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Successful management of invasive rats across a fragmented landscape

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Summary

Introduced mammalian predators are responsible for the decline and extinction of many native species, with rats (genus *Rattus*) being among the most widespread and damaging invaders worldwide. In a naturally fragmented landscape, we demonstrate the multi-year effectiveness of snap traps in the removal of *Rattus rattus* and *Rattus exulans* from lava-surrounded forest fragments ranging in size from <0.1 to >10 ha. Relative to other studies, we observed low levels of fragment recolonization. Larger rats were the first to be trapped, with the average size of trapped rats decreasing over time. Rat removal led to distinct shifts in the foraging height and location of mongooses and mice, emphasizing the need to focus control efforts on multiple invasive species at once. Furthermore, because of a specially designed trap casing, we observed low non-target capture rates, suggesting that on Hawaiʻi and similar islands lacking native rodents the risk of killing non-target species in snap traps may be lower than the application of rodenticides, which have the potential to contaminate food webs. These efforts demonstrate that targeted snap-trapping is an effective removal method for invasive rats in fragmented habitats and that, where used, monitoring of recolonization should be included as part of a comprehensive biodiversity management strategy.

Introduction

Introduced mammalian predators are responsible for the decline and extinction of a disproportionately large quantity of native fauna relative to other introduced guilds and taxa (Doherty et al. 2015). Great effort has gone into monitoring and reducing introduced predators via fencing, culling and poisoning, at an estimated global annual cost of billions of dollars (Courchamp et al. 2003, Doherty et al. 2015). Recent decades have seen an increase in the successful control and eradication of invasive mammals (Courchamp et al. 2003, Jones et al. 2016) and in the documentation of post-eradication benefits for native biodiversity and trophic cascades (Doherty et al. 2016).

Rats (genus *Rattus*, particularly *R. rattus*, *R. norvegicus* and *R. exulans*) are among the most widespread and damaging invasive species, particularly on islands, of which only an estimated 10% remain rat-free (Towns et al. 2006). Numerous case studies from island systems have demonstrated the negative impacts of rats, as well as the recovery of prey species following their eradication (VanderWerf 2001, Fukami et al. 2006, Heath et al. 2008, Mulder et al. 2009, Auld et al. 2010, Pender et al. 2013, Shiels et al. 2014, Russell & Holmes 2015, Tabak et al. 2015). Black rats (alternatively, ship or roof rats; *R. rattus* L.) are particularly damaging as they have been the primary driver of presumed extinctions of at least 60 species worldwide (Towns et al. 2006). The black rat poses significant threats in forested ecosystems because it is an adept tree climber and generalist consumer of fruits, seeds, arthropods, bird eggs and nestlings and carrion (Norman 1970, Cole et al. 2000, Fukami et al. 2006, Matsui et al. 2010, VanderWerf et al. 2011, Shiels et al. 2013, Shiels et al. 2014). Black rats consume bird nest contents directly and also shift bird demography, foraging behaviour and spatial habitat use (Knowlton et al. 2017, Wilson Rankin et al. 2018). Members of the *Rattus* genus can also exacerbate the negative impacts of other invasive species by dispersing non-native seeds or propagules (Shiels 2011), as vectoring pathogens (Meerburg et al. 2009, Smith & Banks 2014) and by serving as alternative prey for higher-level predators (Shiels et al. 2014).

Widespread eradication efforts targeting rats and other invasive mammalian predators on islands are represented by hundreds of successful cases of recovery of native flora and fauna (Jones et al. 2016, Newton et al. 2016, Duron et al. 2017, Wolf et al. 2018), including knock-on secondary extinctions of other invasive species (Lafferty et al. 2018). Key to many successful eradications is the use of aerially broadcast poison baits, formulated with anticoagulants such as diphacinone or brodifacoum, to cover large, spatially isolated areas in short time intervals (Keitt et al. 2015). However, among those successes are problematic failures with non-target effects (e.g., Buckelew et al. 2011) or the spread of toxicants through food webs (Pitt et al. 2015). Snap-trapping avoids some of the negatives associated with poison baiting, namely resistance to anticoagulent rodenticides, which has been documented in *R. rattus* (Tanaka et al. 2012), *R. norvegicus* (Cowan et al. 2017) and *Mus musculus* (Siddiqi 1982, Marquez et al. 2019). For these reasons, toxicant bait broadcast techniques may be logistically and politically unfeasible in some areas (Duron et al. 2017), necessitating strategic development and testing of alternative techniques, such as high-density snap trap grids.

Although rat removal has received a lot of attention in a conservation context, major gaps in our knowledge exist with regards to where rats forage in invaded habitats and whether snap-trapping efficacy scales across a gradient of habitat sizes. Here, we demonstrate the effectiveness of snap traps, continuously maintained over four years, in localized *Rattus* removal from forest fragments on the Island of Hawai‘i and assess the non-target impacts of trapping. By combining snap traps and inked tracking cards placed at three different heights from ground to mid-canopy, we describe how rats utilize forest fragments with regards to distance from edge, overall forest fragment size and vertically into the canopy.

Methods

Study area

Trapping and survey sites were located in 34 *kīpuka* (forest fragments) on the windward north-east slope of Mauna Loa Volcano within the Upper Waiakea Forest Reserve on the Island of Hawai‘i (~19.6°N, –155.3°E). Focal *kīpuka*, isolated by a matrix of lava resulting from historical basaltic lava flows (1852–1881), ranged in size from 0.1 to 12 ha. Distributed from 1500 to 1800 m in elevation, the study area receives moderate levels of orographic precipitation (~2500 mm per year; Giambelluca et al. 2013), with mean annual temperatures at the centre of this study system of 12.5°C (Giambelluca et al. 2014). Similar to contiguous Hawaiian mesic forests, the *kīpuka* canopies are compositionally simple and dominated by mature stands of Hawaiian endemics including *Metrosideros polymorpha* Gaudichaud-Beaupré (‘*ōhi*‘*a lehua*) and *Acacia koa* Gray, although forest height increases and gap density decreases with increasing fragment size (Vaughn et al. 2014, 2015). The *kīpuka* are separated by a relatively homogeneous lava matrix, which may serve as a partial barrier to rat movement among *kīpuka*. Early successional matrix habitat, on a mixture of ‘*a*‘*ā* and *pāhoehoe* lava substrates (Macdonald et al. 1983), features scattered, short-statured ‘*ōhi*‘*a* along with shrubs, ferns and sedges (Raich et al. 1997). Both native and non-native animals inhabit these forests and use the matrix habitat (Gruner 2004), including birds endemic to Hawai‘i that have been eliminated from lower elevations (<1450 m) due to mosquito-vectored avian pox and malaria (Vanriper et al. 1986, Flaspohler et al. 2010, Samuel et al. 2015). Hawai‘i has only one native terrestrial mammal, the Hawaiian hoary bat (*Aeorestes semotus* (H. Allen)); thus, the mammalian predators present in the study system are all non-native, including the Polynesian rat (*Rattus exulans* (Peale)), house mouse (*Mus musculus* L.), Javan mongoose (*Herpestes javanicus* (Saint-Hilaire)) and the pervasive black rat (*Rattus rattus*).

Rodent trapping

We selected 16 of 34 *kīpuka* for rat removal, with each removal *kīpuka* paired with a similarly sized control *kīpuka* and spatially positioned to ensure that they were at least 500 m away from any untreated *kīpuka* (Supplementary Fig. S1, available online; Wilson Rankin et al. 2018, their fig. 1(b)). In each removal *kīpuka*, Victor M326 Pro Rat snap traps were deployed in corrugated plastic boxes with a rat-sized opening on one side (Stanford IACUC, no. 1776; Fig. S2(a) & S2(b)). Covered traps force rats to approach the traps directly, which promotes a quick kill, while the small opening reduces non-target captures. These trap boxes were distributed in a 25 m × 25 m grid system with additional traps every 12.5 m around the forest fragment perimeters (Pender et al. 2013). Prior to the first setting of traps, each trap was pre-baited with locally sourced fresh coconut 6 and 3 days prior to setting the traps. During initial trapping in June 2011, traps were set and checked daily. After the first week of trapping, take from traps decreased substantially. Episodic control efforts in continuous forest tracts on Hawai’i Island, even in combination with diphacinone bait stations, may sustain high recolonization rates between trapping periods (Nelson et al. 2002). Thus, after the first week, traps were subsequently checked and maintained every 2 weeks from July 2011 to May 2015. Trap baits were cycled between three consecutive trapping periods with commercially available peanut butter and then one trapping period with locally sourced fresh coconut.

During initial daily trapping (June 2011), catch species in each trap was recorded on site and traps were immediately rebaited and set. Baits were always changed when traps were checked, regardless of whether there was a capture. Trapped *Rattus* spp. were taken back to the US Department of Agriculture (USDA) Forest Service’s Institute for Pacific Island Forestry (Hilo, HI) for detailed analysis. We identified each collected specimen to the species level where possible, assessed sex and measured body mass, body length and tail length. After processing, carcasses were disposed of as hazardous waste.

During biweekly trapping (July 2011–May 2015), the sex and body length of the rat carcasses were recorded and tissue samples were collected for genetic work, but no additional dissections were conducted. In instances where posthumous predation or advanced decay occurred, specimens were identified to the narrowest taxonomic distinction possible. We recorded any non-target taxa caught in snap traps, including *M. musculus, H. javanicus,* kalij pheasant (*Lophura leucomelanos* (Latham)), red-billed leiothrix (*Leiothrix lutea* (Scopoli)) and slugs (Veronicellidae). During biweekly trapping, all carcasses were buried on site. Snapped traps with no sign of capture, indicating an unintended triggering, an escaped animal or the remains being removed by a scavenger, were noted.

Vertebrate survey: tracking tunnels

To assess the efficacy of our rodent trapping methods, we monitored each *kīpuka* for the presence or absence of rats and other small vertebrates using tracking tunnels. This technique attracts animals to a baited tunnel where they step on an inked tracking card and then leave ink tracks on adjacent white ends of the card as they exit. In 2009, for *kīpuka* that were larger than 0.64 ha in area, two representative trees in each *kīpuka* were selected, with one located near the *kīpuka* centre and another on the perimeter. At each tree, standard Black Trakka™ tunnels (10 cm × 10 cm × 50 cm; Gotcha Traps Ltd, New Zealand) were deployed on the forest floor, at 6 m and at 12 m. This approach allowed us to track rodent presence at the forest floor and into the canopy. For smaller *kīpuka* (<0.64 ha), we used only one survey tree located in the *kīpuka* centre. Aboveground tunnels were attached to wooden platforms ('artificial branches') and secured to the tree with an L-bracket and aluminium nails (Fig. S2(c)). A loop of 7-strand nylon parachute cord passing through the tunnel and extending to the ground was attached to a plastic base plate that fit inside the tunnel (Fig. S2(d)). The aboveground tunnels were baited by attaching a fresh ink card to the base plate, with coconut bait wired to the centre, which could be raised and lowered from the ground by reeling in the parachute cord loop. Tunnels were coconut baited once prior to the initial snap-trapping and thereafter quarterly for 4 years concurrent with the trapping efforts. Cards were left during each baiting session for 1 week before retrieval and track identification (Fig. S2(e) & S2(f)). The tracks left on each card were identified and used to confirm the presence or absence of rats in each *kīpuka*, although we were unable to distinguish the tracks of *R. rattus* from those of *R. exulans*. In addition, we could identify non-target taxa such as *M. musculus*, *H. javanicus* and introduced skinks, *Lampropholis delicata* (De Vis), from these tracking cards. To assess the efficacy of our limited spatial sampling regime, we baited and deployed an additional, one-time 50-m × 50-m grid of ground-level tracking tunnels for 72 h in all *kīpuka* in summer 2012.

Statistical analysis

To assess changes in trapping rates, we calculated the total number of rats (*Rattus* spp.) trapped each month as the response in linear mixed models, where month–year (e.g., June 2011), rat species and log-transformed *kīpuka* area (hectares) were treated as fixed effects and *kīpuka* identity was treated as a random effect. To assess whether there was any change in the size of rats trapped, body size (body length or tail length) was the response, with sex added to the model framework above as a fixed effect. For by-catch taxa from snap-trapping, we calculated the total number of individuals trapped each month as the response, with the presence or absence of rats, month, by-catch species and log-transformed *kīpuka* area modelled as fixed effects and *kīpuka* identity treated as a random effect. We then analysed the tracking tunnel data in two separate analyses: (1) the quarterly tunnel assessments at ground level, 6 m and 12 m in the canopy (2011–2015); and (2) the grid tracking effort of 2012 (all at ground level). For each, we calculated the number of tracking tunnels with identifiable rat tracks divided by the total number of tracking tunnels in that *kīpuka*. Because the response variable represents the proportion of tracking tunnel cards with a positive result, we used a binomial error structure in generalized linear mixed models. For the quarterly tunnel assessments, rat removal treatment, *kīpuka* area, tunnel height and the interaction between treatment and tunnel height were fixed effects, *kīpuka* identity was a random effect and the model was weighted by the number of tracking tunnels available in each *kīpuka*. In the one-time grid tracking effort in 2012, we excluded tunnel height (as all grid tunnels were at ground level) and included bait type as an additional fixed effect because the attractiveness of two baits was tested (Spam Classic (Hormel Foods Corporation) versus fresh coconut). For by-catch species (e.g., mice, mongoose and skink), we conducted analyses on a combined dataset of regular sampling and the 2012 grid sampling, where proportion of tracking tunnel cards with a positive hit for a non-target species was the response variable using a binomial error distribution. We included non-target species identity, rat removal treatment, *kīpuka* area, tunnel height, bait, interaction between non-target species and treatment, interaction between non-target species and tunnel height and interaction between treatment and tunnel height as fixed effects. The dataset (grid only or quarterly trapping) was nested within *kīpuka* identity as a random effect, and the model was weighted by the number of tracking tunnels available in each *kīpuka*.

For the quarterly tunnel assessments, we also estimated whether pairs of species shared or avoided using the same tracking tunnel following the method of Wells et al. (2004). Calculations were done for seven pairs of species where the calculated number exceeded the critical value of the χ^2 distribution for $p < 0.05$ ($\chi^2_{crit} = 3.84$), with species occurring at a minimum of 25 different tunnels. All model results are reported in the Supplementary Materials (Table S1). All analyses were conducted in *R* v. 3.5.0 (R Core Team 2021) and all means are reported ± SE. Mixed models were conducted using the *lmer* or *glmer* functions in package *lme4* (Bates et al. 2013). Where appropriate, *post-hoc* tests were conducted using the *emmeans* package, with false-discovery rate adjustments for multiple comparisons (Lenth 2019).

Results

Rodent trapping

Overall, we captured 660 rats, including 503 rats that we were able to identify to the species level. Black rats (*R. rattus*) represented 81.5% of the rats that were identifiable to the species level and 62.1% of all rats captured (n = 410). The less commonly trapped Polynesian rat (*R. exulans*) comprised 14.1% of all rats captured (n = 93). Overall, monthly averages of rats trapped significantly decreased over time (Fig. 1(a); $F_{1,367} = 14.97$, $p = 0.0001$), resulting in a 95% decrease over the course of the project. Similarly, non-target by-catch decreased over time (Fig. 1(b); $F_{1,311} = 10.71$, $p = 0.001$) regardless of species, although mice dominated the by-catch (327/423). By-catch in snap traps had a marginally significant positive correlation with the presence of rats ($F_{1,316} = 3.43$, $p = 0.065$). The number of rats trapped increased with *kīpuka* area (Fig. 1(c); $F_{1,367} = 14.79$, $p = 0.0001$). Both rat body size and tail length decreased over time (Fig. 2(a) & 2(b); body length: $F_{1,446} = 9.66$, $p = 0.002$; tail length: $F_{1,446} = 74.36$, $p < 0.0001$). In 2011, trapped *R. rattus* had a mean body length of 14.7 ± 0.2 cm, but this decreased to 12.6 ± 1.3 cm by 2015. The average tail length of trapped *R. rattus* followed a similar trend. In 2011, tails were an average of 17.9 ± 0.2 cm, but the mean was 14.6 ± 1.1 cm in 2015. Trapped *R. exulans* body size decreased by a similar magnitude from 2011 to 2014 (11.8 cm body and 12.5 cm tail, 9.9 cm body and 10.6 cm tail, respectively), but increased back to 2011 levels in 2015.

Tracking tunnels

For the quarterly checks, untreated *kīpuka* had a significantly higher mean proportion of tunnels with tracks of 0.51 ± 0.02 per week (n = 1336), while rat removal *kīpuka* had a mean proportion of 0.09 ± 0.01 per week (n = 1004; $F_{1,30} = 26.25$, $p < 0.0001$).

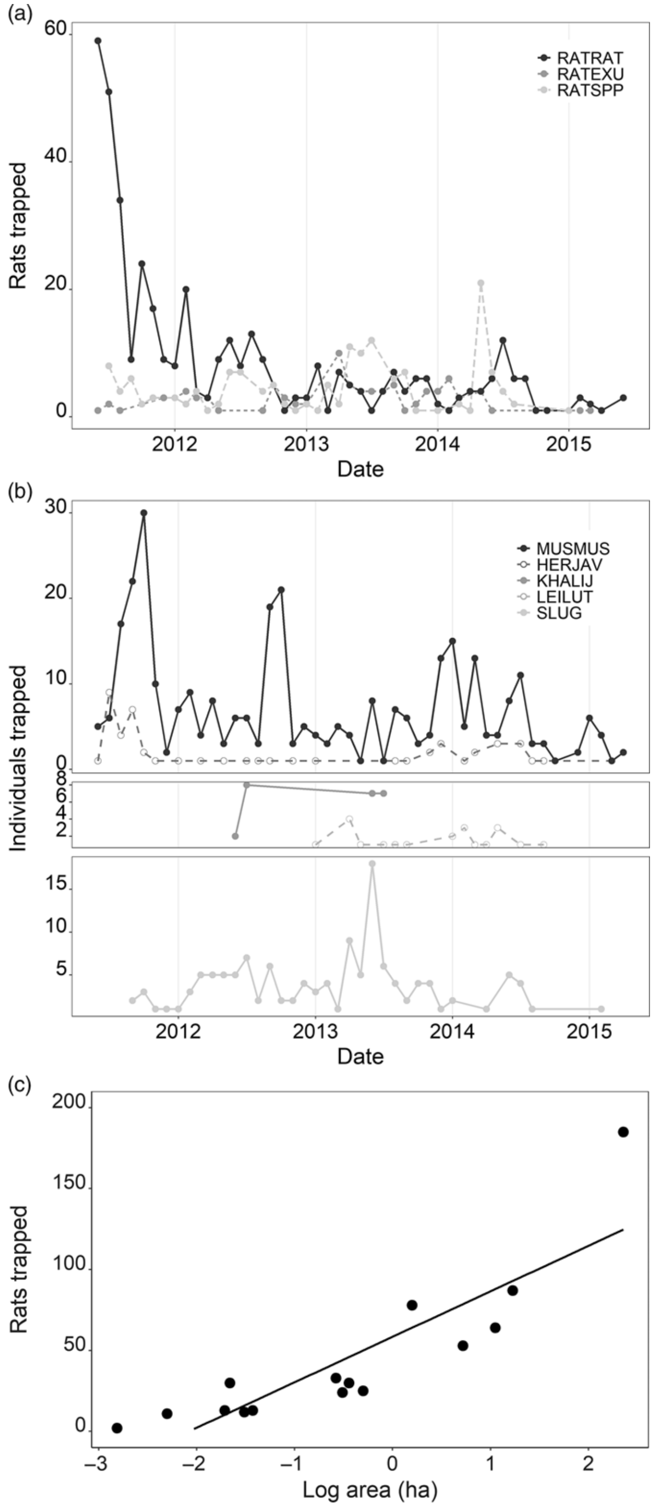

Fig. 1. Take from snap traps from July 2011 through May 2015 from 16 *kīpuka*. (a) Trapped *Rattus* individuals summed by species and month over time. (b) Non-target taxa trapped summed by species and month over time. (c) Relationship between total trapped *Rattus* individuals over entire trapping period in each *kīpuka* and log-transformed *kīpuka* area. Grey line indicates line of best fit. HERJAV = *Herpestes javanicus*; KHALIJ = *Lophura leucomelanos*; LEILUT = *Leiothrix lutea*; MUSMUS = *Mus musculus*; RATEXU = *Rattus exulans* (Polynesian rat); RATRAT = *Rattus rattus* (black rat); RATSPP = *Rattus* species; SLUG = undetermined slug species.

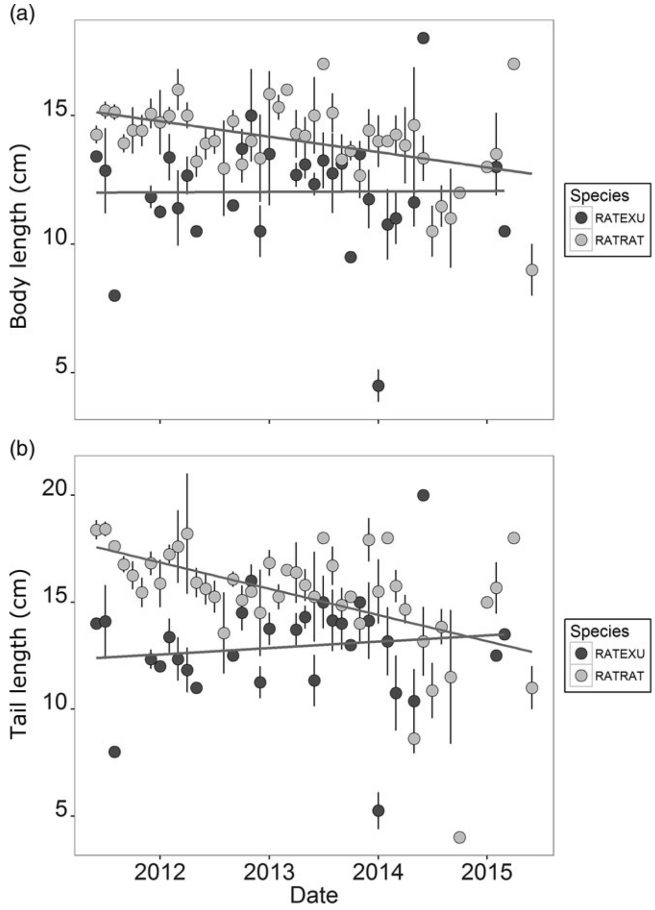

Fig. 2. Monthly mean *Rattus* (a) body length and (b) tail length in centimetres by species over time with standard error bars. RATEXU = *Rattus exulans* (Polynesian rat); RATRAT = *Rattus rattus* (black rat).

The proportion of tracking cards with tracks per week varied with location of the tracking tunnel ($F_{2,42} = 184.02$, $p < 0.0001$), with the highest proportion located on the ground and the lowest proportion at 12 m (Fig. 3; ground: 0.53 ± 0.02, 6 m: 0.23 ± 0.02, 12 m: 0.12 ± 0.02). Additionally, there was a significant interaction between treatment and tunnel height ($F_{2,43} = 7.76$, $p = 0.001$). Rat tracks were more common in untreated *kīpuka* as compared to removal *kīpuka* at all tunnel heights (ground: $\chi^2 = 113.31$, $p < 0.0001$; 6 m: $\chi^2 = 26.37$, $p < 0.0001$), except at 12 m, where there was very low detection of rats in both treatments ($\chi^2 = 0.91$, $p = 0.34$). There was only a marginal effect of *kīpuka* size on the proportion of tracking tunnels with rat tracks ($F_{1,30} = 4.2$, $p = 0.05$) and no effect of time ($F_{1,42} = 0.004$, $p = 0.95$).

When additional tracking tunnels were deployed weekly on ground-level grids in the summer of 2012, similar trends were observed. The proportion of tracking tunnels with rat tracks was significantly affected by treatment (untreated versus rat removal), tunnel location (grid versus perimeter) and bait type (coconut versus Spam). The mean proportion of tracking tunnels with rat tracks was higher in untreated *kīpuka* (0.46 ± 0.03) than rat removal *kīpuka* (0.081 ± 0.02; $F_{1,31} = 35.27$, $p < 0.0001$). The mean proportion of tracking tunnels with rat tracks was higher when Spam Classic was used as bait (0.51 ± 0.06) compared to fresh

Table 1. Proportion of tracking tunnels with tracks for each recorded species in the summer 2012 grid based on bait type in *post-hoc* tests across species.

	Mean proportion and standard error of tunnels with tracks		
Species	Coconut bait	Spam bait	χ^2 statistics
Rattus spp.	0.364 ± 0.05	0.513 ± 0.06	$\chi^2 = 28.57$, $p < 0.0001$***
Mus musculus	0.020 ± 0.01	0.125 ± 0.03	$\chi^2 = 6.36$, $p = 0.011$*
Herpestes javanicus	0.000 ± 0.00	0.240 ± 0.04	$\chi^2 = 33.01$, $p < 0.0001$***
Lampropholis delicata (Scincidae)	0.003 ± 0.01	0.030 ± 0.01	$\chi^2 = 2.65$, $p = 0.11$

*p < 0.05, **p < 0.01, ***p < 0.001.

Table 2. Number of tracking tunnels with tracks for each recorded species by treatment.

	Untreated			Treated			
Species	Ground	6 m	12 m	Ground	6 m	12 m	Total
Rattus spp.	471	191	49	77	16	3	807
Mus musculus	38	7	3	114	3	0	165
Herpestes javanicus	12	0	0	34	1	0	47
Lampropholis delicata (Scincidae)	12	1	4	7	0	1	25

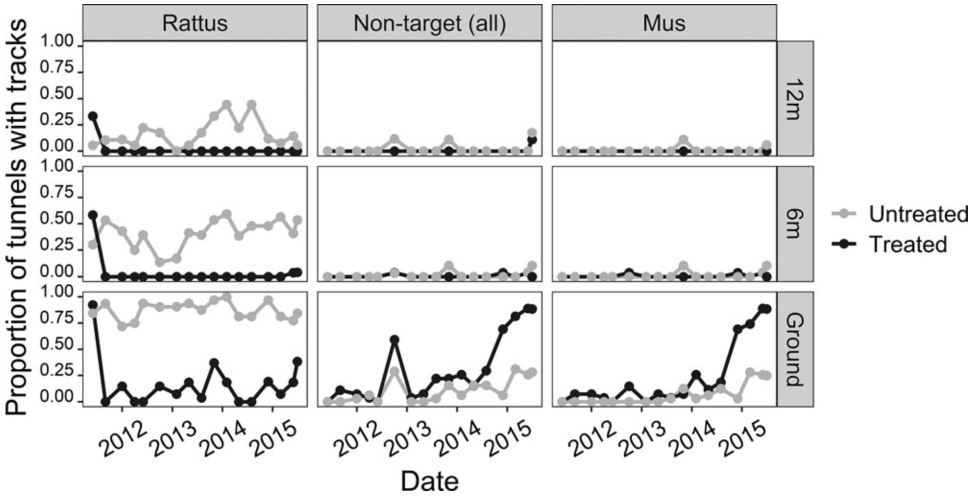

Fig. 3. Proportion of tracking tunnels with tracks over time in untreated and treated (rat removal) *kīpuka* (untreated: n = 1336, treated: n = 1004) for all *Rattus*, all non-target taxa and all *Mus musculus*.

coconut (0.36 ± 0.05; $F_{1,105} = 45.37$, $p < 0.0001$). Overall, more grid tunnels were positive for rat tracks (0.49 ± 0.06) than perimeter tunnels (0.39 ± 0.05; $F_{1,106} = 18.29$, $p < 0.0001$). There was no significant effect of *kīpuka* size on proportion of ground-level tunnels visited by rats ($F_{1,38} = 0.57$, $p = 0.46$).

Effect of rats on other vertebrate taxa

In addition to *Rattus* spp., Javan mongoose, house mouse and skink were recorded on the tracking cards. To examine how these non-native taxa used the *kīpuka*, we reran analyses on a combined dataset of the monthly trapping and the summer 2012 grid. There was a significant treatment effect (Fig. 3; $F_{1,24} = 30.90$, $p < 0.0001$), with a higher proportion of non-rat hits to tracking tunnels in treated *kīpuka* as compared to *kīpuka* with rats. There were differences among the species as well ($F_{2,715} = 68.03$, $p < 0.0001$), where house mice were by far the most common visitors to the tracking tunnels, followed by both Javan mongooses and skinks. A similar pattern for the effect of tunnel height was detected ($F_{2,671} = 32.96$, $p < 0.0001$), with the ground tunnels having the highest proportion of hits (Fig. 3). Similarly to the rats, there was a preference for Spam Classic baits ($F_{1,759} = 58.83$, $p < 0.0001$); non-target taxa – mongoose and house mouse – were significantly more attracted to Spam Classic than fresh coconut baits (Table 1). There was a significant interaction between species and treatment ($F_{2,715} = 4.94$, $p = 0.007$), where there was no difference among the non-target taxa in the proportion of tunnels hit in untreated *kīpuka*, but mice hit a higher proportion of tunnels in treated *kīpuka* as compared to mongooses and skinks. We also detected an interaction between tunnel and species ($F_{4,715} = 2.98$, $p = 0.019$): at the ground level, mice were more common than mongooses and skinks. At all other heights, there were no species differences. Similarly, there was a treatment by tunnel height interaction ($F_{2,669} = 6.60$, $p = 0.0015$), where the most non-target taxa were recorded at ground level in treated *kīpuka*.

To gain additional insight into how these species overlapped, we then examined the co-occurrence of different species of vertebrates at a specific tracking card (Table 2). There were six species pairs with each species occurring at a minimum of 30 tunnels. There was significantly higher tunnel overlap between mongoose and house mouse than expected by chance alone ($\chi^2 = 10.62$, $p = 0.0011$). There was significantly lower tunnel overlap between *R. rattus* and mongoose than expected by chance ($\chi^2 = 4.61$, $p = 0.032$), as well as lower tunnel overlap between *R. rattus* and house mouse than expected ($\chi^2 = 16.27$, $p < 0.0001$).

Discussion

Snap-trapping has a long history in the successful management of non-native, invasive predatory mammals (Shiels et al. 2014), with recent case studies showing sizable rat reductions (Armstrong et al. 2014, referenced in Simberloff et al. 2019) or even short-term eradications of populations from forest fragments (King et al. 2011). Here, we show that continuous control of rats over a 4-year period was effective at greatly reducing rat numbers in managed fragments. While colonists continued to be trapped over time, levels of colonization were low in comparison to other studies (e.g., King et al. 2011, Pender et al. 2013). The rocky, exposed habitat matrix of lava flows, which is less likely to sustain rat densities comparable to forests, may impose a partial barrier that lowers colonization rates in this study system. Comparisons across both removal and untreated *kīpuka* demonstrate that tracks of *Rattus* spp. were significantly more common on tracking cards within the grid compared to at the perimeter. This suggests that rats prefer the vegetated *kīpuka* to the lava matrix and are therefore probably using the associated edge habitats at reduced rates. Our findings are consistent with other studies of *R. rattus* that documented increased capture rates with increasing distance from the forest edge (Ruffell et al. 2014) and showed that *R. rattus* spent most of its time under vegetation rather than in open habitats (Shiels 2010). In such environments where the habitats between fragments are inhospitable or less utilized, trapping efforts may be focused on fragment interiors.

The presence of rats in removal *kīpuka*, quantified by capture rate and tracking surveys, dropped to low levels after a single week of trapping. The continued trapping of intermittent individuals after this period was likely due to immigration by individuals from nearby patches. Innes et al. (2010) found that rats recolonized similarly sized forest fragments (range 2–10 ha) within 33 days of eradication. Thus, we would expect low but steady arrival of immigrants to our removal *kīpuka*, which is consistent with our trapping data. This explanation is further supported by the greater incidence of rat tracks in the removal *kīpuka* on ground tracking tunnels than on tree tunnels. Moreover, body size metrics also decreased in removal *kīpuka* over the trapping period. Maturity and body length are often correlated in rats (Himsworth et al. 2014). One potential explanation for this trend is that resident adults were trapped first and younger remaining rats were trapped as they became more exploratory and moved into unoccupied territories in treated *kīpuka*. While this suggests that continuous trapping may be needed to prevent fragments from being recolonized, our adjacent, experimental untreated *kīpuka* were likely a source pool of these immigrants.

We used fresh coconut, commercial peanut butter and, for a portion of the study, Spam Classic as bait types, rotated to reduce the potential for trap shyness or acclimation. While Spam Classic was the most attractive bait for *Rattus* spp., it also attracted other predators such as *H. javanicus* and *M. musculus*. In Hawai‘i, these species are also introduced, and studies have demonstrated their negative impacts on the native flora and fauna (Hays & Conant 2007, Angel et al. 2009, Harris 2009, St Clair 2011, Harper & Bunbury 2015). In other locations where additional native mammals may be trapped, bait type should be considered as one way to limit non-target captures.

Omnivorous rats are often deeply embedded within invaded systems, and with their removal other invasive competitors or prey species may emerge upon ecological release from rats (Roemer et al. 2002, Caut et al. 2007, Angel et al. 2009, Mulder et al. 2009, Ruscoe et al. 2011, Shiels et al. 2017). Interestingly, we found that the proportion of tracking cards with non-target taxa was affected by rat removal treatments when we combined data for all species. Our data suggest that the presence of rats led to shifts in the foraging behaviours of mongooses and mice, which were both less likely to co-occur at the same tracking tunnel where rats would forage. Co-occurrence of mongooses and mice was significantly higher than expected by chance, which suggests that these two non-native species may fill the void left by black rats. While snap-trapping did result in the trapping of some non-target taxa, our data suggest that snap-trapping had limited effects on their populations (Fig. 1(b)). Additionally, our study sites may be particularly suitable for removal of *Rattus* spp. because the lava matrix is a poor reservoir habitat for mice and rats. Therefore, rats and mice may be more likely to compete for habitat in the *kīpuka* themselves (Caut et al. 2007). By contrast, in a recent study on the neighbouring island of Maui, Shiels et al. (2017) observed that black rats dominated a restored native dry forest, while house mice prevailed over rats in the adjacent grassland. Thus, management strategies aimed at removing all invasive rodents may need to incorporate multiple methods to control both rat and mice populations.

Our study demonstrates that rats can be effectively controlled from partially isolated forested areas using snap traps. This trapping work was sustained by two full-time field technician positions visiting each of the 873 traps on a biweekly schedule. Though labour-intensive, snap-trapping can be a reasonable alternative in areas where long-term use of rodenticide is logistically impractical or unwanted (Shiels et al. 2019, Duron et al. 2020). Furthermore, on islands without native rodents the risk of by-catch in snap traps is low, whereas anticoagulants have the potential to contaminate food webs and impact other vertebrate species, scavenging species in particular (Shiels et al. 2014, Pitt et al. 2015). In areas such as our study system, where full eradication may not be possible, rat control efforts must be implemented instead to protect vulnerable native species. Thus, we recommend snap-trapping as an option in such cases, either alone or in tandem with integrated programmes where toxicants can be delivered and carefully monitored as part of an integrated management strategy (Shiels et al. 2014, Keitt et al. 2015).

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Data availability. The dataset for this study has been uploaded to a public repository and will be available at https://doi.org/10.6086/D1PD72.

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Conflict of interests. None.

Ethical standards. This research was approved by the State of Hawai'i Department of Land and Natural Resources Division of Forestry and Wildlife (Protected Wildlife permit no. WL13-02), the Michigan Technological University Institutional Animal Care and Use Committee (IACUC, no. 332879-4) and Stanford University IACUC (IACUC, no. 1776).

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