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RESEARCH ARTICLE

# Shifts in an invasive rodent community favoring Black rats (*Rattus rattus*) following restoration of native forest

Aaron B. Shiels<sup>1,2</sup>, Arthur C. Medeiros<sup>3,4</sup>, Erica I. von Allmen<sup>3</sup>

One potential, unintended ecological consequence accompanying forest restoration is a shift in invasive animal populations, potentially impacting conservation targets. Eighteen years after initial restoration (ungulate exclusion, invasive plant control, and out planting native species) at a 4 ha site on Maui, Hawai'i, we compared invasive rodent communities in a restored native dry forest and adjacent non-native grassland. Quarterly for 1 year, we trapped rodents on three replicate transects (107 rodent traps) in each habitat type for three consecutive nights. While repeated trapping may have reduced the rat (Black rat, *Rattus rattus*) population in the forest, it did not appear to reduce the mouse (House mouse, *Mus musculus*) population in the grassland. In unrestored grassland, mouse captures outnumbered rat captures 220:1, with mice averaging 54.9 indiv./night versus rats averaging 0.25 indiv./night. In contrast, in restored native forest, rat captures outnumbered mouse captures by nearly 5:1, averaging 9.0 indiv./night versus 1.9 indiv./night for mice. Therefore, relatively recent native forest restoration increased Black rat abundance and also increased their total biomass in the restored ecosystem 36-fold while reducing House mouse biomass 35-fold. Such a community shift is worrisome because Black rats pose a much greater threat than do mice to native birds and plants, perhaps especially to large-seeded tree species. Land managers should be aware that forest restoration (i.e. converting grassland to native forest) can invoke shifts in invasive rodent populations, potentially favoring Black rats. Without intervention, this shift may pose risks for intended conservation targets and modify future forest restoration trajectories.

**Key words:** Auwahi, endangered species conservation, Hawaii, House mouse, mainland island, *Mus musculus*, non-native grassland, tropical dry forest

## Implications for Practice

- Converting non-native grassland to native forest can shift the invasive animal community from House mouse (*Mus musculus*) dominated to Black rat (*Rattus rattus*) dominated.
- Heightened populations of invasive Black rats (*Rattus rattus*) can threaten native and endangered plant and animal species, perhaps especially large-seeded tree species.
- Land managers should be aware that habitat enhancement, particularly forest restoration, can invoke shifts in invasive rodent communities, potentially to the detriment of intended conservation targets.

## Introduction

Restoration projects intentionally and inevitably invoke changes in a site's ecological functioning, and generally these support conservation goals. However, there is the potential for restoration-induced changes to sidetrack or even act counter to original conservation goals (Zavaleta et al. 2001; Bergstrom et al. 2009; Suding 2011). For example, reduction of an invasive feral pig (*Sus scrofa*) population on a California island caused eagles to switch from feral pig prey to the endangered native foxes that were the primary target of restoration (Collins et al. 2009). Elimination of non-native feral goat (*Capra hircus*) populations in parts of Hawai'i promoted unanticipated invasion

and fuel loading of fire-adapted African grasses to the point that native biota were threatened and further ecosystem recovery was curtailed (Tunison et al. 2001). Efforts to restore riparian corridors through removal of the invasive tree *Tamarix ramosissima* in the Southwestern U.S. have caused unintended and unanticipated losses to local and migratory bird habitat (Sogge et al. 2008). Despite these examples, literature documenting unintentional outcomes to restoration is comparatively uncommon (Bergstrom et al. 2009), perhaps in part owing to the tendency to preferentially report positive restoration outcomes.

As a result of extensive anthropogenic impacts, tropical dry forests are among the world's most threatened ecosystems (Hoekstra et al. 2005; Miles et al. 2006). Hawaiian dry forests have been reduced to less than 10% of their former extent (Bruegmann 1996; Pau et al. 2009) owing to replacement

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<sup>1</sup>USDA, APHIS, WS, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521, U.S.A.

<sup>2</sup>Address correspondence to A. B. Shiels, email aaron.b.shiels@aphis.usda.gov

<sup>3</sup>Pacific Cooperative Studies Unit, University of Hawai'i, 3190 Maile Way, Honolulu, HI 96822, U.S.A.

<sup>4</sup>U.S. Geological Survey, Pacific Island Ecosystems Research Center, PO Box 369, Makawao, HI 96768, U.S.A.

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by agriculture, urbanization, wildfires, and non-native ungulates, plants, and rodents. In terms of federally recognized rare plant species, Hawaiian dry forests provide primary habitat for 89 Threatened and Endangered species, or about 9% of the U.S. total (Medeiros unpublished data). Hawaiian dry forests have relatively high species diversity but persist today largely as 0.5–200 ha relictual tracts scattered across the Hawaiian Islands. For many decades, reproduction of native species by seed in Hawaiian dry forests has been poor, and non-native plant invasion plus herbivory and seed predation by non-native mammals are among the likely contributing factors (Medeiros et al. 1986; Cabin et al. 2000; Medeiros et al. 2014). These remaining relatively small but highly diverse tracts of dry forests are important conservation targets for both biological (Olson & Dinerstein 2002) and cultural (Abbott 1992) value.

On isolated tropical islands such as Hawai‘i, no group of invasive organisms has been more destructive to native biota than has introduced mammals, and of these, rodents have driven species extinctions and whole ecosystem changes (Townsend et al. 2006; Drake & Hunt 2009; St Clair 2011). Hawai‘i’s invasive rodent fauna of three rats (*Rattus exulans*, *R. rattus*, *R. norvegicus*) and one mouse (*Mus musculus*) species has had devastating impacts on native plants, arthropods, land snails, and terrestrial and marine avifauna (Athens et al. 2002; Hadfield & Sauffer 2009; Shiels et al. 2013), largely because of the lack of native rodents and adaptations to cope with them.

Our investigation builds upon work initiated in 1997, with the goal of restoring a tract of native dry forest by converting a non-native grassland at Auwahi, Maui, by fencing and excluding ungulates, applying glyphosate-based herbicides to thick non-native grass mats, and planting seedlings of native trees and shrubs at high densities (ca. 1 indiv./m<sup>2</sup>; Medeiros et al. 2014). At the start of restoration in 1997, non-native graminoids dominated (>75% cover); following 15 years of restoration efforts in a 4 ha fenced area, native shrub cover increased by 75%, non-native plant cover decreased by 72%, and most of the 49 native tree species began to reproduce naturally from seed (Medeiros et al. 2014). Despite this, a number of dry forest tree species either failed to produce seedlings or produced them very infrequently; this was especially puzzling considering the often abundant production of viable seed (Medeiros et al. 2014). Evidence on site, such as chewed seeds frequently observed in husking stations (A. Medeiros 2013, USGS, personal observation), suggested invasive rodents, particularly rats, may be an important factor limiting plant recruitment. Invasive rodents, especially Black rats, are known for their nearly ubiquitous occurrence in island forests such as in Hawai‘i (Shiels 2010; Shiels et al. 2014), and are notorious for their predation of many native seeds (Chimera & Drake 2011; Shiels & Drake 2011; Shiels et al. 2013).

The primary objective of this study was to compare invasive rodent communities in restored native forest and adjacent non-native grassland, seasonally, to assess if and how native forest restoration reshapes invasive rodent communities. Our study also provides insight into how these shifts in invasive rodent



Figure 1. Aerial image of the Auwahi dry forest restoration project, leeward Haleakalā volcano, Maui, with the 4 ha native forest restoration area (dark green rectangle), and the surrounding unrestored non-native grassland (light green and brown) containing scattered native trees.

communities potentially influence conservation outcomes and future restoration trajectories.

## Methods

### Study Site

Auwahi dry forest (20°38′24″N, 156°20′24″W) is located at 1,160–1,250 m elevation on the leeward side of Haleakalā volcano, on privately owned ‘Ulupalakua Ranch, Maui Island, Hawai‘i. Mean annual precipitation is approximately 730 mm with a pronounced dry season from April to September (Giambelluca et al. 2011) and mean monthly temperatures are 13.9–18.3°C (Scholl et al. 2007). Unrestored portions of Auwahi are functionally non-native grasslands (Fig. 1), dominated by the mat-forming East African grass, Kikuyu (*Cenchrus clandestinus*, Poaceae), and having less than 10% tree cover; the grassland is used intermittently as cattle pasture. Common tree species of the restored forest area include *Olopua* (*Nestegis sandwicensis*, Oleaceae), Halapepe (*Chrysodracon auwahiense*, Agavaceae), ‘Akoko (*Euphorbia celastroides* var. *lorifolia*, Euphorbiaceae), Kōlea (*Myrsine lanaiensis* and *M. lessertiana*, Primulaceae), ‘Iliahi-a-loe (*Santalum ellipticum*, Santalaceae), and ‘Iliahi (*S. haleakalae* var. *lanaiense*, Santalaceae); dominant shrub species include ‘A‘ali‘i (*Dodonaea viscosa*, Sapindaceae) and ‘Ūlei (*Osteomeles anthyllidifolia*, Rosaceae).

Aside from invasive rodents (described below), other non-native vertebrates at the study site include feral House cat (*Felis catus*), Lesser Indian mongoose (*Herpestes auropunctatus*), Jackson’s chameleon (*Trioceros jacksonii*), Wild Turkey (*Meleagris gallopavo*), Ring-necked Pheasant (*Phasianus colchicus*), Peafowl (*Pavo cristatus*), Barn Owl (*Tyto alba*), Red-billed Leiothrix (*Leiothrix lutea*), Japanese White Eye (*Zosterops japonicus*), Northern Cardinal (*Cardinalis cardinalis*), and Eurasian Skylark (*Alauda arvensis*). Native vertebrates at Auwahi include the indigenous Hawaiian Owl (*Asio flammeus* ssp. *sandwichensis*) and two endemic

passerines, Hawai'i 'Amakihi (*Chlorodrepanis virens*) and 'Apapane (*Himatione sanguinea*).

### Study Species

Three rat species (*R. exulans*, *R. rattus*, *R. norvegicus*) and the House mouse (*M. musculus*) are invasive and well-established in both developed and natural areas in Hawai'i. Collectively, the four rodent species' range extends from sea level to over 3,000 m elevation (Tomich 1986). *Rattus exulans* (Polynesian or Pacific rat) was the first rodent introduced to Hawai'i, accompanying Polynesian colonization about 800 years ago (Wilmschurst et al. 2011). It has colonized native forests and agricultural lands (Sugihara 1997; Lindsey et al. 1999), but is apparently less common at elevations above 1,600 m (Amarasekare 1994; Cole et al. 2000). *Rattus rattus* (Black, Roof, or Ship rat) is the most common invasive rodent in forest habitats in Hawai'i and most other Pacific islands (Shiels et al. 2014), and has been noted as perhaps the most destructive to native biota (Cole et al. 2000; VanderWerf 2001; Shiels et al. 2014). *Rattus norvegicus* (Norway or Brown rat) is generally restricted to urban areas and farm environments, and is less common in natural areas (Tomich 1986). The House mouse (*M. musculus*) is broadly distributed in Hawai'i, occurs from sea level to approximately 3,750 m, is prone to population irruptions, and likely has significant impacts on native arthropods (Cole et al. 2000; Shiels et al. 2013).

All four rodent species are opportunistic omnivores. However, Norway rats and House mice generally consume more animal- than plant-based foods, while Black rats and Pacific rats consume more plant- than animal-based foods, particularly fruits and seeds (Cole et al. 2000; Shiels et al. 2013; Shiels & Pitt 2014). House mouse diet on islands is frequently dominated by arthropods and grass seeds (Cole et al. 2000; Shiels & Pitt 2014); however, tree seed predation during mast years has been well documented in New Zealand (Wilson et al. 2007).

### Experimental Design

In February 2014, we established three replicate transects (lengths 190, 230, and 260 m) in the 4 ha restored forest and three replicate transects in the adjacent grassland (>150 m from the forest edge). Along each transect we placed rodent traps (Victor snap-traps; Lititz, PA, U.S.A.) every 10 m (mouse) and 20 m (rat). In total, we positioned 107 traps (71 mice and 36 rats) in the forest and 107 traps in the grassland (71 mice and 36 rats). The three parallel transects in restored forest were spaced at minimum 25 m from the forest-grassland edge with approximately 50 m between adjacent transects. In the grassland, spacing between parallel, adjacent transects was also 50 m. We considered each of the three transects as independent within the forest and grassland based on rodents in Hawai'i moving less than 25 m linear distance, on average, in a night when studied in three mesic forests in the Wai'anae Mountains, O'ahu; Black rats moved a maximum of 31 m linear distance per night and House mice moved a maximum of 21 m linear distance per night (Shiels 2010).

Seasonal abundance of rodent populations at Auwahi was assessed by trapping quarterly for 1 year. Each trapping period consisted of three consecutive nights and traps were checked and rebaited daily. However, one trapping period (August) was shortened by a night because of interference from a tropical storm. Therefore, the four periods for which trapping occurred in 2014 were: 25–27 February, 6–8 May, 6–7 August, and 12–14 November. Three to four days prior to arming traps (trap night 1), we prebaited them by depositing coconut flakes within 50 cm of each trap. On the first night in a sampling period, we baited traps with fresh coconut (2 × 2 cm pieces for rat traps, 1 × 1 cm for mouse traps); we refreshed with new pieces of coconut in subsequent days as needed. Each trap was checked within 24 hours of arming. Trapped animals were identified to species, and when possible their sex and weight were determined. Total biomass of trapped rodents was calculated at the end of the study, and in each habitat, by summing weights of all individual rats, 162 mice, and by determining the average mouse weight ( $n = 162$ ) and multiplying by the number of mice that were not weighed. Traps that had been sprung were noted, and in some cases the presence of mouse and rat hair that remained on the trap was also noted. Rodent hair caught in the trap indicates a rodent was killed and scavenged by another rodent or rodent scavenger; such findings have been noted in other studies within and outside of Hawai'i (Shiels 2010). Our rodent captures were based only on the numbers of carcasses found. However, as the presence of rodent hair on traps occurred only in the forest and not the grassland, there is a possibility that our estimates of rodent abundance at the native forest study site were conservative.

Abundance of each rodent species was determined by the number of individuals captured per 100 trap nights (Innes et al. 2001; Shiels 2010) for each trapping period for each transect ( $n = 3$  for each of forest and grassland) by dividing the number of animals caught within a transect during the 3-day trapping period by the total number of traps armed for the 3 days (or 2 days for August sampling). A trap night is equal to one rodent trap armed for one night. As mice are often trapped in both rat and mouse traps, all 107 traps per night per location (forest and grassland) were used for calculations of mouse abundance. However, aside from a single instance, rats were caught only in rat and not mouse traps, so we used only 36 rat traps per trap night per location as the basis for calculations of rat abundances.

### Statistical Analysis

Repeated measures analysis of variances (ANOVAs) were used to determine whether mouse and rat abundances differed between forest and grassland, as well as seasonally among the four sampling periods. In order to meet ANOVA assumptions, rat abundances were log-transformed and mouse abundances were square-root transformed. ANOVA was also used to compare weights of adult rats in the restored forest over the four sampling periods. Statistical analyses were performed in R version 2.12.0.

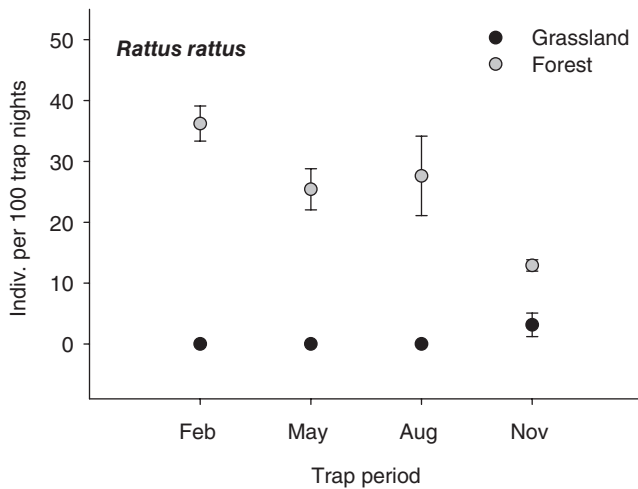


Figure 2. Mean  $\pm$  SE invasive Black rat captures per 100 trap nights in non-native grassland and adjacent restored native forest, Maui, Hawai'i. Trapping occurred in 2014. There was a significant difference in rat abundance between grassland and forest ( $p < 0.0001$ ).

## Results

During this investigation only two of the four species of invasive rodents established in Hawai'i were trapped; the Black rat and House mouse. In the forest, Black rats dominated over all sampling periods, averaging 9.0 captures per night. Black rat abundances were clearly and strongly significantly higher in the forest than in the grassland ( $df$  [degrees of freedom] = 1, 4;  $F = 296.95$ ;  $p < 0.0001$ ). In fact, no rats were captured at all in the grassland until the final (November) sampling period, when three individuals were captured. Mean Black rat abundances (25.5 indiv. per 100 trap nights) ranged seasonally from 13 to 36 indiv. per 100 trap nights in the forest, and 0–5 indiv. per 100 trap nights in the grassland (Fig. 2). There was no significant effect of time when Black rat abundance was averaged across forest and grassland environments ( $df = 3, 12$ ;  $F = 0.53$ ;  $p = 0.6692$ ). However, Black rat abundances in the forest declined successively during our study (treatment by time interaction:  $df = 3, 12$ ;  $F = 8.50$ ;  $p = 0.0027$ ), with abundance in the first census (February) approximately threefold greater than in the final (November) census (Fig. 2).

In marked contrast to Black rats, mouse abundances were significantly higher in the grassland than in the forest ( $df = 1, 4$ ;  $F = 298.41$ ;  $p < 0.0001$ ; Fig. 3). Here, mice were trapped nearly exclusively and at consistently high levels (average of 56.7 captures each night we trapped), outnumbering Black rat captures by 220:1. In the forest, mice were trapped in each of our trapping periods but at low levels, averaging 1.9 mice per sampled night and never exceeding 6 individuals per 100 trap nights (Fig. 3). When mouse abundances were averaged across forest and grassland, there was a significant time effect ( $df = 3, 12$ ;  $F = 27.45$ ;  $p < 0.0001$ ), and there was a significant treatment by time interaction ( $df = 3, 12$ ;  $F = 11.26$ ;  $p = 0.0008$ ), which apparently is reflected by the high abundances of mice (>100 mice per 100 trap night) in the grassland at Auwahi during May and especially August (Fig. 3).

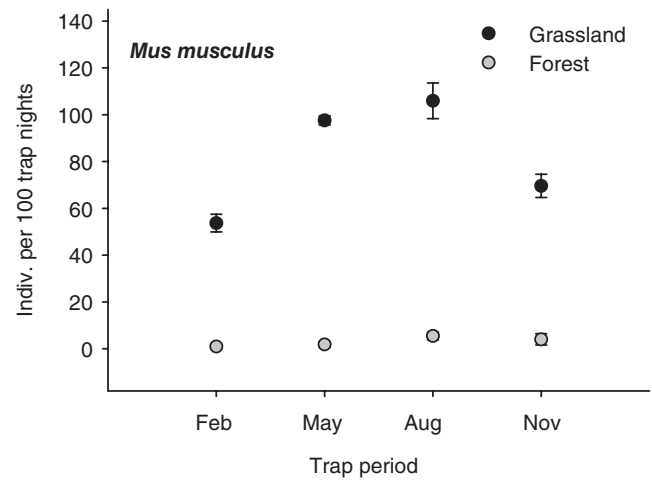


Figure 3. Mean  $\pm$  SE of invasive House mouse captures per 100 trap nights in non-native grassland and adjacent restored native forest, Maui, Hawai'i. Trapping occurred in 2014. There was a significant difference in mouse abundance between grassland and forest ( $p < 0.0001$ ).

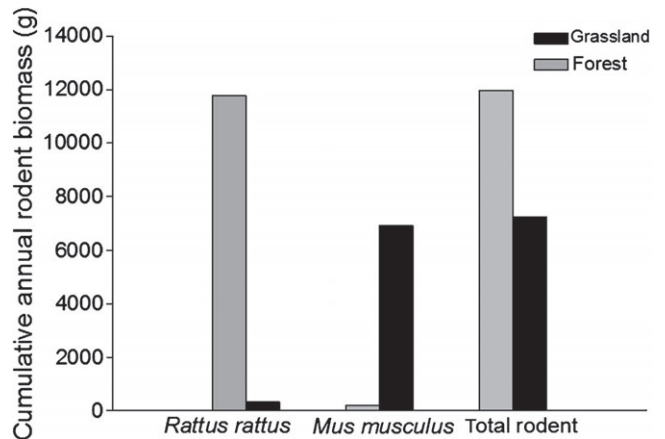


Figure 4. Cumulative annual rodent biomass (g) from four trapping periods in approximately 4 ha of restored forest, and the surrounding unrestored non-native grassland containing scattered native trees, Maui, Hawai'i.

We also documented that relatively recent ecological forest restoration has increased rodent biomass (mass of all rodents trapped during the project) by 65% (Fig. 4). In the grassland, rodent biomass totaled 7,240 g, 95% made up by mice (6,911 g), while in restored native forest rodent biomass totaled 11,968 g of which 98% was made up by Black rats (11,772 g). In other words, native forest restoration spurred a 36-fold increase in Black rat biomass while reducing mouse biomass 35-fold (Fig. 4).

Seasonally, body weights of Black rats and mice showed nearly opposite patterns. Mean weight of trapped mice was generally highest in winter and lowest in summer, while Black rat mean body weight increased throughout trapping periods from late winter through fall. Mean weight of trapped mice (grassland) was highest in February (12.6 g), decreased successively in May (11.2 g) and August (10.5 g), and increased again in

November (12.4 g). In contrast, mean weight of Black rats (forest) was lowest in February (114.6 g), and increased through May (128.1 g), August (130.3 g), and November (136.0 g). Mean Black rat mass ( $129.8 \pm 3.8$  g) was not significantly different among sampling periods ( $df = 3, 81$ ;  $F = 0.48$ ;  $p = 0.696$ ). Juvenile Black rats (identified by a nonperforated vaginal orifice or a lack of descended testes) were trapped in the forest in February (15%) and May (7.7%) samplings and absent in August and November.

The sex ratios of trapped mice were skewed towards females in all sampling periods except May; specifically, female to male (February, May, August, November): 1.9:1, 0.7:1, 1.6:1, 3.3:1. Except for the increase in females in late fall, the sex ratios of trapped Black rats, female to male, was fairly even throughout trapping periods (February, May, August, November): 1.3:1, 1:1, 0.7:1, 3:1.

Inadvertently, two species of non-native passerines, including eight Red-billed Leiothrix and two Northern Cardinals, were trapped in the forest. No native birds were captured. Despite the open stature of the grassland where traps were clearly visible at substantial distances, no birds or feathers were found in traps.

## Discussion

Island conservationists have traditionally viewed exclusion of non-native ungulates and control of invasive plant species as the primary essential components of ecosystem protection (Cabin et al. 2000; Brooks et al. 2009). As such, efforts to protect or restore native species and habitat on islands are typically initiated with ungulate exclusion through fencing and removal programs (Cabin et al. 2000; Cole et al. 2012; Medeiros et al. 2014). Our findings indicate that forest restoration also had the unintended effect of increasing invasive rodent biomass and shifting dominance within the invasive rodent community from House mouse to Black rats. Although the impact of Black rat on native biota in Auwahi forest remains relatively unexplored, such a shift has potentially serious conservation impacts, including native species loss, stalling or modifying forest recovery, or otherwise compromising or even undoing conservation goals.

### Increases in Black Rats Accompanies Native Forest Restoration

Increases in Black rat numbers and biomass following forest restoration at Auwahi are presumably driven by greater food resources, increased plant structural complexity, and decreased predation pressure. Where successful, forest restoration increases a site's ecological complexity, greatly increasing the abundance and diversity of food resources. Diets of Black rats generally include a wider range of available fruits, seeds, and invertebrates, while the House mouse diet is often dominated by grass (seed and vegetative material) and invertebrates (Singleton 1989; Sugihara 1997; Cole et al. 2000; Shiels et al. 2013). Forest restoration and a shift in food availability may therefore disproportionately benefit Black rats over House mice.

Rodent habitat preferences may help explain the shift in abundance to favor Black rats in the restored forest. Black rats

are commonly arboreal, favoring forest or mixed forest habitats especially those with dense understory, deep leaf litter, and numerous vertical stems (Innes & Skipworth 1983; Dowding & Murphy 1994; Cox et al. 2000; Shiels 2010). In contrast, House mice prefer open habitats with dense ground vegetation, especially grass, and mice are rarely found greater than 2 m aboveground (Ruscoe & Murphy 2005; Shiels 2010). At Auwahi, the greater structural complexity of forest habitats may also act to lessen predation pressure from cats, mongooses, and owls. Patrolling owls at Auwahi appear to prefer grassy versus forested tracts for hunting, and regurgitated pellets of undigested prey are commonly found in the grassland and not forest at Auwahi (A. Medeiros 2013, USGS, personal observation). Though Black rats were rarely trapped in the grasslands during this study, a predation event of a rat by a Hawaiian owl was observed in the course of field work in the grassland. Predation pressure on rodents in more open structured habitats at Auwahi may be an important factor shaping resident rodent communities.

Increases in invasive Black rat populations accompanying forest restoration have been reported elsewhere, such as in fenced fragments of forest in New Zealand where Black rat densities (6.5 rats/ha) were 13 times higher than those in unfenced tracts (Innes et al. 2010). Elsewhere in New Zealand, Black rats were more abundant and larger in native forests, despite their logging histories, than in more simply structured, non-native plantation forests (Innes et al. 2001). In both studies, greater vegetation cover, reduced risk of predation, and increased food resources were postulated as factors driving higher Black rat densities in restored forest tracts.

The greatly reduced numbers of House mice in restored forest at Auwahi are presumably the result of shifts in habitat, food resources, and predation and/or competition by Black rats. Snap-trapped House mice in the forest were frequently scavenged before processing, apparently by Black rats; there was no scavenging of mouse carcasses observed in the hundreds of mouse captures in the grassland. The Pacific rat, which is competitively inferior to the Black rat (Shiels 2010) and has an intermediate body size between House mice and Black rats, was absent during our year-long, quarterly trapping efforts. The absence of the Pacific rat during our trapping is somewhat enigmatic considering the species has been reported to co-occur with Black rats elsewhere in native Hawaiian forests (Lindsey et al. 1999; Nelson et al. 2002) including on Maui Island (Sugihara 1997).

### Seasonality and Effects of Trapping on Rodent Populations

Determining the causes of intra-annual population dynamics is a substantial challenge in animal ecology, and rodents are among the most well-known vertebrate groups to experience dynamic population fluctuations (Krebs et al. 1973). The highest Black rat abundances at Auwahi were recorded during the first sampling, in February. In comparison, on O'ahu, Black rat populations in mesic forest typically peaked from October to February (Shiels 2010), and populations in dry coastal forest typically peaked from October to January (Tamarin & Malecha

1971). Throughout the year, House mouse densities at Auwahi varied little in the forest, but peaked strongly in May and August in the grassland. In contrast, Sugihara (1997) found no significant difference in abundance of either rodent species between the winter (November–December) and summer (May–June) in mesic shrubland and wet forest on Haleakalā, Maui. In O‘ahu mesic forest, House mice showed less predictable intra-annual changes in abundance than Black rats (Shiels 2010). The most commonly suggested drivers for these rodent population fluctuations in Hawai‘i are resource availability, precipitation, and temperature (Tamarin & Malecha 1971; Shiels 2010). In southeastern Australian wheatlands, House mouse population dynamics were driven by rainfall, habitat features, and proximity to crops (Singleton 1989).

It is possible that some of the seasonal changes that we found in rodent populations could be due to progressive reductions to the rodent population by our destructive sampling techniques. Although evaluating the feasibility of rodent control was not an original study objective, we note here the conservation implications of decreases of isolated Black rat populations in a forest fragment through quarterly sampling. In contrast and despite the removal of substantial numbers of House mice in non-native grasslands by trapping over successive sampling periods throughout the year, trapping did not appear to affect the large, resident mouse population. For example, following the removal of over 200 mice from the grassland in May, the highest numbers of mice were trapped along the same traplines in the subsequent sampling period (August). In November, the number of captured mice declined as would be expected with the arrival of winter rains and reduction in temperature and food availability. In contrast to mice, the removal of rats from the forest in early sampling periods appeared to not only progressively reduce the numbers of captures but also skew sex ratios of animals trapped in later periods. The larger home ranges and lower densities of Black rats than mice combined with the relatively small area of restored native forest (4 ha) are possible factors to explain the vulnerability of established Black rat populations to control efforts. The apparent absence of mouse population reductions from our trapping probably reflects both the large number of mice in the grassland and the much larger source population surrounding the 4 ha of grassland that we sampled. In the final (November) sampling in the forest, the lowest numbers of Black rat captures coincided with the highest number of mouse captures. If the suppression of Black rat communities in the restored forest is the primary factor that allowed the slight rise in mouse numbers, it is an example of competitive exclusion and maybe the mesopredator release phenomenon (Courchamp et al. 1999; Harper & Cabrera 2010; Goldwater et al. 2012). In addition, the grassland matrix surrounding the restored forest has very low Black rat densities, which should theoretically slow reinvasion or rat incursion into the restored forest once rats have been suppressed in the restored forest (Innes et al. 2010).

### Black Rat Impacts on Native Species and Ecosystems

Black rats profoundly and negatively impact many native bird, invertebrate, and plant species (Shiels et al. 2014; Harper &

Bunbury 2015). Since human contact about 800 AD, numerous frugivorous seed dispersing bird species in Hawai‘i, including thrushes and crows, have gone extinct (James & Olsen 1991; Culliney et al. 2012), thereby depriving large-seeded native plant species of coadapted zoochorous seed dispersal (Shiels & Drake 2011; Culliney et al. 2012; Shiels & Drake 2015). Without zoochorous seed dispersal, both the greatly reduced seed shadows and the unprocessed nature of the deposited fruit (e.g. pulp still attached) can result in higher levels of rodent seed predation (Moles & Drake 1999; Chimera & Drake 2011).

Of particular concern for dry forests are the negative impacts of Black rats on plants via seed predation of large-seeded (>5 mm longest length) species (Chimera & Drake 2011; Shiels & Drake 2011; Shiels & Drake 2015). Large-seeded native tree species of the Hawaiian Islands often have threatened or endangered status with restricted populations and ranges (Wagner et al. 1999). As an example, Mahoe (*Alectryon macrococcus* var. *auwahiensis*; seeds 5–10 mm longest length), considered endangered by the U.S. Fish and Wildlife Service with 11 individuals of the variety remaining in the wild (all residing in the Auwahi region), rarely produces seeds, but when it does, most seeds suffer rat predation (A. Medeiros 2013, unpublished data).

Black rats are serious predators of eggs, young, and tending adults of birds (VanderWerf & Smith 2002; Towns et al. 2006; Harper & Bunbury 2015). The heightened Black rat population in the Auwahi restoration area may be suppressing and reshaping the local bird populations, and possibly influencing pollination and seed dispersal services. Following initial forest restoration, the two endemic honeycreepers, Hawai‘i ‘Amakihi and ‘Apapane, were observed and heard frequently in the Auwahi restoration area; ‘Amakihi were thought to be nesting in the restored forest. However, both species subsequently appeared to become less common in the restoration area and the apparent failure of ‘Amakihi to become established in the restored forest may be due to heightened Black rat populations. In contrast to the lack of colonization of the Auwahi restoration area by native honeycreepers, two non-native passerine species, the Red-billed Leiothrix from Asia and Northern Cardinal from North America, have colonized and achieved substantial populations in the forest, as compared to adjacent grassland where passerines are uncommon or lacking. Scolding by Red-billed Leiothrix has been observed in the forest at Auwahi, which likely indicates nesting of this common passerine. Colonization of the restored forest by the Red-billed Leiothrix and Northern Cardinal may have occurred because of adaptations gained in their native ranges to better cope with vertebrate predators.

Black rats are notorious predators of native invertebrates (St Clair 2011) including nearly all species in the remarkable adaptive radiations of Hawaiian land snails, such as *Achatinella* and *Partulina* (Hadfield & Saufler 2009). Predation of invertebrates by Black rats also may suppress populations of pollinators (e.g. Lepidoptera), potentially modifying pollination and reducing fitness of native plant species (Shiels et al. 2013). Black rats clearly threaten a wide range of native species and can modify ecosystem functions on islands. Without intervention by land managers, heightened Black rat populations may modify future

forest restoration trajectories and even pose significant risks for intended conservation targets.

### Potential Management to Suppress Negative Impacts of Rodents

Best practice management options for landscape-level control of invasive rodents include the use of predator-resistant fencing, toxicants, and traps (Saunders & Norton 2001; Burns et al. 2010; Pender et al. 2013; Young et al. 2013). Predator-resistant fencing is highly effective in excluding non-native mammals from native ecosystems, often yielding significant conservation benefits but is costly, both initially and in its maintenance (Burns et al. 2010; Scofield & Cullen 2011; Young et al. 2013). A complicating factor of Black rat suppression or removal is the potential for dramatic increases of House mice, a so-called mesopredator release phenomenon (Innes & Hooker 1995; Gillies et al. 2003; Harper & Cabrera 2010). Mice, especially at high densities such as in sites experiencing mesopredator release, also present potentially serious ecological problems to native biodiversity (Ruscoe & Murphy 2005; St Clair 2011).

In many respects, the Auwahi project is functionally similar to some of New Zealand's mainland island projects (Saunders & Norton 2001). Mainland islands are native forest remnants ("islands"), managed for conservation, located within much larger pastoral landscapes. The low density of forest-adapted pests in surrounding habitats coupled with intensive pest control within the managed "mainland island" area, especially at forest-pasture margins, allows substantial conservation benefits with relatively low financial costs (Saunders & Norton 2001).

In mainland island situations, such as Auwahi, current methods for suppression of Black rats in the absence of predator-resistant fencing are trapping and poisoning (Gillies et al. 2003). Although both toxicant and trap uses have limitations (e.g. nontarget impacts, efficacy over time, resetting, or rebaiting frequency), elsewhere in Hawai'i they have been shown to provide substantial benefits for both birds (VanderWerf & Smith 2002) and plants (Pender et al. 2013). An alternative to continuous, large-scale rodent control is the strategic targeting of suppression efforts spatially (under canopies of vulnerable large-seeded tree species) and/or temporally (such as during fruiting or nesting seasons) to maximize conservation benefits (Pender et al. 2013). Conservation benefits achieved with such short-term efforts, such as the establishment of seedling cohorts of native tree species, may be substantial and durable because once established and protected from ungulates they tend to have excellent survivability and be long-lived (Medeiros et al. 2014). Although conservation of large tracts of native habitats is clearly desirable, restoration of small tracts of highly depleted forest types offer disproportionately significant conservation benefits and should be an important component of a holistic natural resource management strategy (Saunders & Norton 2001).

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