 2005; Townes et al., 2006), with some notable exceptions being work in the northern Pacific, the Galápagos and Mexico (*inter alia* Tomich, 1970; Wirtz, 1972; Clark, 1980; Harris and McDonald, 2007; Samaniego-Herrera, 2014). In addition, several reviews of rat impacts on islands have been written (*inter alia* Townes et al., 2006; Jones et al., 2008; St Clair, 2011; Shiels et al., 2014), and record the global scale of the deleterious impact of rats on insular species and ecosystems, as these effects became obvious through the 1980s and 1990s. Tools and techniques to eradicate rats were developed concurrently and invasive rats have been removed from an increasing number of islands of progressively larger size (Howald et al., 2007). Most of these islands have been temperate or sub-Antarctic, because eradication techniques have been developed and refined there. The focus is shifting to the tropical islands where rats have been eradicated from a cumulative 5000 ha thus far (Varnham, 2010), although rat eradications on tropical islands have been significantly less successful than on temperate islands (Keitt et al., *in press*). The poor success is possibly due to one, or a combination of, factors such as the year-round availability of food in contrast to temperate islands, bait interference by terrestrial crabs, lack of seasonal cessation in breeding (Rodríguez et al., 2006; Wegmann et al., 2011; Keitt et al., *in press*), and these possible reasons in themselves suggest that the ecology and control of invasive rats on tropical islands is not well understood. Rat population biology likely differs in tropical climates as the usual seasonal constraints in food availability present in higher latitudes can be absent (Melillo et al., 1993; Russell et al., 2011). Moreover, the native fauna of tropical islands comprises a contrasting suite of species to temperate islands, particularly as more terrestrial crustaceans and diverse reptile taxa are present, so the impacts of, and interactions with, introduced rats are probably novel. Hence there is a need to summarise the known population ecology of invasive rats on tropical versus temperate islands, in contrast the review of Shiels et al. (2014) that deals only with black rats in the Pacific Ocean. Equally important is the need to highlight their impacts on native species, and outline gaps in knowledge to provide a focus for future research and eradication planning.

Although the tropics lie between 23.5° south and north, tropical or equatorial climates are regarded as areas where the mean monthly minimum temperature is $\geq 18^\circ\text{C}$ and can extend above and below these parallels, for example at eastern Africa/Madagascar at 26° S, the Bahamas at 25° N, and the Gulf of California up to 32° N (Kottek et al., 2006). Equatorial climate is grouped into four zones depending on seasonality of rainfall; the Equatorial humid zone has precipitation adequate for vegetative growth spread evenly through the year; and three zones, where rainfall is adequate for vegetative growth but is seasonal: the monsoonal zone and two zones with winter or summer minima in rainfall. Within the tropics there are also arid zones (Kottek et al., 2006). The geomorphology of tropical islands broadly fall into three types; atolls, formed from coral; cays, made up of gravel or sand lying on a coral reef; and rocky islands, often volcanic like Hawaii. All these island types within the tropical or equatorial climate zones are relevant to this review, although reference to temperate islands will serve as a contrast of rat ecology in cooler climates. It should be noted that the bulk of research on invasive rats in the temperate zone has been conducted in New Zealand, which de facto becomes the principal 'temperate' comparison point for this review.

Although all three rat species are genetically distinct, Aplin et al. (2011) recognised several clades within the *Rattus rattus* lineage and overlap with the Asian Rat *R. tanezumi*. They concluded that at present *R. tanezumi* should remain as a

clade within the *R. rattus* group so, for the purposes of this review, *R. tanezumi* will be referred to as *R. rattus*. Moreover their behaviour and impacts are for all intents and purposes virtually the same as *R. rattus*. Besides being native to SE Asia and Indonesia *R. tanezumi* has only been identified on a few Pacific islands, possibly due to shipwrecks of Asian fishing vessels (Pierce et al., 2008; Rauzon et al., 2008)

1.1. Historic introductions

Atkinson (1985) comprehensively summarised the locations of invasive rats on islands worldwide. They are present on 80% of archipelagos and their establishment has largely been human-assisted, unless the islands are very close to established populations (Spennemann, 1997). A review of the species distributions on tropical islands by geomorphology, i.e., atolls and cays vs. rocky islands, with reference to Atkinson (1985), updated using recent data (Spennemann, 1997; Beaver and Mougil, 2009), revealed that black rats are found on atolls/cays or archipelagos of atolls/cays in approximately 31 of 66 records (47%) and rocky islands for the remaining 53%. Pacific rats are similarly found on atolls/cays for 44% of their 32 recorded tropical Pacific locations. In contrast, Norway rats are only found on atolls/cays for 19% of their 42 recorded locations on islands or archipelagos which is significantly fewer than expected ($\chi^2 = 9.14$, d.f. = 2, $P < 0.05$).

The advent of genetic techniques and increasing focus on rats as damaging invasive species have provided further insights into the origins, chronology and colonisation routes of rat introductions (Matisoo-Smith and Robins, 2008; Aplin et al., 2011). Recent molecular work points to the island of Flores, SE Asia, as the original source site for Pacific rats (Thomson et al., 2014), which subsequently became widely established in the Pacific Islands during the human migrations across Polynesia about 2500 years BP (Matisoo-Smith and Robins, 2004). They finally reached New Zealand about 1000 BP (Prebble and Wilmshurst, 2009), with evidence of repeated introductions there (Matisoo-Smith et al., 1998). Pacific rats are probably now found on more islands in the Pacific than any other introduced rat species due to their long history (Matisoo-Smith and Robins, 2004). For example, in the Marshall Islands, Pacific rats are found on 30 of the 35 atolls of the archipelago, whereas black rats are only found on nine, and Norway rats a mere two (Spennemann, 1997).

Research suggests Norway rats originated in southern China and spread to Europe during the 15th Century, with virtually all of the invasions since then being derived from the European stock (Song et al., 2014). Similarly, black rats that have invaded most of the world are thought to be derived from south Indian stock (Aplin et al., 2011) which had spread to the Arabian Peninsula by 4000 BP and on to Europe, aided by human trade (see Brouat et al., 2014).

There are thought to have been three 'waves' of introductions of black and Norway rats to most tropical islands except in the Western Indian Ocean (see below), firstly by black rats before the 1700s, then mainly Norway rats until the 1850s as they displaced black rats in Europe (Atkinson, 1973), followed by a mixture of both species into the twentieth century (Atkinson, 1985). A review of the frequency of occurrence of seabird predators on selected archipelagos suggests that black rats are the strongly predominant of the two 'European' derived rats likely to be found on tropical islands (Towns et al., 2011). The relative lack of Norway rats in the tropics with respect to black rats in particular, could be due to several factors, including timing of introduction, along with competition with existing conspecifics, which relegates them to commensal habitats for example, or the species being less suited to tropical or arid climates with a need to access free-standing water (Norman, 1975). In Mexico for example, both Norway and black rats occur on the mainland but only black rats occur on the islands, which are mainly arid in the north and wet tropical in the south (Samaniego-Herrera et al., 2011). On Cuban islands Norway rats are mainly commensal whereas black rats are the ones most likely to invade natural ecosystems (Borroto-Páez, 2013).

In the Indian Ocean, the invasion of black rats appears to have begun at least as early as the ninth Century, aided by traders from the Arabian Peninsula, with definite records of black rats in eastern Madagascar and the Comoros by this time (Cheke, 2010; Tollenaere et al., 2010), with likely invasions of the Seychelles islands during this period (Cheke, 2010; GH & Seychelles Islands Foundation, unpubl. data). Norway rats did not invade the Seychelles until the late 1970s–1980s (Cheke, 2010). In Mauritius black rats were recorded as very numerous by 1598, were present on Rodrigues by 1691 and arrived on nearby Reunion about 1670 (Cheke, 1987, 2010). Norway rats were first recorded in Mauritius and Reunion in 1735. In the Maldives rats (species unknown) were present before 1900, probably from shipwrecks or sailing vessels that plied seasonally between Sri Lanka and Male for trade (Bentley and Bathard, 1959). The timing of introductions to many of the other widely scattered islands in the Indian Ocean is less clear and requires further research.

Black rats are thought to have become established in the Caribbean with the initial contact by Europeans around 600 BP (Macphee et al., 1999) and continued wherever Europeans settled. For example, black rats arrived at Barbados in 1613, shortly after the establishment of the British colony, but Norway rats were not recorded until 1840 (Wingate, 1991). In the Pacific, black rats became established in the Galapagos Islands between 1600 and 1700, shortly after the first European contact (Clark, 1978), and now inhabit 35 islands, or 90% of the land area, in the archipelago (Harper and Carrion, 2011).

Since the 1800s, further invasions likely occurred throughout the more remote tropical islands as commercial operations were established for enterprises like copra growing. On Little Cayman Islands for example, the establishment of buildings for coconut plantations resulted in black rats arriving (Hounsome, 1980). Rats invariably arrived at the outset or during the servicing of these settlements (Chasen, 1933). In the Seychelles black rats arrived on Bird Island in thatching in 1967 (Racey and Nicoll, 1984) and Norway rats on Frégate Island in groceries in 1995 (Thorsen et al., 2000). With an increase in sea traffic, and a concomitant increase in shipwrecks, increasing numbers of invasions occurred, like the black rat invasion

on the Cocos Keeling islands from a shipwreck in early 1800s (Tate, 1950). There was a spike in the rate of rat invasions during 1940–60 (Atkinson, 1985) associated with the establishment of military bases in the Pacific during World War 2 (Spennemann, 1997) and later, nuclear tests (Atkinson, 1985). For example, black rats arrived on Eniwetok a little before 1952 during the nuclear tests there (Jackson, 1969) and are still found there despite the nuclear tests. This ability of black rats to colonise apparently devastated ecosystems is reinforced by the establishment of a population on Karakatau, Indonesia, within 50 years of the massive eruption there in 1883 (Rawlinson et al., 1990).

Rats are now widespread on islands in all the tropical oceans. For example, only five atolls of the ca. 120 islands in French Polynesia are currently known to be free of all rats. Invariably these atolls are remote, less than 300 ha in area, and often uninhabited (Meyer and Butaud, 2009). With increasing globalisation rat invasions continue to occur. Norway rats were first found at the main ports of the Galápagos and the Seychelles Islands by the 1980s and spread to other islands shortly afterwards (Key and Muñoz, 1994; Cheke, 2010). Black rats invaded Clipperton Island, a remote uninhabited atoll in the Eastern Pacific, after two large fishing boats were shipwrecked there in 1999 or 2000 (Pitman et al., 2005). Black rats are thought to have invaded Futuna (central South Pacific) in 2007 or 2008, probably from a cargo ship (Theuerkauf et al., 2010). The widespread distribution of black rats, their ability to exploit virtually all available tropical island habitats and competitive dominance over congenics on forested islands (Harper, 2006; King et al., 2011) make them the most likely invasive rat species to continue spreading.

2. Rat biology on tropical islands

2.1. Habitat use and activity patterns

Invasive rats are successful on oceanic islands mainly due to the paucity of other small rodents able to compete with them, in contrast to very large near-shore islands or continents with a more diverse range of functionally equivalent competitors (Corlett, 2010; King et al., 2011). Rats have wide fundamental niches, so in the absence of congenics they will occupy all available habitats on islands at varying densities depending on the habitat suitability and presence or absence of predators (Harper et al., 2005; Russell et al., 2011). With other rat species present, rats occupy a more constrained 'realised' niche with varying degrees of overlap with conspecifics (Harper et al., 2005). All three species can be commensal and the degree to which they occupy human habitation will depend on which other species are present, with Norway rats apparently dominating in this 'habitat' (Nicholson and Warner, 1953). Black rats usually occur in forest or shrubland but can exist on islands with minimal vegetation (Rodríguez and Herrera, 2012). In Hawaii they live at 2100 m altitude (Amarasekare, 1993), where they can be highly arboreal and exploit habitat that Pacific and Norway rats are less suited to. For example, black rats inhabit mangrove forest (Frith, 1976; Dunson and Lazell, 1982; Sánchez et al., 2001), and in Guadeloupe were the only species trapped in this forest despite sharing adjacent terrestrial forest with Norway rats (Delattre and Le Louarn, 1980). Black rats can be more arboreal when Norway rats are present (Key and Woods, 1996) although no black rats have been found to be exclusively arboreal with or without rat species present (Howald et al., 2004; Ringle et al., in press). On Palmyra Atoll radio-tagged black rats in coconut forest used both the tree canopy and forest floor. Rats trapped in trees spent 51% of their time on the forest floor, whereas ground-trapped rats were located in the canopy for 29% of observations (Howald et al., 2004). When Pacific rats are found in native forest, they appear to be more arboreal when black rats are absent (Marples, 1955; McCartney, 1970; Twibell, 1973) although when other rat species were absent Wegmann et al. (2011) found them more often on the ground both day and night and on average were recorded as active approximately equally diurnally and nocturnally. When other congenics are present Pacific rats will tend to prefer habitat with thick ground cover like grass or fern (Baker, 1946; Nicholson and Warner, 1953).

In general, where Norway rats are present on tropical islands with congenics they tend to be commensal, inhabiting areas of agriculture or human habitation (Nicholson and Warner, 1953; Marples, 1955; Jackson and Strecker, 1962; Twibell, 1973; Key and Muñoz, 1994), although a few can be trapped in forest many kilometres from areas of human activity and are thought to be dispersing animals (Nicholson and Warner, 1953; Lindsey et al., 1999). Norway rats on 210 ha Frigate Island, Seychelles, where other rat species were absent, were found in all habitats (Thorsen et al., 2000). They tend to prefer wetter rather than arid habitats (Key and Muñoz, 1994; Phillips, 2010) and are known to forage in the inter-tidal zone (Navarette and Castilla, 1993; Harper, 2006), although this has not been recorded in the tropics. When predators are absent, diurnal activity in black rats appears to be related to density. On Palmyra, recorded diurnal activity was thought to be in response to either, the high percentage of canopy cover and understory foliage cover and lack of predators, and/or the high density of rats competing for resources (Howald et al., 2004). However, diurnal activity has been recorded during periods of high rat densities in xeric forests on Buck and Great St James Islands in the Caribbean (Campbell, 1991) and by Pierce et al. (2008) on McKean Island in 2006 when rat density was approximately twice as high as in 2008, whereas in 2008 no diurnal activity was recorded. Similarly, diurnal activity was noted on Picard, Aldabra Atoll, in the Seychelles, when high rat densities were high (GH & Seychelles Islands Foundation, unpubl. data). None of these islands have mammalian predators, which suggests that high population density is the predominant driver of diurnal activity and possibly tied to competition for food.

Table 1Maximum, minimum and point estimated population densities of Pacific rats *Rattus exulans* on tropical and temperate islands.

Reference	Location	Maximum	Point estimate	Minimum
Tropical islands				
Strecker (1962) ^a	Ponape	113		17
Wodzicki (1969) ^a	Tokelau	288		–
Tomich (1970) ^c	Hawaii Island, Hawaii	34.6		1.2
Wirtz (1972) ^a	Kure Atoll	185		50
Williams (1974) ^d	Fiji	137		24
Adams et al. (2011) ^a	Marianas		55	
Range		288	55	1.2
Temperate islands				
Moller and Craig (1987) ^d	Tiritiri Matangi, northern NZ	108		6
Harper (2006) ^b	Pearl Island, southern NZ		0.79–3.68	
Range		108	0.79–3.68	6

Density estimate methods:.

^a Mark–recapture.^b Removal trapping (Zippin, 1958).^c Live trapping.^d Minimum number alive.**Table 2**Maximum, minimum and point estimated population densities of black rats *Rattus rattus* on tropical and temperate islands.

Reference	Location	Maximum	Point estimate	Minimum
Tropical islands				
Uchida (1969) ^a	Ifaluk, Caroline Islands	119	–	–
Tomich (1970) ^d	Hawaii, Hawaiian islands	34.6	–	1.2
Delattre and Le Louarn (1981) ^a	Guadeloupe, Caribbean	15.7	–	4.3
Vogt (2004) ^e	Diego Garcia, Indian Ocean	–	25.7	–
Russell et al. (2011) ^a	Europa and Juan de Nova, Mozambique channel	34.6 & 65	–	26
Samaniego-Herrera et al. (in press) ^a	Cayo Norte, Banco Chinchorro, Yucatan, Mexico	66	–	–
Harper et al. (2014) ^a	Aldabra Atoll, Seychelles	70.5		20.2
Range		119	25.7	1.2
Temperate islands				
Shapiro (2005) ^a	Pounui Island, Northern NZ	22.43	–	6.04
Latham (2006) ^b				
Hooker and Innes (1995) ^b	Rotoehu, North Island, NZ	–	6.2	–
Blackwell et al. (2002) ^c	Lake Waikaremoana, North Island, NZ	–	–	8.2
Wilson et al. (2007) ^a	Orongorongo Valley, North Island, NZ	–	4.9 & 8.7	–
Harper (2006) ^c	Pearl Island, southern NZ	–	0.13 & 1.38	–
Range		22.43	0.13–8.7	6.04

Methods used to estimate density:.

^a Mark–recapture.^b Telemetry.^c Removal trapping (Zippin, 1958).^d Live trapping.^e Observation transect.

3. Population biology

3.1. Density and home ranges

Pacific and black rats on tropical islands generally attain maximum population densities or measures of relative abundance that exceed those recorded during seed–mast events in temperate sites (Tables 1 and 2), when huge quantities of food are available, albeit only for a few months (Harper, 2005). In many cases methods for deriving density estimates have not been clearly stated, so the accuracy of specific estimates are open to question, but recent work supports the conclusion that rat population densities are generally higher on tropical islands. In Tables 1 and 2, densities are given as rats hectare^{−1}, and in many cases are converted from imperial measurements.

Contemporary research on Europa and Juan de Nova atolls in the Mozambique Channel, showed black rats attained high densities in forest in the wet season and lower densities at the beginning of the dry season, while in grassland, black rat densities were lower and higher in the wet and dry seasons respectively. Lower densities were recorded where predators

Table 3Home range size estimates of black rats *Rattus rattus* on tropical islands.

Reference	Location	Habitat	Male home range (ha)	Female home range (ha)	Combined home range
Lindsey et al. (1999) ^a	Hawaii	Rainforest	–	–	3.6
Samaniego-Herrera et al. (2010) ^a	Isla Isabel, Mexico	Deciduous forest	–	–	0.17
Howald et al. (2004) ^a	Palmyra Atoll	Rainforest	0.13	0.04	
Low et al. (2013) ^a	Christmas Island, Aust.	Settlement	0.54	0.38	
Ringler et al. (2014) ^b	Europa	Dry forest	0.45–0.6	0.35–0.5	
	Juan de Nova	Dry forest	0.4–0.85	0.35–0.75	
	Europa	Grassland	1.5–2	1.3–1.7	
	Juan de Nova	Grassland	1.45–3.1	1.25–2.6	
Harper et al. (2014) ^b	Aldabra	<i>Pemphis</i> scrub	0.79–1.2		
	Aldabra	Mixed scrub	0.5–0.8		
	Aldabra	Mangrove	0.57–0.65		

Methods used to estimate home range:.

^a Telemetry.^b SECR estimate.

(cats) and competitors (mice) were present (Russell et al., 2011). Samaniego-Herrera et al. (in press) recorded maximum black rat densities varying from 66 ha⁻¹ on Cayo Norte Island, a wet tropical island, to 38 ha⁻¹ on Isabel Island, a seasonally wet–dry tropical island, and only 19 ha⁻¹ on dry Pérez Island. On Aldabra Atoll black rat population densities were 20–70.5 ha⁻¹ in three habitats in the wet season (Harper et al., 2014). Uchida (1969) recorded black rats population density on Ella Islet on Ifaluk Atoll (Table 3) but, when sympatric with Pacific rats on nearby Falarik, the density halved. In mangrove forest in the French Antilles, black rats attained a moderate to high densities (Delattre and Le Louarn, 1980). Pierce et al. (2008) noted black rats at 12–64 ha⁻¹ using transects on McKean Island, Kiribati in 2006 and 2008.

When predators and competitors are absent, Pacific rats appear to reach higher densities than their conspecifics, possibly related to their smaller size (Table 2). When Pacific rats co-occurred with two competitors, mice *Mus musculus* and rice rats *Rattus diardii*, and a mammalian predator, feral cats *Felis catus*, on Guam before the introduction of the brown tree snake *Boiga irregularis*, their population density was only 3–21 ha⁻¹ (Baker, 1946).

In temperate climates without predators or competitors, Pacific rats on Tiritiri Matangi Island, northern New Zealand, reached densities somewhat lower than tropical islands (Table 1) with maximum densities recorded in grassland in autumn and declining to lower densities in winter and early spring.

Sufficient home range data for rats on tropical islands was only available for black rats (Table 3), with only two studies on Pacific rats by Wirtz (1972) and Lindsey et al. (1999) Wirtz used a live-trapping grid on Kure Atoll to estimate home ranges of 0.18 ha (range: 0.012–0.74) for adult males and 0.08 ha (0.012–0.49) for breeding females and Lindsey et al. recorded a mean home range for adults of 3.0 ha in Hawaiian rainforest. No data on Norway rat home ranges or population density on tropical islands was available in the literature. Black rat home range size estimations are mainly derived from telemetry studies, although recently home ranges are being estimated from spatially explicit capture–recapture (SECR) data (Ringler et al., 2014). Male black rats tend to have larger home ranges than females although on Isabel Island there was no significant difference between sexes (Samaniego-Herrera et al., 2010). Black rat home range size can vary due to a suite of often interacting factors such as available food, an animal's sex, the breeding season, population density and predation (Russell et al., 2011; Ringler et al., 2014). No comparisons with black rats on temperate islands were possible due to the small sample size and certainly there is a need for more home range data on all rat species, but particularly Norway and Pacific rats.

Rat population densities on mesic tropical islands are generally higher than on temperate islands. Where there is adequate rainfall, this is probably, at least partially, related to higher primary productivity due to continually warm temperatures (Melillo et al., 1993; Schurr, 2003), which likely results in increased reproduction and recruitment of young rather than increased survival (Adler, 1998; Prevedello et al., 2013). Clark (1980) observed that vegetation density had a positive relationship with black rat population densities and concluded that food was a limiting factor on population size. In contrast, on more arid tropical islands, or seasonally dry islands population densities are lower probably due to lower primary productivity. Xeric forest and arid shrubland can have net primary productivity substantially less than half of tropical evergreen forest (Melillo et al., 1993) and precipitation becomes the principal exogenous factor driving population dynamics, by influencing resource availability (Madsen and Shine, 1999; Previtali et al., 2009; Russell and Ruffino, 2012; Russell and Holmes, in press). Pierce et al. (2008) noted that on McKean Atoll rat population density was ca. 50% lower two years after a previous visit and suggested that this was, in part, due to a recent drought. In the Galápagos black rat population density was estimated at only 3.5 ha⁻¹ on arid Seymour Norte with an average rainfall of 228 mm (Harper et al., 2011), and 4.8 ha⁻¹ on Santa Cruz with median rainfall of 288 mm (Harper and Cabrera, 2010). Clark (1980) also estimated a range of black rat population densities in the archipelago of 0.2–18.9 rats ha⁻¹, which was hypothesised to be a function of lower primary productivity, although food availability has been suggested as a better metric to explain changes in population densities (Prevedello et al., 2013). Even in cases where islands are not sufficiently arid to curtail reproduction, it is highly

Table 4

Mean numbers of embryos recorded per female rat in Pacific rats and black rats on tropical and temperate islands.

Tropical islands		Temperate islands	
Reference	Mean litter size	Reference	Mean litter size
Pacific rat <i>Rattus exulans</i>			
Harrison and Woodville (1950)	4.0	Watson (1956)	4.7
Harrison (1957)	4.5	Hitchmough (1980)	6.7
Nicholson and Warner (1953)	3.0	Dick (1985)	4.7
Jackson and Strecker (1962)	2.5	Moller and Craig (1987)	6.7
Jackson and Strecker (1962)	3.0	Sturmer (1988)	4.7
Wirtz (1972)	4.0		
Lindsey et al. (1999)	3.4		
Mean	3.49 (s.e.: 0.27)		5.50 (s.e.: 0.49)
Black rat <i>Rattus rattus</i>			
Harrison (1957)	5.7	Morlan et al. (1952)	5.6
Nicholson and Warner (1953)	5.0	Davis (1953)	5.3
Davis (1953)	6.3	Davis (1953)	5.8
Strecker 1969	3.8	Davis (1953)	7.4
Strecker 1969	3.4	Davis (1953)	3.1
Delattre and Le Louarn (1980)	5.4	Davis (1953)	6.4
Clark (1980)	5.3	Davis (1953)	5.1
Lindsey et al. (1999)	4.3	Davis (1953)	5.6
Harper et al. (2014)	2.9, 3.0, 4.1	Davis (1953)	3.0
		Best (1968)	5.9
		Daniel (1972)	6.1
		Sturmer (1988)	5.9
		Miller and Miller (1995)	7.0
		King and Moller (1997)	6.3
		Innes et al. (2001)	4.2, 5.9
		Efford et al. (2006)	4.4, 5.0
Mean	4.47 (s.e.: 0.34)		5.44 (s.e.: 0.28)

likely rats will have sub-optimal body condition during the dry season (Samaniego-Herrera et al., in press). Adams et al. (2011) noted that Pacific rats were detected more often after rain in the Marianas and suggested the population was water stressed due to a lack of readily available water.

3.2. Breeding

Both Pacific rats and black rats on tropical islands have significantly smaller mean litter sizes than in temperate sites (Pacific rats: $t = -3.347$, d.f. = 9, $P = 0.009$; black rats: $t = -2.179$, d.f. = 27, $P = 0.019$; Table 4). Wirtz (1972) recorded Pacific rats on Kure Atoll most often producing only one litter per female per year. On Tiritiri Matangi Island in northern New Zealand, Pacific rats produced 2.3–2.6 litters per female per year (Moller and Craig, 1987).

There is little information on mean numbers of embryos in female Norway rats on tropical islands, although it does seem to be higher than either of the other species. In New Caledonia, Nicholson and Warner (1953) recorded an average 9.3 embryos per female in commensal Norway rats and Delattre and Le Louarn (1980) recorded mean pregnancy rates of 5.8 embryos per litter in forest on Guadeloupe.

3.3. Juveniles

In Guadeloupe juvenile black rats were present year-round, although there was a peak in captures during the wet season in winter (Delattre and Le Louarn, 1980, 1981). On Aldabra Atoll, Seychelles, production of juveniles in mixed-scrub was curtailed during the dry season, whereas in adjacent evergreen *Pemphis* and mangrove forest, juveniles were present year-round (Harper et al., 2014). In Hawaii, the highest pregnancy rates were in Pacific rats in late spring, and in black rats in summer, with no pregnant rats of either species trapped in winter (Tamarin and Malecha, 1971; Lindsey et al., 1999). Juveniles of both species were present year-round, but highest numbers were in autumn and could comprise up to 70% of the population. Wirtz (1972) trapped juveniles and sub-adults from June to January (summer to mid-winter) on Kure Atoll.

Unfortunately, despite breeding data being available for Pacific and black rats, there is very little information for Norway rats on tropical islands. The sparse data on juvenile survival and recruitment, however, is probably more crucial to understanding why rats on tropical islands can apparently reach very high population densities, and future population studies should seek to obtain this data.

Although breeding by invasive rats can occur year round on tropical islands with little seasonal difference in rainfall (Delattre and Le Louarn, 1980; Lindsey et al., 1999), on islands with seasonal rainfall, breeding fluctuates, generally in relation

to wet seasons (Gomez, 1960; Tamarin and Malecha, 1971; Clark, 1980; Delattre and Le Louarn, 1980; Russell and Holmes, *in press*). In contrast, on temperate or sub-tropical islands, where seasonal temperature changes are the principal constraint on primary productivity, breeding is restricted to seven to eight months (Moller and Craig, 1987; Harper and Veitch, 2006; Harper, 2006). At high densities it appears that density-dependent effects can become the endogenous factor regulating population abundance in concert with resource restriction (Previtali et al., 2009). For example Wirtz (1972) concluded that for Pacific rats on Kure Atoll, production of young over the summer resulted in high densities by early winter, which declined over winter and early spring apparently due to intra-specific competition for resources and/or shelter. However, Wirtz still recorded a minimum density of 50 ha⁻¹, which is significantly higher than the minimum recorded on temperate islands (Table 2). The very sparse data does not suggest that survivorship in the tropics is higher as monthly survival of Pacific rats on Kure Atoll (Wirtz, 1972) (0.7–0.8) is similar to a temperate New Zealand island (0.72–0.97; Moller and Craig, 1987). Hence there are generally smaller litter sizes and little apparent difference in survival for rats on tropical versus temperate islands, which suggests alternative drivers for higher population densities on tropical islands, such as more litters produced per annum. Food supplementation experiments with tropical small rodent species reveal increased recruitment of young, along with immigration, as the principal cause for the observed high population densities, which may be due to higher food availability and/or food quality (Adler, 1998; Castellarini and Polop, 2002; Prevedello et al., 2013). Although some comprehensive research has been conducted on tropical rat population dynamics, particularly in Hawaii, comparative work investigating the link between relative food availability and habitat with population dynamics, in particular production, recruitment and survival of young, is worth investigating to explain the higher densities attained on tropical islands.

4. Diet

Rats are omnivorous, so their diets are highly variable, likely in response to available prey. In general plant material forms the basis of all rat diets and leaves, stems and fruits are all eaten. Arthropods, usually insects, have been recorded as providing most of the animal protein for all three rat species, although it is becoming increasingly evident that terrestrial crustaceans can form a substantial portion of the diet (Samaniego-Herrera, 2014). Of the three species *R. norvegicus* generally consume the most vertebrate prey (Bassford et al., 2007).

For Pacific rats on Kure Atoll, Wirtz (1972) recorded 62% of their diet as plant material, with berries and seeds of low-growing *Scaevola* and *Earagrostis* and the seeds of the grass *Boerhavia* being favoured. *Scaevola* also predominated in the diet of Pacific rats on Niwetok atoll (Fall et al., 1971) and Jackson and Strecker (1962) found about 90% of their diet was plant material. On Kure Atoll, 30% of the diet was insects, predominantly grasshoppers, spiders, cockroaches and flies (Wirtz, 1972). Fall et al. (1971) only found insects in 10% of stomach samples. Wirtz (1972) noted 8% of the diet as vertebrate flesh, mainly seabirds. Somewhat surprisingly, Shiels et al. (2013) found that Pacific rats occupied a higher trophic position than the larger black rat, which was apparently due to the larger percentage of invertebrates relative to plant material in Pacific rat diet.

The diet of black rats is dominated by plant material. On Europa and Juan de Nova atolls in the Mozambique Channel, plants occurred in 90%–100% of 220 rats sampled in 2007–2008 (Russell et al., 2011; Ringle et al., *in press*). On Surprise Island, New Caledonia, plant material occurred in 100% of gut samples (Caut et al., 2008). Invertebrates occurred in 72%–98% of samples from the Mozambique Channel islands and 38%–83% of samples from Surprise Island. Feathers or flesh were found in 0%–17% of rats from Juan de Nova, which was tied to the arrival of sooty terns (Feare et al., 2007; Russell et al., 2011). On Surprise Island seabird feathers were found in 56% of gut samples, along with skink remains in 13%. Seabird eggs and sea turtle hatchlings were also taken.

This short section highlights the highly opportunistic foraging nature of rats and when coupled with the high population densities it is little surprise they have significant effects on island ecosystems. Although it is apparent rats can exploit virtually any available food source, more long-term research needs to elucidate the response of rats, at an individual and population level, to seasonal food availability and quality when it fluctuates due to seasonal aridity or breeding by seabirds for example.

5. Impacts of rats

There is a burgeoning literature on the impacts of rats on tropical islands, although most comprise circumstantial evidence; for example, declines in populations of native species after rat invasions, differences in population sizes between islands with and without rats or population increases after rat eradication. Most of these records likely represent examples of rat impacts but cannot be separated from other possible agents of decline like habitat degradation, direct human impacts or other invasive species. Even when rat predation is directly observed the relationship with population decline or extinction cannot be proven (Towns et al., 2006; Banks and Hughes, 2012). In contrast there have been a few manipulative experiments, with replicated controls and treatments, which have provided the most compelling data of rat impacts on native tropical island species (e.g. Seto and Conant, 1996; VanderWerf and Smith, 2002; Pender et al., 2012). Black rats dominate the literature with regard to impacts of invasive rats on tropical islands, with most of the remaining literature focusing on

Pacific rats. The almost total absence of Norway rats in this section may be due to the reasons discussed in the *Birds* section.

5.1. Plants

Research on deleterious effect of rats on tropical island plants initially focused on commercial crops, particularly coconut *Cocos nucifera*, from the mid-20th century (Bentley and Bathard, 1959) and sugar cane (Kami, 1966). Both Pacific and black rats can cause severe damage to coconut crops. Twibell (1973) estimated at least 50% of the coconut crop on Hunga, Tonga, was destroyed by black rats gnawing holes in green coconuts to access liquid and the fleshy fruit. Williams (1974) noted that most damage in Fiji was caused by black rats on 3–6 month old (green) coconuts and mainly on palms <10 m high. In the Tokelau Islands Pacific rats also preferred green coconuts, with severity of damage being positively related to the density of surrounding undergrowth and not to rat population density (Wodzicki, 1969). Both species were recorded using coconut shells for nests. Similar damage to coconuts has been recorded from the Caribbean to the Indian Ocean (Bentley and Bathard, 1959; Hutson, 1975; Dunson and Lazell, 1982). Pacific rats have also been recorded eating pineapples (Twibell, 1973).

Any of the three invasive rat species can alter the composition of native forest, which is thought to have led to total forest collapse through continuous predation of native seed banks (Athens et al., 2002; Hunt, 2006; Athens, 2009), through preferential predation of seeds, by killing palms through eating the growing tips or seeds (Pérez et al., 2008; Athens, 2009), spreading weed seeds and predation of the native seed dispersers (Meyer and Butaud, 2007). The families Arcaceae, Elaeocarpaceae, Rubiaceae, Santalaceae, and Sapotaceae appear to be susceptible to seed predation and in French Polynesia woody plants with large-seeded drupes are favoured (Meyer and Butaud, 2009). Several species experience severe seed predation and in one example, the Polynesian sandalwood *Santalum insulare*, over 99% of fruits were eaten. On the Tongan islands the seeds of at least 18 species were found at black rat husking stations (McConkey et al., 2003) However, of 13,555 empty husks located, only 165 were viable seeds and seedlings. The seeds of *Mimosa pudica* were also favoured by Pacific rat (Twibell, 1973). In Hawaii black rats eat the bark, buds, and nectar of native hibiscus species (*Hibiscadelphus*) and can destroy up to 50% of flowers and 90% of seeds which may have led to the present rarity of this genus (Baker and Allen, 1978). Rats were the principal seed predators of four rare plant species in mesic forests and of native species in xeric forests in Hawaii (Pratt et al., 2010; Chimera and Drake, 2011). Black rats also favour the large juicy flowers of cacti on arid islands (A. Samaniego-Herrera, pers. comm).

Rat control operations or eradications can provide strong evidence of the effects of rats on seedlings. In Hawaii only 4% of an endangered lobeliad (*Cyanea superba*) fruit was eaten where rats were controlled in contrast to 47% fruit loss at a non-treatment site (Pender et al., 2012). On Palmyra Atoll, where rats were eradicated in 2011, there was a 130% increase of native seedlings and the first records of native *Pisonia* since monitoring began (G. Howald, pers. comm).

Damage to bark and buds tends to follow a recurrent theme of occurring, or becoming more prevalent, during drought or dry seasons. Rat damage to sandalwood, *Meryta* and small trees in French Polynesia was prevalent during drought (Meyer and Butaud, 2009). On Aldabra Atoll, Seychelles, the bark of native *Sideroxylon inerme* and *Myroxylon aethiopicum* chewed by black rats and rat teeth marks were noted on 80% of branches of *Ficus reflexa* during the dry season (Hambler et al., 1985; Roberts and Seabrook, 1989). *Acalypha claoxloides* (Euphorbiaceae) is particularly attractive and damage to plants increases during dry periods (Seychelles Islands Foundation, unpubl. data). On Midway Atoll black rats severely damage *Scaevola*, especially succulent apical and lateral buds (Apfelbaum and Ludwig, 1983) and Campbell (1991) noted blackship rat damage on buds and bark in xeric forest on Caribbean islands. Bark stripping was recorded on 75% of *Sophora chrysophylla* studied in Hawaii (Duffey and Gardner, 1993). Baker and Allen (1978) noted that bark stripping on *Hibiscadelphus* occurred during summer dry seasons and suggested that the soft, succulent bark was eaten for its moisture content. Meyer and Butaud (2009) noted the bark and stem damage by rats in the Indo-Pacific islands tended to occur in the families Araliaceae, Euphorbiaceae and Malvaceae, which have soft bark. On an island covered in volcanic ash black rats ate more succulent herbaceous stems than seeds, probably for the water content (Yabe, 2004). Norway rats stripped bark from numerous shrubs on Rabida Island, Galápagos, and in some cases ring-barked them. Rats require fresh water to maintain body weight and to breed and, in the case of rats in drought conditions, moisture can be obtained from more vascularised plant tissues, possibly bird eggs (Norman, 1975), or from intertidal invertebrates (Rodríguez and Herrera, 2012). In mangrove forest black rats have a moderate tolerance to drinking seawater (Dunson and Lazell, 1982), and may eat mangrove seeds to obtain liquid. Red *Rhizophora mangle* and black mangrove *Avicenna germinans* propagules are eaten in the Florida Keys (Dunson and Lazell, 1982), and Pacific and black rats occur in mixed mangrove forest in Hawaii where they are thought to consume mangrove propagules (Steele et al., 1999).

Invasive rats also degrade native forest by dispersing small-seeded weed species, e.g. velvet tree *Miconia calvescens*, Peruvian guava *Psidium cattleianum*, roseleaf bramble *Rubus rosifolius*, soapbush *Clidemia hirta*, Asian butterfly bush *Buddleia asiatica*, and Chinese banyan *Ficus microcarpa* and to a lesser degree, bishop wood *Bischofia javanica*, casuarina *Casuarina equisetifolia*, kiawe *Prosopis pallida* and palm grass *Setaria palmifolia* (Meyer and Butaud, 2007; Shiels, 2011).

The catholic vegetative diet of invasive rats summarised in this short section supports the conclusion that their prolonged selective effects on native plants can severely affect forest composition, leading to forest collapse (Athens, 2009). However, it also begs the question of whether islands with a long history of rat presence exhibit truly 'natural' forest composition and structure.

5.2. Invertebrates

Invertebrates generally comprise a substantial portion of the diet of introduced rats on tropical islands, with large-bodied invertebrates of the orders Coleoptera and Orthoptera in the insects and the phyla Mollusca being the principal prey items (St Clair, 2011). Indeed, snails are likely to be a significant source of protein for Pacific and black rats (Hadfield and Saufler, 2009; Meyer and Shiels, 2009; Harper et al., in press). Littoral invertebrates can also be taken (St Clair, 2011; Rodriguez and Herrera, 2012). Some indication of the scale of impact that rats exert on tropical islands was the recorded 367% increase in arthropod numbers after the eradication of black rats from Palmyra Atoll in 2011 (G. Howald, pers. comm.).

Most information on the effect of rats on invertebrates comes from work in temperate climates, although due to the prevalence of terrestrial crabs in the tropics there is some data to suggest that rats suppress crab populations, often severely. Observations suggest that even large crabs like *Gecarcinus ruricola* in the Caribbean and *G. planatus* on Clipperton Island are depredated by rats (Pascal et al., 2004; Pitman et al., 2005). Other observations, like a substantial increase in the numbers of fiddler crabs (*Uca* spp.) on Palmyra Atoll within 18 months of a rat eradication (G. Howald, pers. comm.) suggest that black rats can severely reduce crab densities, possibly through predation of juveniles. Samaniego-Herrera (2014) recorded species-specific vulnerability to black rats in crabs. The small Mexican crab (*Gecarcinus quadratus*) shifted from being extremely rare prior to a rat eradication to being the most ubiquitous crab, with the larger red crab (*Johngarthia planata*) population subsequently decreasing. Changes in activity patterns followed by recruitment, rather than population density changes, was the likely initial response of the Mexican crab population after the rat eradication. Observations on Diego Garcia, Indian Ocean, suggest that black rats can even compete with the large coconut crabs (*Birgus latro*), through active defence of food supplies (J. Schleyer, pers. comm.). Pacific rats are also known to eat land crabs (Moseby et al., 1973).

In an excellent example of a feedback-loop that can occur when rats are introduced to an island, newly arrived rats on Clipperton Island depredated red land crabs *Gecarcinus planatus*, a large terrestrial crab, which in turn increased the vegetation cover as the crabs are vegetarian, resulting in a decrease in masked boobies *Sula dactylatra* which require clear ground to take off. Furthermore, the increased vegetative cover provided shelter for rats, which responded with increased numbers and further predation pressure on the crabs (Pitman et al., 2005).

Although rat diet studies on tropical islands have recorded the consumption of insects and snails, which mirrors data from temperate zones, they have not generally noted crab predation. These effects are only becoming apparent from observations of interspecific interactions and population changes after rat removal. Similarly, there are tantalising data on rats impacts in the intertidal zone, which hints at rats effecting not only terrestrial island ecosystems but also the adjacent marine environment.

5.3. Herpetofauna

Case and Bolger (1991) reviewed the effects of introduced species on island reptiles and concluded that the introduction of predators, with or without exotic reptile introductions, cause extinctions and severe reductions in the numbers of native reptiles on islands. Subsequent to this paper more information has supported the supposition that rats on tropical islands have a detrimental effect on reptile species of all sizes. In the case of large reptiles, the rats can impact populations by preying on eggs and young, whereas smaller reptiles can be depredated at all life stages.

Hayes et al. (2004) recorded significantly lower density of iguanas (*Cyclura* spp.) on four rat infested cays ($10.2 \text{ ha}^{-1} \pm 3.1$) in the Bahamas than on six rat-free cays ($59.9 \text{ ha}^{-1} \pm 18.1$) and low recruitment in the San Salvador Island iguana *C. rileyi rileyi* on rat-infested islands. On Half Moon Cay, Belize, rats are thought to affect the population structure of both the green iguana (*Iguana iguana*) and the black spiny-tailed iguana (*Ctenosaurus similis*) whereby juveniles and sub-adults are absent or in low numbers (Platt et al., 1999). Similarly the endemic Belize leaf-toed gecko *Phyllodactylus insularis* on Half Moon Cay is depredated by rats (Meerman, 1996). On Christmas Island, Indian Ocean, the blue-tailed skink (*Cryptoblepharus egeriae*) is thought to have declined in population size due to black rat predation (Low et al., 2013). Rats also are recorded as predators of lizards in the Seychelles (Cheke, 1984; Racey and Nicoll, 1984). Mortality in the St Lucia whiptail lizard *Cnemidophorus vanzoi* increased after black rats invaded (John, 1999). Populations of reptiles have been recorded to increase rapidly after rat eradication on islands. The Antigua racer (*Alsophis antiguae*) population doubled in 18 months after black rat eradication on 10 ha Great Bird Island (Daltry, 2006) and on Mexican islands several species of reptiles, including snakes, are recovering after rat eradications (Samaniego-Herrera et al., 2011). The discovery of a previously undescribed gecko species found on Rabida Island, Galápagos islands, after Norway rats were eradicated in 2011 (K. Campbell, pers. comm.), highlights the conservation value of rat eradications on islands.

Rats can apparently affect populations of turtles and tortoises by taking eggs and young. Witmer et al. (2007) reported harassment of nesting hawksbill sea turtles by black rats along with predation on 10%–20% of sea turtle eggs and hatchlings on Buck Island, Caribbean. Rats were seen feeding on eggs as they were being laid on three occasions. Since the eradication of rats there, predation of turtle nests has ceased. Black rats eat turtle hatchlings on Aldabra Atoll (Racey and Nicoll, 1984) and a rat was observed jumping out of the egg chamber of a green turtle as it was laying eggs there (M. van Dinther, pers. comm.). Pacific and black rats prey on green turtle (*Chelonia mydas*) and hawksbill turtle (*Eretmochelys imbricata*) eggs and hatchlings (Ohashi and Oldenburg, 1992; Meier and Varnham, 2004) and Norway rats can locate and depredate hawksbill turtle eggs and hatchlings within nest chambers (Zeppelini et al., 2007). On Surprise Island, New Caledonia, sea turtles were estimated to comprise as much as 45% of the black rat diet in the hatching season (Caut et al., 2008). Pacific rats also eat

green turtle hatchlings, which they attack initially by biting through the plastron (Fosberg, 1969). The hatchlings of Aldabra giant tortoises (*Aldabrachelys gigantea*) are vulnerable to predation by black rats, along with other native predators, until they are ca. five years old (Coe and Swingland, 1984).

The data collated paints a picture of virtually all tropical island reptile species being potentially adversely affected by invasive rats, but there is no information for amphibians. Again there are hints of the possible effects of rats on the marine ecosystem, through predation of marine turtle eggs and nestlings.

5.4. Birds

Many effects of rats on tropical island birds have not been recorded as many species probably went extinct between the period of first Polynesian, Arabian, or European contact, the likely establishment of black rats, and when the first bird observations were recorded. In the Pacific there was certainly a second wave of extinctions once black rats became established, that continues today as these rats spread to the remaining uninhabited islands. Most recorded extinctions were caused by black rats, which simply extirpated or severely reduced populations that were less susceptible to predation by the smaller Pacific rat, about half the black rats' weight and size (Meyer and Butaud, 2009). Very few records of Norway rat interactions with native birds, or other flora and fauna, are available (Tables 5 and 6). In many cases black rats were the first invasive species to invade an island, especially pre-1700, and had already affected native species and ecosystems before any possible Norway rat invasion. They will also dominate congenics in forest habitat (Harper et al., 2005; Harper, 2006), as they are more agile climbers (King et al., 2011), so Norway rats on tropical islands are often restricted to agricultural or settled areas where native bird populations are already reduced or absent.

As Pacific rats became established on Pacific Islands in concert with the past 3500 years of human colonisation of the ocean basin, virtually all of the effects of Pacific rats on native species were not recorded. Thus remains of extinct species from sites such as caves, middens or sink-holes are used to build a picture of the avifauna at human arrival and these studies are reviewed by Steadman (1995). In summary, the pre-European losses may exceed 2000 species and are principally of rails, pigeons, doves, parrots and passerines, mainly due to predation by non-native mammals—primarily rats, along with the dogs and pigs brought by Polynesians and hunting by humans themselves. Losses of tree-nesting species were almost certainly due to rats, namely the pigeons, doves, parrots and passerines. Graves (1992) generalised that; “It is probable that nearly every vegetated island in southeastern Polynesia the size of Henderson [Island] or larger once supported a flightless rail, one or more pigeons, a lorikeet, and a reed-warbler”. Pacific rats are almost entirely absent from the list of currently affected land birds (Table 5) as any effects appear to have occurred in pre-European times. Black rats have predominated in Table 5 for two likely reasons; they have been introduced during the period of European colonisation when records of impacts were recorded and black rats have likely affected a suite of bird species that were less susceptible to predation by Pacific rats. Experiments with artificial nests clearly show that black rats are adept nest predators, causing 49%–54% of predation on eggs on artificial nests in Mauritius (Carter and Bright, 2002), and rat control in Hawaii reduced rat predation at artificial nests by 55% (VanderWerf, 2001). Black rats were reported as key nest predators of Seychelles black parrots, causing the failure of up to 33% of nesting attempts (Reuleaux et al., 2014). It is therefore unsurprising that Campbell (1991) recorded an inverse relationship between rat abundance and bird diversity on xeric islands in the Antillean Cays. As black rats have been present on many Indian Ocean islands since at least the 10th century, well before records of native species were kept, we simply have no idea of the losses of native species caused by rats there, although it is likely to mirror the catastrophic effects recorded in the Pacific islands, with similar species guilds affected.

Meta-analysis of impacts of rats on seabirds concluded that *inter alia* species that weighed less than 300 g and those exposed to black rats were most in danger of being extirpated (Jones et al., 2008). This threat was apparently mediated by the availability of alternative food for rats when birds were breeding or if terrestrial crabs were present. It is suggested that tropical seabirds have a degree of defence against egg or nest predation due to developing behaviours to circumvent predation by crabs (Atkinson, 1985; Jones et al., 2008). However, when comparing the species affected (Table 6) with seabird species present in the tropics (Diamond, 1978) it appears that almost all species of tropical seabirds up to the size of albatross are vulnerable to rat predation in some form, but unsurprisingly the smaller species such as terns are overly represented. VanderWerf (2006) and VanderWerf et al. (2007) noted that the most limiting factor for seabird nesting in the Kwajalein archipelago and Lehua, Hawaii, was the presence of rats, along with other introduced predators. Although Wirtz (1972) suggested that intensity of seabird predation was positively related to rat density, Woodward (1972) added that predation was exacerbated by seasons with poor plant growth (i.e. drier years) because rats depended on vegetative matter as the principal component of their diet.

5.5. Mammals

Harris (2009) provided a comprehensive summary of the impact of introduced rats on small mammals on islands, recording the extinction of 11 mostly native rats by invasive rats and seven more threatened with their co-existence. One bat species was extirpated on a temperate island and may reflect unrecorded extinctions of other bats in the tropics, but there is virtually no data on possible effects of rats on any bat species, including fruit bats. Most of these species were on tropical islands worldwide, although the Galápagos rice rats comprised at least four of the extinctions. Negative effects

Table 5
Recorded evidence of the impacts of invasive rats on land birds on tropical islands.

Species		Location	Rat species	Evidence	Reference
Micronesian starling	<i>Aplonis opaca</i>	Truk	<i>R. rattus</i>	Observed nest predation of this hole nester	Brandt (1962)
Pacific flycatchers	<i>Pomaera spp.</i>	French Polynesia	<i>R. rattus</i>	Extinction of four subspecies of flycatchers on five islands soon after arrival of rats	Thibault and Meyer (2001)
Rarotonga flycatcher	<i>Pomarea dimidiata</i>	Rarotonga	<i>R. rattus</i>	Nesting success was 20% prior to rat control but increased to 67% after rat poisoning	Saul et al. (1998)
Lorikeets	<i>Vini spp.</i>	Pacific Islands	<i>R. rattus</i>	Extinction of lorikeets soon after arrival of rats	Gill (1995)
Kuhl's lorikeet	<i>Vini kuhlii</i>	Tabuaeran (Fanning Island, Line Islands)	<i>R. rattus</i>	Near extinction of lorikeet population	Watling (1995)
Blue lorikeet	<i>Vini peruviana</i>	Makatea, Tuamotus	<i>R. rattus</i>	Extinction likely between 1902–1922	Thibault and Guyot (1987)
Blue-crowned lory	<i>Vini australis</i>	Tonga	<i>R. rattus</i>	Lories disappeared soon after arrival of rats	Theuerkauf et al. (2010)
Aldabran brush warbler	<i>Nesillas aldabranus</i>	Aldabra Atoll, Seychelles	<i>R. rattus</i>	Extinction of species likely partially due to rats	Roberts (1987)
Aldabran fody	<i>Foudia eminentissima</i>	Aldabra Aatoll, Seychelles	<i>R. rattus</i>	Loss of 81% of 134 fody eggs in one season, mainly to rats. Some of remaining chicks also killed.	Frith (1976)
Mauritius fody	<i>Foudia rubra</i>	Mauritius	<i>R. rattus</i>	Likely nest predation by rats	Safford (1997)
Aldabra bulbul	<i>Hypsitetes madagascariensis rostratus</i>	Aldabra Atoll, Seychelles	<i>R. rattus</i>	Eggs and chicks taken by rats	Racey and Nicoll (1984)
Aldabra white-eye	<i>Zosterops maderaspatana</i>	Aldabra Atoll, Seychelles	<i>R. rattus</i>	Eggs and chicks taken by rats	Racey and Nicoll (1984)
Mauritius olive white-eye	<i>Zosterops chloronothos</i>	Mauritius	<i>R. rattus</i>	Seven out of eight nests depredated by rats	Nichols et al. (2005)
Mangrove finch	<i>Camarrhynchus heliobates</i>	Isabela Island, Galapagos	<i>R. rattus</i>	Nest predation declined from 54% to 30% after rat control	Fessl et al. (2010)
Laysan rail	<i>Porzana palmeri</i>	Midway Atoll Laysan Island	<i>R. rattus?</i>	Thought to be main causal factor in decline of the rail population	Bailey (1956)
Tuamotu sandpiper	<i>Prosobonia cancellata</i>	Tuamotus	<i>R. exulans</i>	Highest densities of sandpipers are on islands without rats and are absent from most islands with rat populations	Pierce and Blanvillain (2004)
			<i>R. rattus</i>		
			<i>R. norvegicus</i>		
Polynesian ground dove	<i>Gallicolumbae rythroptera</i>	Vahanga, Tuamotus	<i>R. exulans</i>	Local extinction thought to have been caused by rats	Pierce and Blanvillain (2004)
Atoll fruit dove	<i>Ptilonopus coralensis</i>	Vahanga, Tuamotus	<i>R. exulans</i>	Local extinction thought to have been caused by rats	Pierce and Blanvillain (2004)
White-crowned pigeon	<i>Patagioenas leucocephala</i>	Great Bird Island, Antigua	<i>R. rattus</i>	Population increased by 16-fold since rat eradication	Daltry et al. (2013)
Sandpiper	<i>Prosobonia sp.</i>	Henderson Island	<i>R. exulans</i>	Local extinction thought to have been caused by rats	Wragg and Weisler (1994)
Laysan teal	<i>Anas laysanensis</i>	Laysan & Midway Islands	<i>R. rattus</i>	Thought to have caused extinction on Midway Island and at least partially responsible for severe population decline on Laysan Island	Fisher and Baldwin (1946); Reynolds et al. (2007)
West Indian whistling duck	<i>Dendrocyna arborea</i>	Great Bird Island Antigua	<i>R. rattus</i>	Apparent increase in reproductive success following rat eradication	Daltry et al. (2001).
Laysan finch	<i>Psittirostra cantans</i>	Laysan & Midway Islands	<i>R. rattus</i>	Thought to have caused extinction on Midway Island and severe decline on Laysan Island	Fisher and Baldwin (1946),
Bokikokiko	<i>Acrocephalus aequinoctialis pistor</i>	Tabuaeran (Fanning Island) Line Islands	<i>R. rattus</i>	Thought to have caused extinction of endemic race of warbler between 1924 and 1967	Watling (1995)

(continued on next page)

Table 5 (continued)

Species		Location	Rat species	Evidence	Reference
Christmas Island white-eye	<i>Zosterops natalis</i>	Christmas Island, Indian Ocean	<i>R. rattus</i>	Arrival of rats associated with decline in white-eye population	Low et al. (2013)
Mao	<i>Gymnomyza samoensis</i>	Samoa	<i>R. rattus</i>	Nest predation recorded on video	R. Stirnemann pers. comm.
Montserrat oriole	<i>Icterus oberi</i>	Montserrat	<i>R. rattus</i> / <i>R. norvegicus</i> ?	Rats videoed in 50% of nest predation events	Allcorn et al. (2012)
Palila	<i>Loxioides bailleui</i>	Hawaii	<i>R. rattus</i>	Mean rat predation on nests (1988–1990) of 6% (s.e.±1) and dummy nests of 4% (±1).	Amarasekare (1993)
Puaiohi	<i>Myadestes palmeri</i>	Kaua'i, Hawaii	<i>Rattus</i> spp.	Rat predation confirmed in 4 out of 9 depredated nests and two adult females killed by rats	Tweed et al. (2006)
			<i>R. rattus</i>	19% of nest failures attributed to rat predation	Snetsinger et al. (2005)
O'ahu 'Elepaio	<i>Chasiempis sandwichensis ibidis</i>	Hawaii	<i>R. rattus</i>	Over four years sites with rat control averaged 58% nest success versus 33% at sites without rat control and 0.7 fledglings per pair vs 0.33. Female survival was higher at rat control sites (0.83) versus non-treatment sites (0.5). Population growth was 0.76 where rats were not controlled and 1.0 with rat control	VanderWerf and Smith (2002)

of the presence of introduced rats were recorded for a further 11 mammal species. Hanna and Cardillo (2013) undertook a meta-analysis of small mammal extinctions on islands and concluded that for small mammal species (<2.7 kg), the presence of black rats was the principal predictor of extinction.

6. Conclusions and research needs

The impacts of invasive rats on tropical islands mirror their effects at higher latitudes, although they are possibly more severe as they can attain particularly high densities which likely compounds their impacts. Rats occur in virtually all habitats, from mangrove forest to rainforest to arid shrublands and bare islands, and will eat all forms of vegetative growth, including bark. Little information is available on their impact on invertebrates but evidence suggests they impact upon terrestrial crustaceans and possibly intertidal habitats more than is currently recognised. Virtually all insular tropical land birds are affected in some way by rats with extinction particularly likely for rail species, small parrots, small pigeons and other small passerines when rats invade. Tropical seabirds up to the size of small albatrosses are deleteriously affected by rats, with observations of smaller tropical species like terns, noddies and petrels being particularly prevalent in Table 6. Any populations of small insular mammals are likely to be deleteriously effected when invasive rats are present, including small bats. In many cases the adverse effects of rats have gone unrecorded and are only inferred from the absence of species, as shown by research on the prehistoric losses of birds in the Pacific (Steadman, 1995). It is highly likely that unrecorded endemic species have been lost in the Western Indian Ocean islands for example, where black rats have been present for a millennia. Palaeoecological research on other tropical islands will likely show similar trends in extinctions as recorded in the Pacific.

Although the distribution of introduced rats on tropical archipelagos has been well recorded, and their likely routes and timing of invasions have largely been confirmed, their population biology is generally relatively poorly researched in most of the tropics except Hawaii, which hinders management and eradication planning. Of the three species, very little is known about Norway rats, their impacts and why they are the least widespread species in the tropics. Their inter-specific interactions and the three species' relative competitive advantages in different tropical habitats are only known at a general level (Russell et al., in press). To improve the understanding of invasive rat biology and impacts on islands further, research in areas like the Caribbean, and the South Pacific and North Indian Oceans require some focus for black and Norway rats in particular. The identified bias towards temperate studies in New Zealand will be difficult to correct, although there is some scope for studies on isolated islands in the temperate zones of most oceans (Figure 6; Atkinson, 1985).

What sets invasive rat ecology on tropical islands apart is largely the differing drivers of primary productivity. On temperate islands invasive rat breeding appears to be principally constrained by lulls in primary productivity driven by cool temperatures. The uniformly high primary productivity or food availability in the tropics is only restricted by aridity, either permanently on dry islands or seasonally (Russell and Holmes, in press). With consistently warm conditions, where rainfall is evenly spread throughout the year, rats can apparently reach very high densities for extended periods, and population

Table 6
Recorded evidence of the impacts of invasive rats on seabirds on tropical islands.

Species		Location	Rat species	Evidence	References
Xantus murrelet	<i>Synthliboramphus cravieri</i>	San Pedro Mártir, Gulf of Mexico	<i>R. rattus</i>	Nesting reported for first time in 16 years after rat eradication	Rodriguez & Herrera 2012
Lesser noddy	<i>Anous tenuirostris</i>	British Indian Ocean Territories	<i>R. rattus</i>	Significantly lowered population density compared with rat-free islands	Symens (1999)
Brown noddy	<i>A.stolidus</i>	British Indian Ocean Territories	<i>R. rattus</i>	Lowered population density compared with rat-free islands	Symens (1999)
		Hardy Islet, Fr. Antilles	<i>R. rattus</i>	Breeding success improved from 5% prior to rat eradication to 85–90% in two years post eradication Predation of chicks, losses possibly as high as 28% in two weeks	Pascal et al. (2004)
		Kure Atoll	<i>R. exulans</i>	Mass predation of roosting noddies observed	Bratley in Kure 1967, Woodward (1972)
		Iles du Lys, Iles Glorieuses	<i>R. rattus</i>	Substantial increase in population size after rat eradication	Van de Elyst & Prys-Jones 1987
White tern	<i>Gygis alba</i>	Great Bird Island, Antigua	<i>R. rattus</i>		Daltry (2006)
		Midway Atoll	<i>R. rattus</i>	Predation of eggs and chicks	Johnson 1945, in Norman (1975)
		Tomelin Island, Indian Ocean	<i>R. norvegicus</i>	Began breeding on island for first time in 150 years after rat eradication	Le Corre et al. (in press)
Grey-backed tern Bridled tern	<i>Sternus lunata</i> <i>S. anaethetus</i>	Kure Atoll Great Bird Island, Rabbit and Redhead Islands, Antigua	<i>R. exulans</i> <i>R. rattus</i>	Egg & chick predation noted Substantial increase in population sizes after rat eradication	Woodward (1972) Daltry (2006); Daltry et al. (2013)
Roseate tern	<i>S. dougallii</i>	Congo Cay, US Virgin Islds	<i>R. rattus</i>	Rats destroyed 27% of nests in 1998.	Savidge et al. (2012)
		Little St James Island, Caribbean	<i>R. rattus</i>	Possible extirpation of two colonies by rats	Campbell (1991)
		Green Island, Antigua	<i>R. rattus</i>	Substantial increase in population following rat eradication	Daltry et al. (2013)
Sooty tern	<i>S. fuscata</i>	Kure Atoll	<i>R. exulans</i>	Egg and chick predation observed	Kepler (1967),
		Seychelles	<i>R. rattus</i>	Rats seen carrying eggs away from colony	Woodward (1972)
		Europa, Mozambique Channel	<i>R. rattus</i>	Rats destroyed eggs and young	Vesey-Fitzgerald (1941)
		Clipperton Island	<i>R. rattus</i>	Predation of eggs and chicks	Feare et al. (2007),
		Great Bird Island, Antigua	<i>R. rattus</i>	Egg predation	Pitman et al. (2005)
		Ascension Island	<i>R. rattus</i>	Substantial increase in population size after rat eradication	Daltry (2006); Daltry et al. (2013)
		Europa and Juan de Nova, Mozambique Channel	<i>R. rattus</i>	Predation of 52%–100% of monitored chicks	Hughes and Wearn (2006)
		Isabel Island, Baja California	<i>R. rattus</i>	Sooty tern remains recorded in 71% and 44% of rat stomachs from each island respectively	Ringler et al. (in press)
Least tern	<i>Sternula antillarum</i>	US Virgin Islands	<i>R. rattus</i>	Recorded nesting again after rat eradication	Samaniego-Herrera et al. (2011)
Elegant tern	<i>Thalasseus elegans</i>	Rasa Island, Baja California	<i>R. rattus</i>	Predation on eggs & hatchlings	Witmer et al. (1998)
Brown booby	<i>Sula leucogaster</i>	Surprise Island, New Caledonia	<i>R. rattus</i>	Population has increased 4-fold since rat eradication	Samaniego-Herrera et al. (2011)
				25% egg predation in one week	Caut et al. (2008)

(continued on next page)

Table 6 (continued)

Species		Location	Rat species	Evidence	References
		Tromelin Island, Indian Ocean	<i>R. norvegicus</i>	Began breeding on island for first time after rat eradication	Le Corre et al. (in press)
		Rabbit & Redhead Islands, Antigua	<i>R. rattus</i>	Substantial increase in population following rat eradication	Daltry et al. (2013)
Red-footed booby	<i>Sula sula</i>	Tromelin Island, Indian Ocean	<i>R. norvegicus</i>	Averaged 23% population growth every year since rat eradication	Le Corre et al. (in press)
Masked booby	<i>Sula dactylatra</i>	Tromelin Island, Indian Ocean	<i>R. norvegicus</i>	Averaged 22% population growth every year since rat eradication	Le Corre et al. (in press)
Brown pelican	<i>Pelecanus occidentalis</i>	Rabbit & Redhead Islands, Antigua	<i>R. rattus</i>	10-fold population increase in 10 years following rat eradication	Daltry et al. (2013)
Red-tailed tropic bird	<i>Phaethon rubricauda</i>	Kure Atoll	<i>R. exulans</i>	54–65% egg loss, 90–100% chick loss 64–94% chick mortality without rat control and an 'appreciable decrease' in chick mortality when rats were controlled Increase in breeding success following rat eradication	Fleet (1972); Woodward (1972) Wirtz (1972)
		Europa, Mozambique Channel	<i>R. rattus</i>	300% increase in population size since rat eradication 6 years prior	Russell and Le Corre (2009)
		Great bird island, Antigua	<i>R. rattus</i>	Rats recorded attacking unguarded chicks. Breeding success increased from 4.8% to 32% once rats were controlled	Varnham (2001)
		Europa, Mozambique Channel	<i>R. rattus</i>		Ringler et al. (in press)
White-tailed tropic bird	<i>P. lepturus</i>	Puerto Rico	<i>R. rattus</i>	Increase in nesting success from 12% to 46% after rat control	Schaffner (1988)
Red-billed tropic bird	<i>P. aethereus</i>	Great Bird Island & Galley Islands, Antigua	<i>R. rattus</i>	Substantial increase in numbers of nests and four-fold population increase after rat eradication	Ross (2000), Daltry (2006), Daltry et al. (2013)
		Farallón de San Ignacio, Baja California Baja	<i>R. rattus</i>	Chick survival and nest occupancy increased by 20% & 60% respectively after black rat eradication	Rodriguez and Herrera 2012
Heerman's gull	<i>Larus heermanii</i>	Rasa Island, Baja California	<i>R. rattus</i>	Breeding success increased five-fold after rat eradication	Samaniego et al. 2011
Laughing gull	<i>Leucophaeus atricilla</i>	Great Bird & Galley Islands, Rabbit and Redhead Islands, Antigua	<i>R. rattus</i>	Substantial increase in populations following rat eradications	Daltry et al. (2013)
Bonin petrel	<i>Pterodroma hypoleuca</i>	Kure Atoll	<i>R. exulans</i>	Predation of chicks	Kepler (1967)
				Nesting success of 90% where rats poisoned and 46% in non-treatment site over 2 years	Seto and Conant (1996)
Bulwer's Petrel	<i>Bulweria bulwerii</i>	Lehua Islet, Hawaii	<i>R. exulans</i>	Populations have disappeared on islands with invasive rats and recovered where rats eradicated	VanderWerf et al. (2007)
Bermuda petrel	<i>P. cahow</i>	Bermuda	<i>R. rattus</i>	No breeding where rats present	Murphy and Mowbray (1951)
			<i>R. norvegicus</i>	Four chicks recorded eaten by <i>R. rattus</i>	Dobson and Madeiros (2009)

(continued on next page)

Table 6 (continued)

Species		Location	Rat species	Evidence	References
Dark-rumped petrel	<i>Pterodromaphaeopygia phaeopygia</i>	Floreana Island, Galápagos	<i>R. rattus</i>	Previous losses of nesting petrels halted by initiation of rat poisoning programme	Cruz and Cruz (1987)
Murphy's petrel	<i>Pterodroma ultima</i>	Henderson Island	<i>R. exulans</i>	Predation of chick observed	Brooke (1995)
Kermadec petrel	<i>Pterodroma neglecta</i>	Henderson Island	<i>R. exulans</i>	Predation of chick observed	Brooke (1995)
Wedge-tailed shearwater	<i>Puffinus pacificus</i>	Kure Atoll	<i>R. exulans</i>	Suspected predation Tooth marks on eggs	Wirtz (1972) VanderWerf et al. (2007)
Audubon's shearwater	<i>P. lherminieri</i>	Hardy Islet, Fr. Antilles	<i>R. rattus</i>	Breeding success improved from 0% prior to rat eradication to 61%–63% in two years post eradication	Pascal et al. (2004)
Laysan Albatross	<i>P. immutabilis</i>	Kure Atoll	<i>R. exulans</i>	Observed predation of adults and chicks	Kepler (1967)
Black-footed albatross	<i>Phoebastria nigripes</i>	Kure atoll	<i>R. exulans</i>	Predation of chicks recorded	Woodward (1972)
Western reef heron	<i>Egretta gularis schistacea</i>	Hara Biosphere Reserve Straits of Hormuz	<i>R. rattus</i>	Egg & chick predation causing up to 49% reproduction failure in mangrove forest	Etezadifar et al. (2010)

cycles appear to be driven by intra-specific competition and/or resource restriction. It is likely that this results in increased production, recruitment and possibly survival of young when compared with populations in temperate climates but there is little comparative information to provide a firm conclusion.

Several habitats that are unique to the tropics have received little attention with regard to rats. There has been some research on rats in coconut palms for example, but little in tropical rainforest or mangroves. All these habitats are problematic for eradication practitioners, as they provide year-round food (Russell and Holmes, *in press*). For example, rats in mangrove forests are likely have different population dynamics to purely terrestrial habitats and the habitat complexities can pose significant barriers for rat poison application (Harper et al., 2014). Of particular interest is the emerging picture of tropical island rats having an effect on the marine environment, as observations of predation of marine molluscs, crustaceans, turtles and seabirds would suggest. These records hint at possibly larger effects on complex marine–terrestrial ecosystem interactions similar to those caused by other invasive species on islands (Croll et al., 2005; Kurle et al., 2008). For example, rat predation may cause seabird-vectored nutrient additions to the marine environment to cease in local waters, with a cascade of effects through the marine food chain and back to an island through other marine species (McCauley et al., 2012). Further research of this nature will likely provide a greater understanding of the breadth of rat impacts on tropical islands.

For most other species except birds there are few data on the impacts of rats or of their interactions on tropical islands. Most of the limited work on rats with terrestrial crabs for example, has focused on the relative off-take by crabs of poison intended for rat eradication, rather than the direct interactions between species. There are several species, including amphibians, large lizards, snakes, tortoises and other reptiles, along with various terrestrial invertebrates, about which we have virtually no knowledge in relation to invasive rats. As most tropical islands are repositories for high numbers of endemic species and are often biodiversity hotspots (Meyers et al., 2000), the need to understand rat population dynamics, use experimental techniques to assess their impacts on native species and, in many cases, control or eradicate them is urgent.

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