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Special Issue Article: Tropical rat eradication

The response of black rats (*Rattus rattus*) to evergreen and seasonally arid habitats: Informing eradication planning on a tropical island

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ABSTRACT

Rat eradications on tropical islands have been less successful than operations in temperate climates. This is likely due to poor understanding of the factors unique to tropical regions that rat populations respond to, such as high numbers of land crabs, aseasonal climates and habitats not found at higher latitudes. On Aldabra Atoll, southern Seychelles, black rats were monitored for one year in three habitats over three climatic seasons to investigate changes in density and breeding to inform planning for a possible rat eradication. Rats bred all year in mangrove forest and in two of three seasons, including the dry season, in *Pemphis* forest, probably resulting from the saline tolerance of these habitats: lush vegetation and seeds were available there during the dry season. In contrast, rats from the adjacent mixed-scrub habitat only bred in the wet season due to desiccation of vegetation and lack of fresh water during other times of the year. Bait consumption trials showed that all rats ingested dyed bait when applied at 15 kg/ha, despite high rat densities and substantial bait interference by non-target species, but not at an application rate of 10 kg/ha. A novel 'bola' technique was tested for distributing bait into mangrove forest, where aerially applied rat bait would normally be lost due to tidal inundation. The method is likely to improve rat exposure to bait in mangrove forest and other habitats on tropical islands, and warrants further development.

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1. Introduction

The introduction of invasive rats (*Rattus exulans, Rattus rattus, Rattus norvegicus*) to tropical islands has resulted in reductions of native animal and plant populations, often to extinction. Rats disrupt ecosystem function by causing cascades of collapse, through interruption of nutrient pathways and pollination, and by seed predation (Towns et al., 2006; Towns, 2009; Kaiser-Bunbury et al., 2009; Hilton and Cuthbert, 2010; Gibson et al., 2013).

As tropical islands are often biodiversity hotspots with high levels of endemism (Meyers et al., 2000), rat invasions have had an arguably worse impact on these islands than on temperate islands (Russell and Holmes, 2015). Island ecosystems damaged by rats can be restored through rat removal (Towns et al., 2006), and eradication techniques have been developed over the past 30 years. Rats have been successfully extirpated from islands of increasingly larger size (Howald et al., 2007) particularly on temperate islands. Although rat eradications are increasingly carried out on tropical islands they have been less successful overall (Holmes et al., 2015). Several possible factors, often unique to tropical islands, account for the reduced success, including higher productivity, bait interference by terrestrial crabs (Howald et al., 2004) and other non-target species, and/or the constant food availability on aseasonal humid tropical islands promoting year-round breeding and high population densities, in contrast to seasonal higher latitude islands (Rodriguez et al., 2006; Wegmann et al., 2011).

The lower eradication success and likely causal factors indicate that the role of invasive rat ecology in eradications on tropical islands is not yet well understood. This is also evident in the timing of tropical island eradications, which has to date been on a case-by-case basis in contrast to temperate islands (Ringler et al., 2014). Tropical islands invariably have unique native species assemblages and habitats which likely result in novel interactions with invasive rats, and differences in their population biology (Russell et al., 2011). Increasing the success of rat eradications on tropical islands therefore depends on improving understanding of both invasive rat biology and population dynamics in these ecosystems, and the effectiveness of eradication techniques in the presence of non-target species.

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Tropical islands also often contain extensive areas of mangroves. Mangroves present a unique challenge to rat eradications since these areas are subject to regular tidal inundation which thwarts the current bait distribution technique of aerial pellet application (Ringler et al., 2014). As a result, eradication of rats from mangroves has only been achieved on a few small islands (<30 ha) where baits are manually attached to mangroves along with bait 'bolas' thrown onto the mangrove forest canopy (Wegmann et al., 2008; Rodríguez and Samaniego, 2012). The problem mangroves pose for large-scale eradications is also confounded by the lack of knowledge of rat ecology in mangroves. Rats are known to not only occur (Delattre and Le Louarn, 1981; Ringler et al., 2014) but to thrive in mangroves: rats trapped in mangroves have been found to be larger and heavier than rats trapped in other habitats (Harper et al., in press). More information on seasonal dynamics of rats in mangroves is critical for eradication planning on islands with mangroves and is therefore a key focus of this research.

Here we present the results of research into the population dynamics of black rats *R. rattus* in three different habitat types, including mangroves, on the seasonally arid tropical atoll of Aldabra in the southern Seychelles. Our specific aims are threefold: first we assess seasonal and habitat differences in rat breeding, population density and survivorship to identify the optimal season for eradication. During the dry season rats would be expected to be more constrained by limited fresh water and food availability (Russell and Ruffino, 2012) and therefore in poorer condition and at lower densities than in the wet season (Tamarin and Malecha, 1971; Clark, 1980; Previtali et al., 2009). We also expected rats trapped in mangroves to show higher productivity and survivorship, and a longer breeding season relative to other habitats. Secondly, using small-scale trials, we assess the likelihood that toxic bait would be available to all rats in three habitat types during an aerial rat eradication attempt and quantify bait removal by non-target species. Finally, we conducted an initial trial of bait distribution by hanging 'bolas' in mangroves to assess uptake rates in this habitat. Aldabra's 2000 ha of mangroves encircle a 30 km long lagoon, making manual bait application logistically and economically unfeasible, especially as part of a larger eradication operation. An effective new technique would have potential to be developed for rat eradications in a habitat previously not possible to tackle on a large scale. The overall objective of our research is to inform planning for eradications on tropical islands, particularly those with large areas of mangroves, including Aldabra, by improving knowledge of rat ecology and the effectiveness of control methods in these ecosystems.

2. Methods

2.1. Study site

Aldabra Atoll (9°24′S, 46°20′E), a UNESCO World Heritage site, is part of the Seychelles archipelago in the Western Indian Ocean (Fig. 1). With a terrestrial area of 152.6 km², Aldabra is among the largest elevated coral atolls in the world at *c.* 34 km long by 14.5 km wide. It is *c.*18 m above mean sea level at its highest point, although the greater part of the land lies only *c.* 5–8 m above mean sea level. The atoll consists of four main islands that are separated by tidal channels, the widest being 300 m across. A research station on Picard Island was established in 1971 (Fig. 1). Aldabra is managed and protected by the Seychelles Islands Foundation for the Seychelles Government. Mean annual rainfall for Aldabra is approximately 975 mm unevenly distributed throughout the year, with most rain (~600 mm) falling from December to April and the remainder of the year being dry or very dry, averaging <10 mm/

month in September and October (Walsh, 1984, SIF Unpubl. data). Temperatures vary little seasonally with the mean minimum temperature in the coldest month (July; 22.2 °C) only 2.7 °C less than the warmest month and similarly the mean maximum temperature (February; 31.2 °C) is only 3.6 °C warmer than in July.

Aldabra's rock formations comprise two main types: highly pitted and eroded limestone known as 'champignon', and smooth flat limestone called 'platin'. The three principal vegetation types relevant for this study are; 'Mixed scrub', a variable community of shrubs 3–5 m tall which may have a very open or closed canopy and thin soil; 'Pemphis scrub', dominated by *Pemphis acidula*, which often forms dense pure stands up to 6 m tall on champignon, with little soil and a saline water table; and 'Mangrove forest', up to 10 m tall, which comprises eight mangrove species and covers most of the lagoon coastline. On Picard, *Pemphis* covers the largest area, while mangrove forest covers *c.* 150 ha.

Aldabra's native terrestrial fauna includes the Aldabra giant tortoise *Aldabrachelys gigantea*, whose population exceeds 100,000 individuals, several species of native gecko and skink, a large population of nesting green turtles *Chelonia mydas*, one endemic land bird species (Aldabra drongo *Dicrurus aldabranus*) and 11 subspecies of breeding landbird including the flightless Aldabra rail *Dryolimnas cuvieri aldabranus*. Several seabird species breed on the atoll, including boobies, large numbers of frigatebirds, several tern species, and a subspecies of tropical shearwater, *Puffinus lherminieri colstoni*, apparently confined to Aldabra. Four species of bats occur, three of which are endemic. Of the insects, *c.* 38% of the estimated 1000 species are endemic. Several mammal species were introduced to Aldabra by 1900 following settlement (Stoddart, 1971). Of these, only two species remain, feral cats *Felis catus*, and black or ship rats *R. rattus.* Cats no longer occur on Picard where this research was undertaken. On Aldabra, rats are known to prey on many native invertebrate, reptile and bird species (including several life stages) and also eat seeds, seedlings and damage vegetation (Frith, 1976).

2.2. Habitat differences in breeding seasonality and productivity

Rat trapping transects were set up in all three habitats on Picard (Fig. 1), using Victor™ snap-traps for three nights. Fifty traps on a transect were zip-tied to trees at 25 m intervals about 1.5 m above ground (See Harper et al., in press for further details). Three sessions of kill-trapping were completed in 2013; January/February (wet season), June (transitional season), and October (dry season). The breeding status of trapped female rats, including the number of uterine scars and embryos, was recorded by dissection. Any possible differences in the number of embryos per female among habitats were tested using a GLM with Poisson distribution. Statistical analyses were performed using R 2.03 (R Core team, 2013). Results are presented ± SE unless stated otherwise.

2.3. Rat population density, home range estimates and survivorship

To estimate rat population density and factors influencing it, and estimate survivorship, live-trapping grids were established in all three habitat types, consisting of a seven by seven trap grid at 10 m spacing (covering *c.* 0.36 ha). We conducted three trapping sessions in 2013 to cover seasonal changes; February/March (wet season), July (transitional season), and October (dry season). Rats were trapped for 10 consecutive nights. Trapped rats were given a mild anaesthetic (Halothane®) in a plastic bag before each rat was ear-tagged with an individually-numbered metal fingerling tag. Sex, age (adult, juvenile) and weight were recorded before being released. All captures and recapture locations within the grid were noted. Population density was calculated using spatially explicit capture recapture (Borchers and Efford, 2008) with
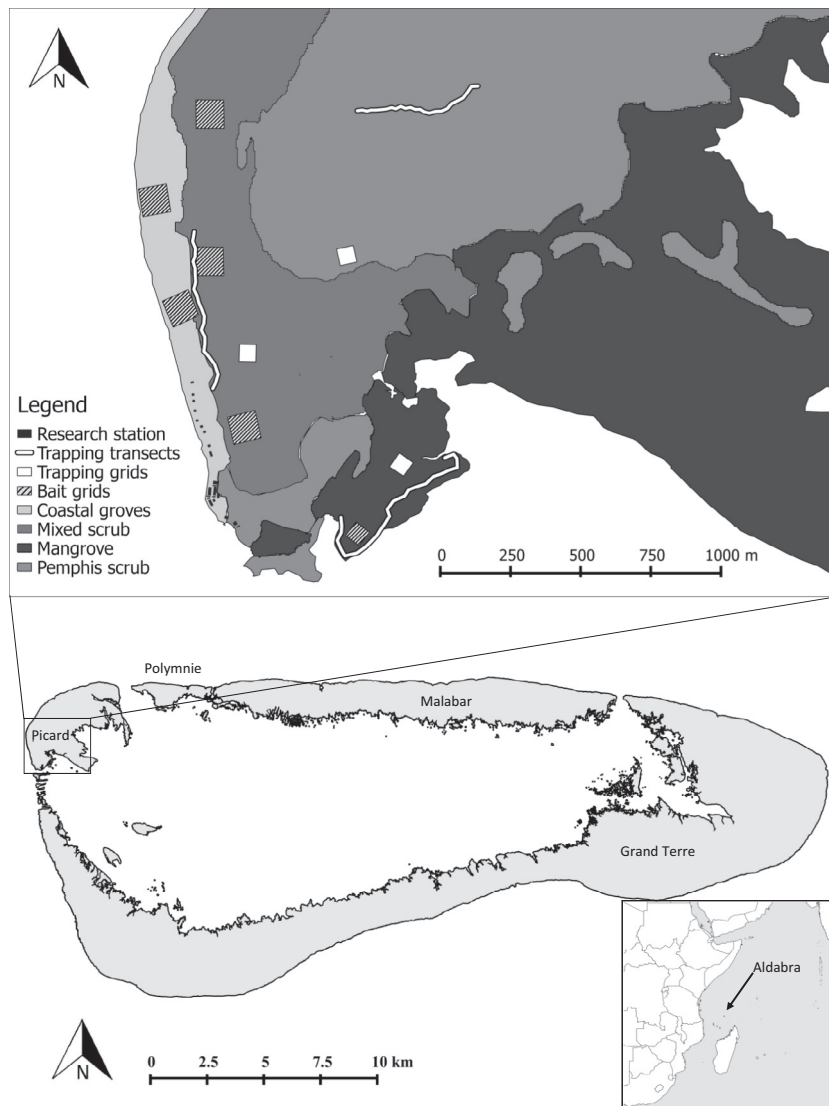
Fig. 1. Location of the trapping grids in three habitats on Ile Picard, Aldabra Atoll, Western Indian Ocean (inset).

package SECR. We assume a half-normal detection curve function adjusted by a combination of g_0, the detection probability at home range centre (range centre and trap coincide), and σ (the spatial scale of detection), and implement a conditional maximum likelihood to incorporate individual covariates for sex and age. Range centres are assumed to be random (Poisson distribution) and rat densities (D) were estimated by using a 100 m buffer around the trapping grid. Given the large number of possible models, we first constructed a series of possible models including the additive effects of habitat and season on g_0 and σ to identify the environmental model with greatest support. Akaike's information criterion (AIC) was used to select between models. From this model, we then constructed all possible models containing additive effects of age and sex on g_0 and σ to identify the environmental–individual model with greatest support. We used the nine grids across seasons and habitats to determine important covariates of density using model selection, but more precisely estimated density across all grids (trial rat bait applications; Section 2.4) using models where density depended only on one session.

For home range estimation of adult males and females in the three habitats we used the technique described in Ringler et al. (2014). Using a circular hazard distribution we calculated the 95% home ranges (HR95) using the spatial detection function as follows: $\pi \times (3.36 \times \sigma)^2$.

An estimate of the apparent overall survival of rats after eight months was calculated from recaptures of previously marked rats after three seasons in each habitat using the formula:

$$\text{Recapture rate}(= \text{apparent survival}) = (N\,mr_3/Nmr_1)$$

where mr_1 animals were marked and released in session 1; mr_3 animals were marked and released in session 3.

An index of habitat favourability (Fv) for rats in each habitat was estimated by combining the recapture data, as a proxy for survival, with mean litter size and annual productivity. In this case recapture rates are assumed to be the same for juveniles, and are likely to be an overestimate. Initially, the mean number of litters produced each year per adult female in each habitat was calculated (Emlen and Davis, 1948; Moller and Craig, 1987). This was then multiplied by the observed average number of embryos produced by pregnant females each season. These totals were added together and the final total multiplied by recapture rates, as follows:

$$\text{Fv} = \left(\sum b^{1,2,3}(t*p/18) \right) * e * s$$

where t = No. of days in breeding season; p = proportion of pregnant females; 18 = days of observed pregnancy; e = average number of embryos produced by pregnant females; b^x = breeding season x; s = observed recaptures over the three seasons. For these calculations each breeding season (t) is assumed to be equal to one of the climatic seasons, i.e. four months (122 days).

2.4. Trial rat bait applications

Small-scale trials were carried out on five bait-trial grids to test the effectiveness of two bait application rates; 15 kg/ha and 10 kg/ha at sites with high and low land-crab densities. The higher application rate is recommended where dense populations of hermit crabs occur, to limit the impacts of bait interference (Griffiths et al., 2011), while the lower application rate is encouraged to reduce non-target bait consumption (Pitt et al., 2015). The bait used in all trials was non-toxic pollard rat bait pellets Bell Labs Conservation 25 W' dyed with pyranine. The grids were 100 × 100 m, with five parallel lines cut at 25-m intervals. Grids were at least 400 m apart to ensure independence. Five tomahawk collapsible cage-traps were set at 25-m intervals on each cut line for a total of 25 traps per grid, and traps were attached to trees 1–1.5 m above ground to avoid non-target captures. Three grids were cut in mixed scrub (low land crab abundance) and two additional grids were established at coastal sites (high land crab abundance) (Fig. 1). Coastal vegetation comprised a mixture of *Casuarina equisetifolia*, native scrub and coconut palms. Rat density was estimated in each of the three mixed scrub grids as described in Section 2.3.

Due to high interference of non-target species with cage traps it was not possible to estimate rat density in the coastal grids. Therefore much smaller Victor snap-traps were set above ground where possible at the coastal grids, for three consecutive nights. To estimate relative numbers of rats at each of these grids, an index of abundance was calculated from the number of rats trapped divided by the number of traps set each night.

Transects were carried out on the cut and marked 100 m traplines to estimate the population density of non-target species within each trapping grid that were likely to consume non-toxic rat bait. Non-target species included giant tortoises, hermit crabs (principally *Coenobita rugosus*), coconut crabs *Birgus latro* and land crabs *Cardisoma carnifex*. Differing detection widths were used to count each species. Transect counts on the marked lines were carried out each day for three days immediately prior to the bait application. We slowly walked along the marked lines counting all animals seen. Tortoises were counted within 5 m of each side of transects while the detection width for hermit crabs was 0.5 m. It is likely that only hermit crabs with shells larger than 1 cm in diameter were counted as refuges small than 1 cm were present. Counts were carried out at dusk during the peak of crab activity.

The bait was hand-spread at 25-m intervals along the grid lines, at a rate of 15 kg/ha in December 2013 in all five grids. A second application of 10 kg/ha was spread at the same sites four months later. Kill-trapping of rats was initiated two to four days after each bait application to estimate the percentage of bait uptake by rats. An internal grid of kill-traps was established within the main grid of all five sites, which consisted of 15 Victor snap traps set on the three internal lines at 12.5-m intervals and 25 m from the outer perimeter of the main grid. This 25-m buffer reduced the risk of trapping rats from outside the grid that had not been exposed to bait. Four 5-m square plots were established randomly within the three internal lines of the grids to measure bait removal over the four days following bait application. Trapping continued for three nights. All kill-trapped rats were dissected to record the number of animals that had consumed the bait (indicated by

pyranine-dyed alimentary tracts). The amount of bait was measured in all of the plots daily and the mean percentage of bait removed from each grid each day was calculated.

2.5. Mangrove bait bola trials

The grid was the same configuration as described in Section 2.3 and located in mangrove forest (Fig. 1). Rat population density within the trial site was measured in March 2014 immediately before the trial, as outlined in Section 2.3. Bait bolas were constructed by drilling 2 mm holes into the centre of 10–15 mm bait pellets and threading a 250 mm length of string through the holes and knotting the ends. A bait pellet on each end of the string formed a two-bait bola weighing c. 4.4 g. Bolas were manually thrown into mangrove trees on the cut grid as described in Section 2.4 at an application rate of c. 10.3 kg/ha. Rats were kill-trapped four days after bait application. Tomahawk collapsible cage-traps were attached to trees c. 1.5 m above the high tide line with cable-ties and baited with a mixture of peanut butter and rolled oats. Rats were trapped in the centre of the grid on the five internal cut lines at 10-m intervals and 10 m from the outer perimeter of the main grid. Trapped rats were transferred to a plastic bag and euthanised with Halothane®. All rats were later necropsied as per the other kill-trap lines.

3. Results

3.1. Habitat differences in breeding seasonality and productivity

Over all three seasons, more rats were kill-trapped in mangrove forest than in mixed-scrub or *Pemphis* habitat (Table 1). Female rats had significantly more embryos per litter in mangrove forest than the other habitats (Table 1; $z = 2.59$, $p = 0.01$). In the wet season pregnant rats were trapped in all habitats. Mangrove was the only habitat where breeding occurred over all three seasons, while in mixed scrub breeding only occurred during the wet season (Fig. 2).

3.2. Rat population density, home range and survivorship

The number of rats caught in the mark-recapture grids is shown in Table 1. The environmental model with highest support (91%) was the fully specified model of habitat and season effects on both g_0 and σ. The final environmental-individual model with highest support (100%) was the fully specified model with age and sex effects on both g_0 and σ. Population densities ranged from 20.2 (±4.1) to 42.0 (±6.1) rats/ha in the three habitats over the three seasons (Fig. 3), g_0 ranged widely from 0.10 to 0.54 and σ from 11.2 to 18.8 m. *Pemphis* habitat had lower g_0 (β: −0.285, s.e. 0.153), but higher σ (β: 0.235, s.e. 0.056). The transitional season had higher g_0 (β: 0.621, s.e. 0.149), while the wet season had higher σ (β: 0.135, s.e. 0.056). Males and juveniles had lower g_0 ($\beta[\male]$: −0.80, s.e. 0.13/β[Juv.]: −0.697, s.e. 0.145) than females. Rat density was broadly similar for all the habitats, except in mangrove forest, when density was higher during the dry season (Fig. 3). The largest estimated 95% home ranges of male rats were in *Pemphis* (Fig. 4). For both sexes in all habitats home range size decreased from a maximum in the wet season to a minimum in the transitional season.

Rats trapped in mangrove forest showed apparent higher survival, as deduced from recapture rates, from initial capture to 8 months than in the other habitats (Table 1). The habitat favourability index was highest for mangrove (Table 1). Although *Pemphis* had high productivity per female, the low recapture rates reduced

Table 1
Black rat trapping results and reproductive and population dynamics in three habitats (mixed scrub, *Pemphis* scrub and mangroves) in three seasons (wet, dry and transitional) on Aldabra Atoll. The total number of trapped rats differs from seasonal totals due to interference with kill-trapped rats by coconut crabs.

|	Mixed scrub				*Pemphis* scrub				Mangroves			
	Wet	Trans	Dry	Total	Wet	Trans	Dry	Total	Wet	Trans	Dry	Total
Kill-trapping												
# Trapped rats	51	40	51	**134**	62	33	23	**109**	65	44	41	**148**
Embryos/litter (±SE)			n/a	3.0 ± 1.0			n/a	2.9 ± 0.2				4.1 ± 0.24
Breeding (yes/no)	Yes	No	No	n/a	Yes	No	Yes	n/a	Yes	Yes	Yes	n/a
Live-trapping												
# Individuals trapped	28	32	34	**60**	36	31	41	**80**	41	30	51	**57**
Apparent survival to 8 months	n/a	n/a	n/a	30%	n/a	n/a	n/a	16.7%	n/a	n/a	n/a	45%
Productivity/female (# embryos)	n/a	n/a	n/a	1.8	n/a	n/a	n/a	21.7	n/a	n/a	n/a	13.3
Habitat favourability	n/a	n/a	n/a	0.05	n/a	n/a	n/a	3.61	n/a	n/a	n/a	6.0

Bold values are the total number of rats trapped.
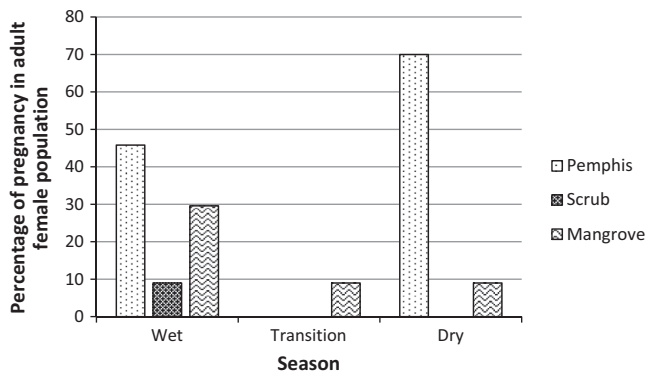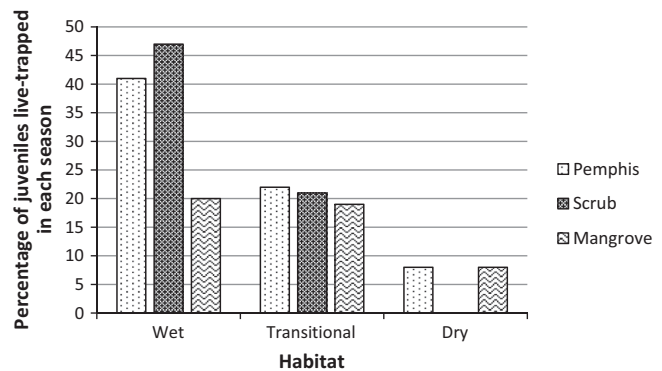

Fig. 2. The percentage of adult female rats breeding in mangrove, *Pemphis* and mixed-scrub over three seasons on Aldabra.
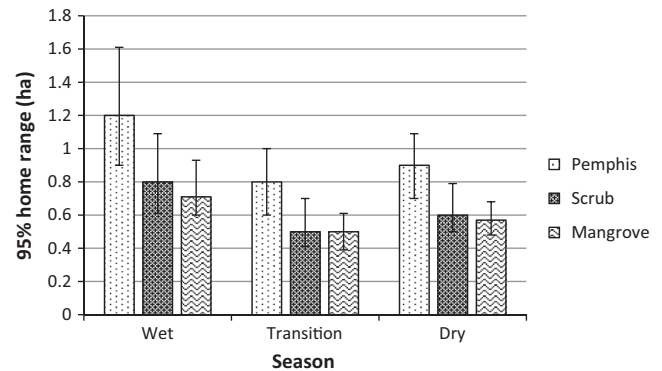
Fig. 4. Seasonal changes in the estimated 95% home range (± 95% C.I.) of male black rats in three habitats on Aldabra.
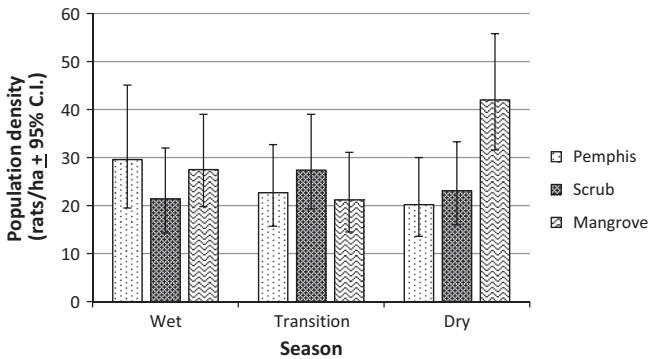
Fig. 3. Seasonal changes in the population density (±95% C.I.) of black rats in three habitats on Aldabra.

Fig. 5. Seasonal captures of juvenile rats on mark-recapture grids in three habitats as a percentage of the total sampled population.

the favourability index and the converse was true for mangrove forest.

Although an overall smaller percentage of juveniles of the sampled populations was live-trapped in mangrove forest than the other habitats, juveniles were trapped every season there (Fig. 5).

3.3. Trial bait applications

Before the first trial, the three mixed-scrub grids had rat population densities of 43.1 (CI: 30.9–60.1) –65.9 (CI: 49.3–88.0) rats/ ha. Densities of hermit crabs were relatively low in mixed-scrub (8–192 crabs/ha) but reached 900–2000 crabs/ha in the coastal grids (Fig. 6). Densities of coconut crabs reached 174/ha in mixed-scrub grid 3 but were lower than this at all other sites.

Cardisoma spp. count range was 0–33 individuals on the mixed-scrub grids only. Like coconut crabs, tortoises reached maximum density in mixed-scrub grid 3 at 16.4/ha. All the other sites had <8 tortoises/ha.

All 79 rats trapped in the five grids had consumed dyed bait. Daily bait loss during the first trial was considerably higher on the coast grids than within the mixed scrub and within three nights all the bait had been removed on the coast (Fig. 7). On the mixed scrub grids at least 20% of the bait was still present after four nights and on grid 2, with the lowest population density, 58% of the bait remained by the fourth night. Rat trapping success was relatively high in the mixed-scrub grids with 20, 17 and 21 rats caught with trapping success of 67%, 57% and 70% on Grids 1–3 respectively. Fewer rats were trapped on the coast grids with
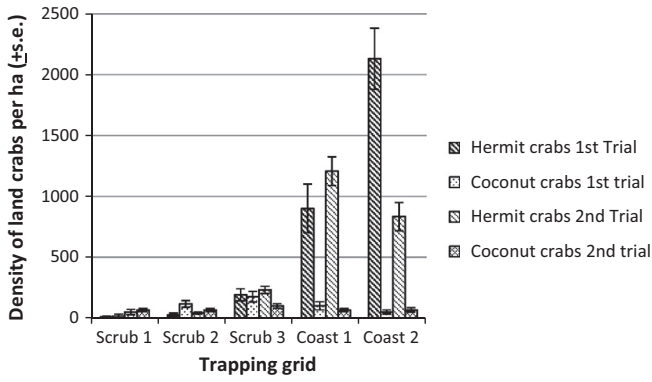
Fig. 6. Density of hermit crabs (*Coenobita* spp.) and coconut crabs (*Birgus latro*) during two bait trials on 1-ha grids in mixed-scrub and the coast on Aldabra.

10 and 12 rats caught and only 22% and 27% trapping success on Grids 1 and 2 respectively. Using this simple index of abundance for the mixed-scrub grids revealed a positive correlation with the observed population density four days prior ($R^2 = 0.99$). Using the regression equation, we estimated rat densities on the coast grids at 24–28 rats/ha. Many hermit crabs were observed consuming bait at the coast grids and tortoises were observed eating bait at the coast grids and in Grid 3 in the mixed-scrub.

For the second trial application at 10 kg/ha, the densities of all species were similar to the first trial (Fig. 8). One of the mixed scrub grids had only 2% of the bait still present after three nights so further counts were stopped. On grid 2, with the lowest population density, 54% of the bait remained by the third night.
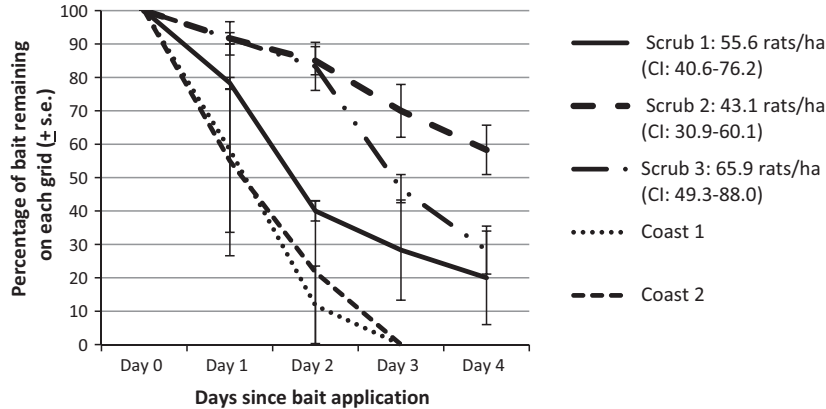
All 63 rats trapped in the mixed-scrub grids had consumed dyed bait but of the 20 rats trapped on the coast grids one adult female had no trace of dye in her alimentary tract. The index of abundance for the mixed scrub grids showed a positive correlation with the observed population density ($R^2 = 0.90$) and the regression equation suggests that rat population density on the coast grids was approximately 19–28 rats/ha. Again many hermit crabs and tortoises were observed consuming bait at the coast grids.

Relatively long-distance movements of >100 m were noted between the various mixed-scrub grids and to and from the coast grids as well as between the mangrove live-trapping grid and the mangrove kill-traps between trapping seasons. All observed long-distance dispersals were by adults and significantly more male ($n = 11$) than female ($n = 1$) animals dispersed >100 m ($\chi_1^2 = 6.74$, $p = 0.009$). The longest recorded dispersal was 650 m by an adult male trapped on the *Pemphis* kill line in March 2014 after being tagged in the *Pemphis* grid in October 2013.

3.4. Mangrove bait trial

In the mangrove bait trial trapping grid a total of 25 rats (10 adult males, nine adult females, six juveniles) were live-trapped over 10 days and the population density was estimated at 18.4 ± 3.8 rats/ha. Five days after 'bola' bait application 19 rats (nine adult males, seven adult females, three juveniles) were kill-trapped in the inner grid. Four of these rats were not captured during the live-trapping (three adult males, one adult female). Necropsy revealed that all 19 of these rats had consumed dyed bait. Rats that had eaten dyed bait were also caught on the nearby trapping transect one week after trial completion.

Fig. 7. Removal of rat bait applied to 1-ha grids in mixed-scrub and the coast on Aldabra at a rate of 15 kg/ha.

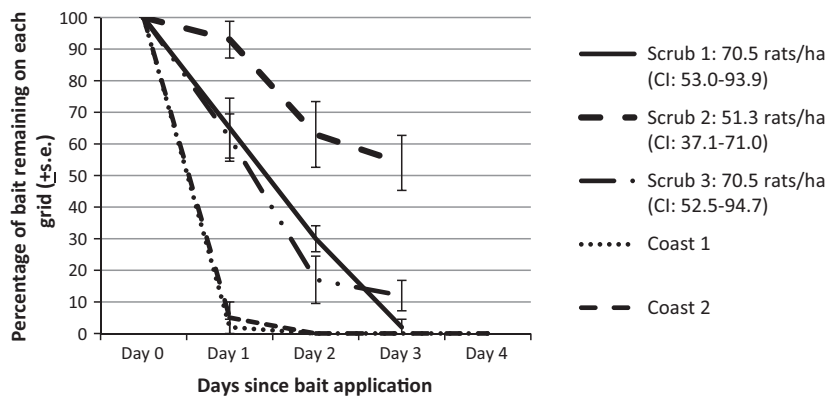**Fig. 8.** Removal of rat bait applied to 1-ha grids in mixed-scrub and the coast on Aldabra at a rate of 10 kg/ha.

4. Discussion

4.1. Rat population dynamics in three habitats

Tropical mangrove forest appears to be a particularly favourable habitat for black rats, with high productivity and apparent survival. Breeding was also recorded in all seasons in contrast to the 'terrestrial' habitats. Although *Pemphis* forest and mixed scrub had similar population densities and fecundity, survival was the lowest in *Pemphis*. Rats in *Pemphis* bred through the dry and wet season with no breeding in the transitional season, while in mixed scrub, breeding was restricted to the wet season. Population densities on Aldabra were similar to black rat populations in forest on islands in the Mozambique Channel (Russell et al., 2011). The high rat densities recorded in the mixed-scrub trial grids in December appears to be a due to increased breeding and numbers of juveniles associated with a flush of resources at the start of the wet season (Figs. 2 and 5).

The lack of breeding in mixed-scrub outside the wet season may be due to the state of the foliage leading into the dry season, which became increasingly desiccated with substantial leaf loss. Indeed the dry season is when most bark stripping by rats is recorded in mixed-scrub (Seychelles Islands Foundation, unpubl. data) which suggests the rats are suffering from water stress. *Pemphis* scrub is evergreen with fruit present all year (Seychelles Islands Foundation, unpubl. data), as it is tolerant of the saline water table which permeates the limestone. Breeding occurred all year in mangrove forest which is similarly tolerant of salt water and remains green throughout the dry season. The sustained breeding in mangrove forest in contrast to the transitional season breeding hiatus in *Pemphis* may be caused by the continuous availability of high-quality protein prey in the form of marine molluscs in the mangroves (Harper et al., in press). In this case it appears that breeding constraints on rats, caused by resource restriction due to seasonal aridity, have only occurred in mixed-scrub. The saline tolerant sites on Aldabra appear to be functionally similar to 'wet-tropical' islands where rats can breed more or less continuously due to year-round availability of sufficient fresh water and hence, resources (Russell et al., 2011).

Some emigration might have occurred between habitats, but recorded large-scale movements were mainly by adult males, suggesting it was largely driven by competition for females. Mangrove forest would be expected to be a 'source' population, as it appears to have high quality resources and the high apparent survival there suggests low population turnover. Although there were an apparently large number of juveniles being produced, judging by the litter size relative to the other habitats, juveniles comprised a smaller percentage of captures in mangroves than in other habitats. Elsewhere, subordinate animals' access to higher quality resources appear to be restricted through intra-specific territorial interactions (Ruffino et al., 2011; Russell and Ruffino, 2012), which in this case may result in increased juvenile dispersal out of mangrove forest. Further intensive trapping across habitat boundaries near existing live-trapping grids, or radio-telemetry, could be used to investigate the timing, scale and composition of any inter-habitat dispersal.

Although pregnant rats in mangrove forest produced more embryos per litter than in other habitats on Aldabra, it was fewer than recorded on other tropical islands. The average number of embryos per litter recorded for black rats on Guadeloupe (Antilles), the Galapagos, New Caledonia and Hawaii were 5.4, 5.0, 5.3, and 4.3 respectively (Nicholson and Warner, 1953; Clark, 1980; Delattre and Le Louarn, 1981; Lindsey et al., 1999). The lower litter sizes recorded at Aldabra are probably offset by better survival than on the other islands, likely related to the lack of introduced mammalian predators on Picard.

4.2. Bait consumption by rats and non-target species

At an application rate of 15 kg/ha the highest bait loss on two mixed-scrub grids occurred where the rat population density was the highest, suggesting that rats were removing baits at a rate positively related to population density. At the lower rate this relationship disappeared, probably due to the relatively high bait removal by non-target species and curtailed temporal availability of bait. It is possible that the one female rat that did not consume bait in the second trial was not exposed to it if she had immigrated from outside the grid, but the high bait loss due to land crabs appears a more likely explanation.

During the first trial all the bait from the coastal grids was consumed within three nights and although the apparently small number of rats there had all eaten dyed bait, most bait is likely to have been consumed by the dense population of hermit crabs. In the second trial all the bait was consumed by the second day. This mirrors the magnitude of bait loss caused by hermit crabs elsewhere on tropical islands, with similar estimated crab densities (Howald et al., 2004; Wegmann, 2008). If almost all the bait consumption was by hermit crabs, the approximately 800–2000 crabs present on the coast grids would have consumed about at least 5 g or two of the 2.4 g baits each per night, which is apparently achievable for this species due to their habit of seeking out and forming dense aggregations around food sources (Wegmann, 2008). Activity in other crab species is depressed by aridity elsewhere and there is a marked seasonality in the activity of coconut crabs, with the fewest individuals being observed in the dry season (Seychelles Islands Foundation, unpubl. data). Indeed the lower numbers of land crabs and tortoises recorded in the second trial on all grids was likely due to dispersal as climatic conditions were more humid, whereas dry conditions prevailed during the first trial at the end of the dry season. This has clear implications in regard to bait loss during a rat eradication operation and where possible timing of an eradication during likely dry conditions should reduce bait interference by crabs.

In the first bait application trial all rats subsequently kill-trapped on the five bait grids had eaten dyed bait but not in the second trial with a third less bait applied. These results support the conclusion of Griffiths et al., (2011) that above a threshold bait application rate of 15 kg/ha, rats are able to access bait even when substantial populations of land crabs are present. However, it should be noted that on the mixed-scrub grids with low numbers of land crabs all rats consumed bait at both application rates. Bait application rates as low as 3 kg/ha have resulted in successful rat eradications on tropical arid islands with few non-target species (Harper and Carrion, 2011; Harper et al., 2011), which highlights the effects of contrasting climatic conditions and non-target bait interference on rat eradication success on tropical islands. In this case the higher application rate appears to be sufficient to eradicate rats from the 'terrestrial' habitats on Aldabra Atoll at the end of the dry season. Elsewhere, trial assessments of bait consumption within a rat population in the face of likely substantial bait loss from land crabs should be undertaken until practitioners better understand the interactions between rats, crabs and poison bait (Pott et al., 2015).

Tortoises did not appear to contribute to any significant bait loss attributable to non-target species. On one mixed-scrub and the coast grids tortoises were observed eating large amounts of bait during both trials but bait loss within the grid sub-plots did not appear to reflect this.

Several bird species including the Aldabra rail are also likely to remove small amounts of bait. Although this bait loss is unlikely to result in an eradication failure, birds in particular are highly susceptible to anticoagulant poison (Eason and Spurr, 1995). Some species, like the Aldabra rail, would require management to

prevent severe declines in numbers during an eradication operation. Giant tortoises in the Galapagos are apparently little affected by anticoagulants (Fisher, 2011) but additional trials on the Aldabra tortoises would be prudent as they are a different genera.

At this stage, the most promising period for an eradication attempt on Aldabra appears to be during the transition months of July–September when rat breeding is at the lowest, but a longer seasonal data set would give more certainty to this conclusion.

4.3. Mangrove bait trial

The initial small scale trial of bait bolas in mangrove forest shows promise, with all rats consuming baits, suggesting that the technique is worth pursuing. At this stage the technique of aerial application of 'bola' baits into trees is in its formative stages (Savarie and Tope, 2004) and unlikely to be available in the near future. Aspects of the technique, such as the effective application rate for rat eradication for example, would also require trials. However, our results suggest that black rats are actively foraging in mangrove canopy and do not require access to mudflats, which has been observed in continuously flooded mangrove forest in Mexico (A. Samaniego, pers. comm.). Although the delivery of bait to the ground achieved high consumption rates by rats, there are likely to be advantages in applying bait to terrestrial and littoral forest canopies where black rats are foraging. Likely advantages of bola baits would be longer availability of baits, a reduction in bait interference by crabs, and resilience to cyclonic flooding events, all of which are a probable cause of some rat eradication failures (Russell et al., 2015).

5. Conclusions

The saline tolerant habitats of Pemphis and in particular mangrove forest, remain evergreen during arid conditions and these habitats are favourable for rats on Aldabra. In contrast vegetation in the adjacent mixed-scrub became increasingly water stressed with the onset of the dry season with a consequent restricted breeding season in the rat population. This situation is a microcosm of the response of invasive rats to wet tropical and arid conditions normally found on distinct tropical islands.

Eradication appears feasible in the terrestrial habitats of Aldabra Atoll and is likely to be most effective at an application rate of 15 kg/ha during the transitional season when breeding has ceased, contrary to expectations of reduced breeding in the dry season. Poison bait interference was recorded by several non-target species, of which hermit crabs removed substantial amounts of bait at both application rates.

Bola rat baits distributed in the canopy of mangrove trees appeared to be an effective technique to deliver rat bait in a habitat where tidal inundation makes other bait delivery methods ineffective. Although the continued application of rat bait onto the ground will remain the fundamental method for eradications, the mangrove bola bait trial presented suggests the technique has a promising future. Black rats apparently spend a large proportion of time on the ground (Howald et al., 2004) but arboreal bola baits are likely to increase the exposure of black rats to poison baits. Combinations of ground and tree baiting could improve tropical rat eradication success in future.

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