

Micro- and Macrohabitat Preferences of Invasive Rodents on St. Eustatius, Caribbean Netherlands

Authors: Madden, Hannah, Eggermont, Eline, and Verdel, Kevin

Source: Caribbean Journal of Science, 50(2) : 202-211

Published By: University of Puerto Rico at Mayagüez

URL: <https://doi.org/10.18475/cjos.v50i2.a1>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Micro- and Macrohabitat Preferences of Invasive Rodents on St. Eustatius, Caribbean Netherlands

HANNAH MADDEN^{1,2,*}, ELINE EGGERMONT³, AND KEVIN VERDEL³

¹Caribbean Netherlands Science Institute (CNSI), St. Eustatius, Caribbean Netherlands

²NIOZ Royal Netherlands Institute for Sea Research, and Utrecht University, Texel, The Netherlands; ORCID: 0000-0002-3163-2241

³University of Utrecht, Utrecht, The Netherlands; e.d.c.eggermont@gmail.com; kgm.verdel@gmail.com

*Corresponding author: Hannah.madden@cnsi.nl

ABSTRACT—We studied the micro- and macrohabitat preferences of black rats (*Rattus rattus*) and house mice (*Mus musculus*) on St. Eustatius, a small, inhabited Caribbean island. Our study builds upon a preliminary assessment of invasive alien rodents on St. Eustatius, which has no extant native rodent species. We deployed tracking tunnels (baited cards with ink left overnight to track animal visitors to the card) in 12 macrohabitats to determine the presence and relative abundance of rodent species. Data were collected between July 2017 and May 2019. We collected data in 5 × 5 meter ($n = 120$) plots to determine whether grass cover, leaf litter cover, number of living trees, and other microhabitat components influenced habitat use by rats and mice. Rats were more likely to occur in microhabitats with more live trees, but with fewer logs and less grass and bare ground. Mice were more likely to occur in microhabitats with more bare ground. Rat tracks were recorded in all macrohabitats, whereas mouse tracks were detected in all but four, namely: C, M2, M3, and M5. Based on tracking tunnel data, the relative abundance of rats and mice ranged from 0% to 70%, respectively, in all macrohabitats over the study period. Rat relative abundance in forest macrohabitats differed significantly from that in other macrohabitats. Rat relative abundance in regenerating grassland differed significantly from that in other macrohabitats. There is evidence of habitat selection by rats at the micro- and macrohabitat scale, which could be linked to food availability. However, our study revealed only weak or no patterns of habitat selection by mice. Rat relative abundance differed significantly between the second and third assessment, and between the fourth and fifth assessment. Mouse relative abundance differed significantly between the first and second assessment.

Development has increased in intensity on many Caribbean islands over the last century, and the expansion of global trade and the movement of humans, biological material, and other commodities has provided a range of pathways for the introduction of alien species (Kairo et al. 2003). This has led to significant variation in the availability of spatial and temporal resources on Caribbean islands. Black rats (*Rattus rattus*) and house mice (*Mus musculus*) are two of the world's most successful invasive mammalian 'tramp' species (Clark 1980; Wanless et al. 2007). Thanks to their plasticity and omnivorous diets, these rodents have successfully invaded thousands of islands worldwide via human dispersal. Many, if not most, islands in the Caribbean many have been colonized by one or more species of invasive rodent (Kairo et al. 2003). Furthermore, the warm climate and constant availability of food in the tropics can lead to year-round breeding, although populations may be constrained by other factors, such as net primary productivity, precipitation, and the presence of competitors (Harper and Bunbury 2015). The absence of other competing rodent species allows invasive ro-

dents on oceanic islands to occupy all available habitats at varying densities (Harper et al. 2005; Russell et al. 2011).

A number of empirical studies have been published on spatial and temporal fluctuations in rodent populations in continental systems (Brown and Heske 1990; Ernest et al. 2000; Madsen and Shine 2009; Russell and Ruffino 2012). Whilst fluctuations are apparently maintained by density-independent abiotic conditions, these are also regulated by density-dependent intra- and inter-specific interactions (Kot and Schaffer 1984; Schaffer 1985; Schaffer et al. 1986). Varying patterns have been documented in small mammal populations, including relatively stable populations, annual cycles, multiannual cycles, and irregular multiannual fluctuations (Hansson and Henttonen 1985; Henttonen 1985; Taitt and Krebs 1985). Rodents may perceive and respond to habitat characteristics at a variety of scales. In New South Wales, Australia, Cox et al. (2000) determined that use of habitat by the black rat was influenced by leaf litter cover. In New Zealand, Brown et al. (1996) trapped a similar number of rats in for-

est and scrubland habitats, but captured more mice in scrubland. On tropical forested island systems lacking high-order predators or congeners, the factors and/or processes that regulate small mammal population fluctuations have been poorly studied (Russell and Ruffino 2012). Tropical islands generally support higher rodent densities compared with temperate regions, although these can vary between habitats and among seasons, often related to precipitation rates (Samaniego Herrera et al. 2017). For example, Shiels and de Arellano (2018) documented black rats in all habitats sampled within the Caribbean National Forest, Puerto Rico, whereas mice were only detected along forest edges. Fluctuations in rodent populations on tropical islands are typical, and do not necessarily infer a decrease or increase in abundance. Rodent diet and impacts on native species vary according to species and the availability of resources. Generally, however, invasive rats have a greater local impact compared with mice (Samaniego Herrera 2014).

St. Eustatius, a special municipality of The Netherlands, is situated in the northern Lesser Antilles, and has a human population of approximately 3,900 (Statistics Netherlands 2018). It is home to two terrestrial protected areas (TPAs), which overlap with two Important Bird Areas. Black rats and house mice likely coexisted on St. Eustatius with the native oryzomyine rice rat (*Pennatomys nivalis*) until the latter was extirpated by European settlers in the early 20th century (Brace et al. 2015). Black rats are widely distributed on St. Eustatius, which they co-occupy with house mice in shrublands and other habitats at lower altitudes (Madden et al. 2019). The presence of rats and mice in rural areas can have significant negative impacts not only on native bird species, but also on invertebrates, reptiles, and indigenous flora (Shiels et al. 2013; Samaniego Herrera 2014). Our study builds on a preliminary assessment of invasive alien rodents on St. Eustatius (Madden et al. 2019). The main aim of this study was to measure the relative abundance (RA) of black rats and house mice in 12 vegetation types over 22 months, and to relate their occurrence to micro- and macrohabitats. We predicted that rat RA would differ significantly between vegetation types, especially those with higher floristic diversity, e.g., forested areas compared with grasslands or shrublands. We anticipated that mouse populations would be limited to open, grassy habitats at lower elevations. We further predicted that temporal fluctuations in rat and mouse RA would not differ significantly over the study period. Finally, we hypothesized that micro-

habitat components such as number of stems and/or leaf litter cover would be an important predictor of rat, but not mouse, activity.

MATERIALS AND METHODS

Study Areas

St. Eustatius (21 km²) (17°28'–17°32'N, 62°59'–63°W) comprises two volcanic areas separated by lowlands (Van Andel et al. 2016). Boven (289 m) to the north consists of five extinct volcanic centers, whereas the Quill (600 m) to the south is a dormant stratovolcano (Roobol and Smith 2004). The Quill (~220 ha) and Boven (~320 ha) are TPAs that are actively managed by the St. Eustatius National Parks Foundation (Collier and Brown 2008). Both areas are covered in secondary dry forest (Van Andel et al. 2016). Fieldwork was conducted in 12 of 15 different vegetation types described by De Freitas et al. (2012), which we further examined in 2019 (Fig. 1). Due to their steep topography, we were unable to effectively conduct fieldwork in vegetation types M6 (*Capparis-Antirhea* mountains) and M8 (*Antirhea-Coccoloba* mountains). We excluded vegetation type B (*Coccoloba* beach), since this area was too small for the required fieldwork. Our study did not include any assessment of rodent populations in urban areas.

Vegetation on St. Eustatius varies from xeric shrubland with cacti to seasonal deciduous forest (Roobol and Smith 2004; De Freitas et al. 2014). The former consists of open, grassy shrubland with few trees, while the latter is dominated by *Bourreria bacata*, *Pisonia subcordata*, *Guettarda scabra*, and to a lesser extent *Bursera simaruba* (Van Andel et al. 2016). Annual average precipitation is 986 mm, and vegetation at higher elevations receives more rainfall than elsewhere on the island (De Freitas et al. 2012). There are no natural streams or bodies of fresh water on St. Eustatius, however black rats and mice are believed to obtain sufficient moisture through the consumption of plant material or rainwater droplets (Shiels et al. 2014).

Tracking tunnels

In order to measure the RA of invasive rodent species, data were collected in 12 vegetation types between July 2017 and May 2019. With the exception of the first assessment, which took place over seven months (Madden et al. 2019), tracking tunnels in assessments two to six were deployed quarterly (May 2018, August 2018, November 2018, February 2019, and May 2019). Ten footprint tracking cards were placed in each veg-

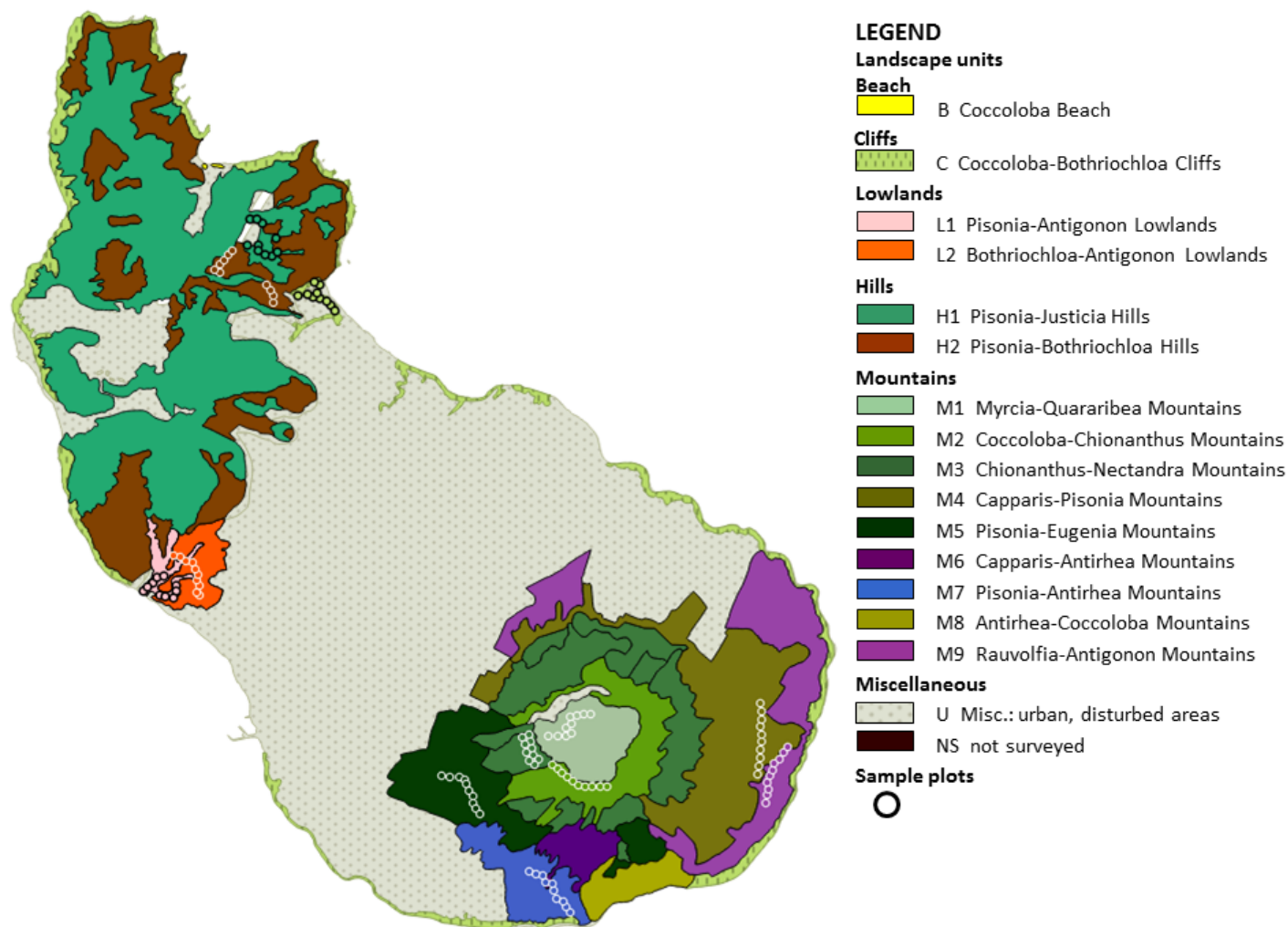


FIG. 1. Landscape ecological vegetation map of St. Eustatius showing locations of tracking tunnels and vegetation plots.

etation type at 50 meter intervals, baited with peanut butter, and tracked over three consecutive nights (first and second assessments; Madden et al. 2019) or overnight (subsequent assessments; Brown et al. 1996). We followed the same methods described by Madden et al. (2019). A total of 1,200 tracking tunnels were deployed over the study period.

Microhabitats

In order to determine whether particular microhabitat components were important predictors of rat and mouse activity, we collected data in a 5 x 5 meter plot at each of the tracking tunnel locations ($n = 130$). We combined all data to produce an average from each vegetation type. The microhabitat components were:

1. Elevation: a Garmin Montana 680t GPS device was used to measure elevation.
2. Rock cover: the percentage of rock cover was estimated by eye on two separate occasions and averaged (Barun et al. 2011).

aged (Barun et al. 2011).

3. Bare ground: the percentage of bare ground was estimated by eye on two separate occasions and averaged (Barun et al. 2011).
4. Grass cover: the percentage of grass cover was estimated by eye on two separate occasions and averaged (Barun et al. 2011).
5. Leaf litter depth: a minimum of five measurements (one in the center and one in each corner) were taken within each plot and averaged to determine leaf litter depth (Cox et al. 2000).
6. Leaf litter cover: the percentage cover of leaf litter was estimated by eye on two separate occasions and averaged (Cox et al. 2000). The four “cover” categories added up to 100%.
7. Number of stems: the number of stems standing between 45° and 90° and ≤ 10 cm in diameter was counted (Van Andel et al. 2016).

8. Number of shrub species: the number of shrub species was counted (Van Andel et al. 2016).
9. Number of tree species: the number of tree species was counted (Van Andel et al. 2016).
10. Number of live trees: the number of living trees was counted (Van Andel et al. 2016).
11. Number of logs: all logs (dead or alive) greater than 10 cm in diameter, lying on or otherwise parallel to the ground, were counted (Cox et al. 2000).
12. Canopy cover: the percentage cover of the canopy was assessed using the same method as for leaf litter cover (Cox et al. 2000).
13. Canopy height: the maximum height of the canopy was measured with a Bushnell Elite™ rangefinder.

Statistical analyses

We transformed percent average rodent relative abundance, percent rock cover, grass cover, leaf litter cover, canopy cover, canopy height, and understory height with an arcsine square root transformation (Sokal and Rohlf 1995) in order to balance variables with large numbers (e.g., counts of ground stems) to those with smaller numbers (e.g., counts of trees). We used a Friedman's chi-square test to determine significant differences in mean rat and mouse RA per vegetation type over the study period, followed by a post-hoc test where relevant. A multiple regression model was constructed to investigate which microhabitat components were the most important predictors of rat and mouse occurrence. All six assessments were combined into one dataset. A correlation matrix including all microhabitat components was calculated to eliminate any highly correlated variables from the regression model. Microhabitat components were deleted from the model if they could be reconstituted by linear combinations of remaining variables; reconstitution was considered acceptable if R^2 exceeded 0.90. Remaining microhabitat components constituted the independent variables for the regression, while rat or mouse RA was used as the dependent variable. The model was accepted when $\alpha \leq 0.05$. The advantage of multiple regression analysis was expected to lie in using data from all six assessments. However, averaging of microhabitat component data had the potential to mask significant rat- or mouse-component associations based on the tracking tunnel data. We performed a Shapiro-Wilks test to determine for normality of the rat and mouse RA datasets (Shapiro and Wilk 1965). We performed an analysis

of variance (ANOVA) to compare rat and mouse RA between each assessment of rats and mice in all vegetation types combined. If the data were not normally distributed, we performed a Wilcoxon rank sum test. All analyses were performed in the R environment version 3.5.0 (2018). Statistical significance was based on $\alpha \leq 0.05$.

RESULTS

Tracking tunnel data revealed rat and mouse RA from 0% to 70%, respectively, at elevations ranging from sea level to 507 meters. The highest mean RA of rat tracks were recorded at elevations of 300–349 meters (51.67%), 350–399 meters (33.05%), and 250–299 meters (30.00%), which fall inside the 250-meter boundary of the Quill National Park. The highest mean RA of mouse tracks were recorded at elevations of 50–99 meters (53.90%) and 0–49 meters (38.88%), which fall outside the boundaries of the terrestrial protected areas. More rat than mouse tracks were recorded above 100 meters, however mouse tracks were also recorded inside the crater of the Quill at elevations of 250–299 meters. Both house mouse and rat tracks were detected in seven vegetation types (L1, L2, H1, H2, M1, M7, and M9; Figs. 1, 2, and 3), at elevations of 0–299 meters. Four vegetation types (C, M2, M3, and M5; Figs. 1, 2, and 3) detected only rats and no mice.

There was a significant difference in mean rat RA over the study period (Friedman $\chi^2 = 14.31$, $df = 5$, $P = 0.01$). A post-hoc test revealed significant differences in rat RA between macrohabitats. In particular, rat RA in vegetation type M5 (lower Quill slope) differed significantly from all other vegetation types except M1 (Quill crater) and M3 (Quill rim; Fig. 2; Table 1). Rat RA in vegetation type M9 (regenerating grasslands) differed significantly from six vegetation types (C, M1, M2, M3, M5, and M7; Fig. 2; Table 1). Similarly, rat RA in vegetation type M4 (lower Quill dry slope) differed significantly from vegetation types in coastal areas and the upper, wetter slopes and crater of the Quill (C, M1, M2, and M3; Fig. 2; Table 1). There was no significant difference in mean mouse RA over the study period (Friedman $\chi^2 = 5.15$, $df = 5$, $P = 0.40$). Rat RA differed significantly between assessments two and three (ANOVA ($F(1,10) = 20.46$, $P = 0.001$) and four and five (ANOVA ($F(1,10) = 14.99$, $P = 0.003$)). Mouse RA differed significantly between assessments one and two (ANOVA ($F(1,10) = 5.46$, $P = 0.04$)).

Inspection of the correlation matrix revealed signifi-

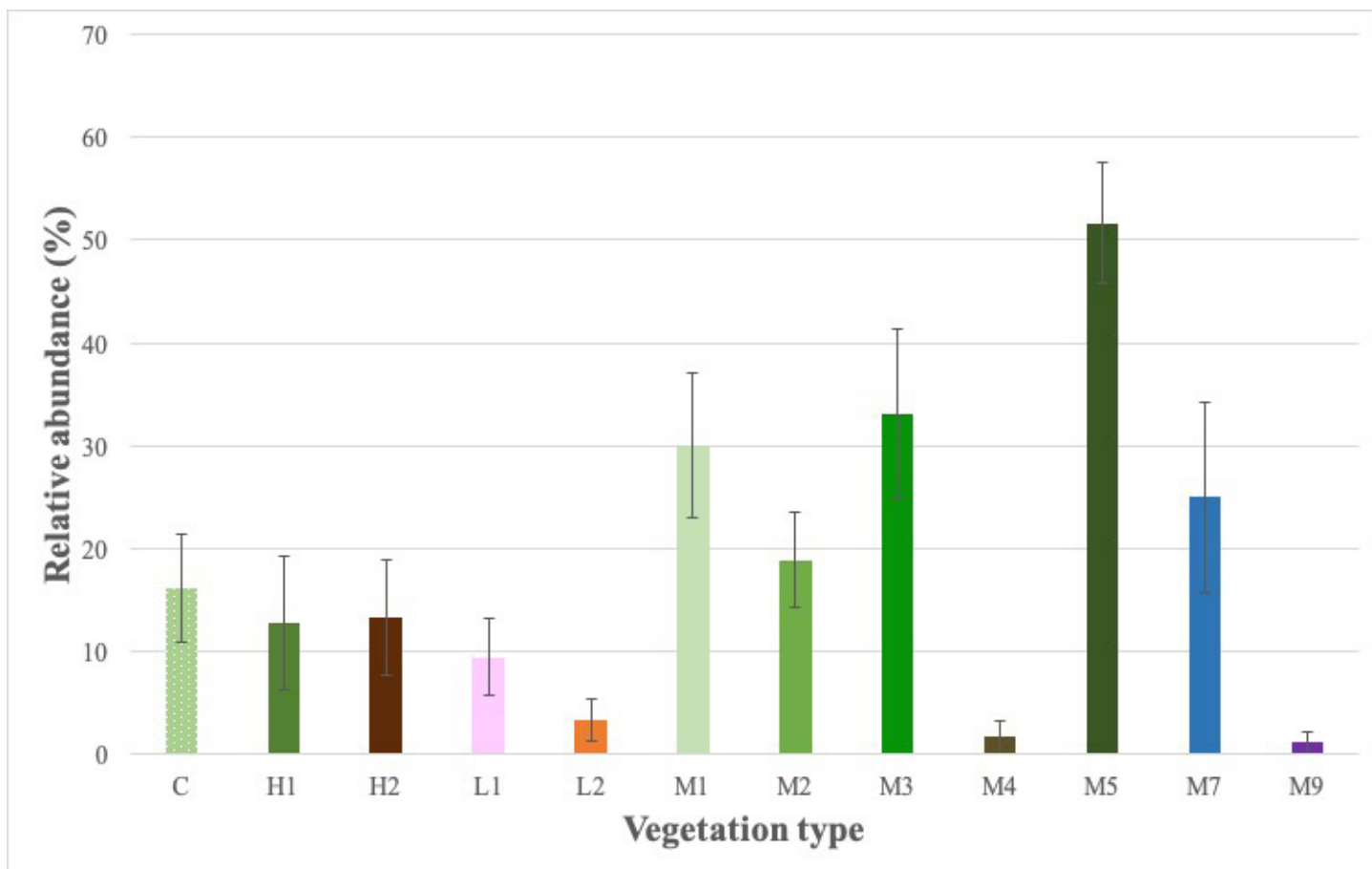


FIG. 2. Relative abundance (\pm SE %) of black rats (*Rattus rattus*) per macrohabitat (vegetation type) on St. Eustatius between July 2017 and May 2019 based on tracking tunnel data.

cant multicollinearity between six microhabitat components, namely: grass cover and canopy cover, number of stems and number of shrub species, and number of trees alive and number of tree species. Consequently, before running multiple linear regression analyses on the rat and mouse datasets we removed canopy cover, number of shrub species and number of tree species from the models. After running an initial model we inspected the variance inflation factor (VIF) of each independent variable and removed four additional components with scores >10 , namely: elevation, grass cover, leaf litter cover and canopy height. Inspection of the VIF of the remaining microhabitat components resulted in values of between 1.25 and 3.62, which we considered acceptable to run a revised model. Multiple regression analysis of the independent variables revealed that rats were more likely to occur in microhabitats with fewer logs ($r = -1.97$; $P = 0.05$), less bare ground ($r = -2.48$; $P = 0.02$), and less grass cover ($r = -2.42$; $P = 0.02$), but with more live trees ($r = 5.15$; $P < 0.001$; Table 2). Conversely, mice were more likely to occur in microhabitats with more bare ground ($r = 2.01$; $P = 0.05$; Table 3).

DISCUSSION

This work builds on an initial study conducted in 2017 and 2018 that combined rat and mouse data (Madden et al. (2019)). In contrast, this study analyzed the two species separately. This allowed us to build a more comprehensive overview of invasive rodent populations in rural areas on St. Eustatius over a longer timeframe. Black rats and house mice were present and unevenly distributed in 12 rural macrohabitats. Black rats were the most abundant and ubiquitous species, detected in all vegetation types; house mice were detected in eight. As expected, more rat tracks were recorded at higher elevations, whereas more mouse tracks were recorded at lower elevations. Studies elsewhere (e.g., Salibay and Luyon 2008; Shiels et al. 2014; Christie et al. 2017) have recorded lower rat densities at elevations $>2,000$ meters, however maximum elevation does not exceed 600 meters on St. Eustatius.

Black rats and house mice exhibited clear and inverse patterns of habitat use on St. Eustatius. Black rats preferentially used microhabitats with less grass and bare ground, fewer logs, but more living trees. Cox et al. (2000) determined that black rats in New South

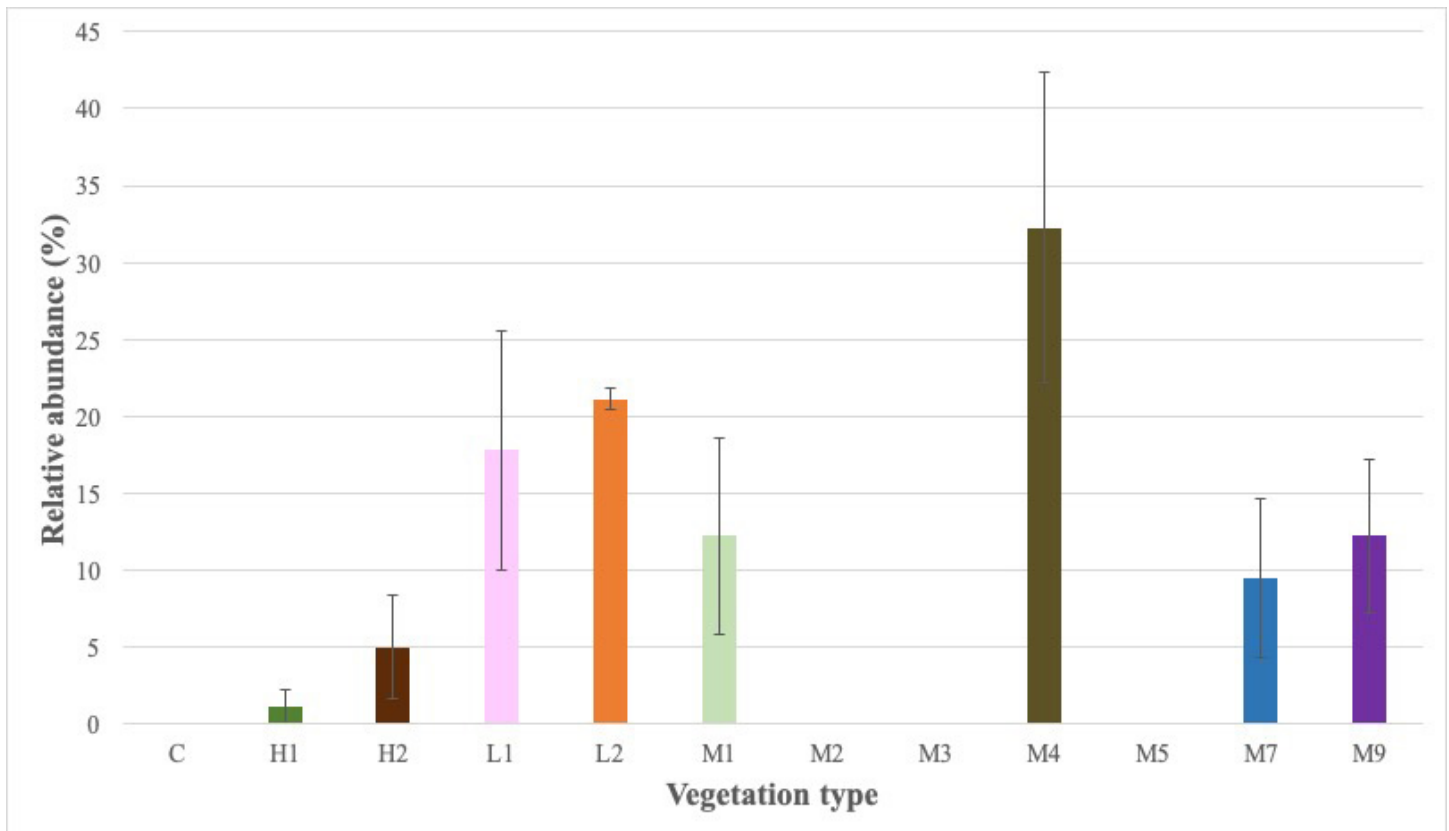


FIG. 3. Relative abundance (\pm SE %) of house mice (*Mus musculus*) per macrohabitat (vegetation type) St. Eustatius between July 2017 and May 2019 based on tracking tunnel data.

Wales, Australia, were more likely to occupy microhabitats with a dense understory, numerous vertical stems, and dense leaf litter cover. Our linear regression model did not reveal a significant relationship between rat RA and leaf litter cover or number of stems within microhabitats. Nevertheless, the number of live trees, logs, bare ground, and grass cover were significant predictors of rat RA. The results of our model do not entirely concur with Cox et al. (2000) or Brown et al. (1996), however they do reveal that rats can persist in a variety of microhabitats and may not necessarily be influenced by the same independent variables in different environments.

At a macrohabitat scale, rat RA exhibited significant differences between vegetation types. Overall, rats had a clear preference for forested areas with a mosaic of macrohabitats compared to forest fragments or grass/shrub habitats. Specifically, rat RA in vegetation type M5 (*Pisonia-Eugenia* mountains) differed significantly from all other vegetation types except M1 (*Myrcia-Quararibea* mountains) and M3 (*Chionanthus-Nectandra* mountains; Fig. 1; Table 1). This is unsurprising considering M1, M3, and M5 are located in the upper, wetter slopes and inside the crater of the Quill, although we expected M2 (*Coccoloba-Chionan-*

thus mountains) to have similar rat RA. Van Andel et al. (2016) describe M2 as “lower and denser than that in the crater bottom, with smaller trees growing on and between large boulders,” which may account for the difference. Rat RA in vegetation type M9 (*Rauvolfia-Antigonon* mountains) differed significantly from vegetation types C, M1, M2, M3, M5, and M7 (Table 1). This is to be expected given the differences in vegetation types, with M9 classified as regenerating grassland dominated by invasive flora such as *Corallita* (*Antigonon leptopus*; Van Andel et al. 2016). Floral composition in vegetation types M1, M2, and M3 is structurally more complex than M9, and thus may provide adequate food, nesting, and other resources. De Freitas et al. (2012) described vegetation type C as consisting of low shrubs/trees, species-poor vegetation, with fruit-bearing *Coccoloba uvifera* being the dominant species. This suggests that resources such as food might be limiting rat populations in M9 compared with C. Similarly, rat RA in vegetation type M4 (*Capparis-Pisonia* mountains) differed significantly from vegetation types C, M1, M2, and M3 (Table 1). M4 is located on the lower, dryer slopes on the south side of the Quill, and is heavily dominated by *Quadrella cynophallophora* and *Ficus citrifolia*, with a shrub and herb layer characterized by *Randia aculeata*

TABLE 1. Post-hoc Pairwise Wilcoxon test between rat relative abundance in 12 vegetation types on St. Eustatius. Significance levels (P -values) are shown. Bold typeface indicates significance.

	B	H1	H2	L1	L2	M1	M2	M3	M4	M5	M7
H1	0.72	-	-	-	-	-	-	-	-	-	-
H2	0.89	0.71	-	-	-	-	-	-	-	-	-
L1	0.22	0.60	0.34	-	-	-	-	-	-	-	-
L2	0.07	0.07	0.07	0.14	-	-	-	-	-	-	-
M1	0.35	0.07	0.04	0.04	0.03	-	-	-	-	-	-
M2	0.67	0.46	0.53	0.20	0.04	0.25	-	-	-	-	-
M3	0.23	0.03	0.03	0.07	0.03	0.50	0.18	-	-	-	-
M4	0.03	0.13	0.13	0.10	0.56	0.04	0.04	0.04	-	-	-
M5	0.03	0.03	0.03	0.03	0.03	0.08	0.03	0.12	0.03	-	-
M7	0.35	0.14	0.14	0.11	0.07	0.75	0.60	0.53	0.07	0.04	-
M9	0.03	0.07	0.07	0.07	0.18	0.03	0.04	0.03	0.66	0.03	0.04

and *Rauvolfia viridis* (Van Andel et al. 2016). As with M9, it is likely that rat populations in M4 are limited by food or other resources compared with those in coastal areas and forested areas on the wetter slopes and inside the crater. Specific microhabitat components may act as cues in determining macrohabitat use by black rats. As suggested by Cox et al. (2000), the strong association between rat RA and microhabitat components could indicate that rats are “opportunistic in macrohabitat use, but within large patches, individuals may preferentially use some microhabitats more than others.”

House mice were more likely to occur in microhabitats with more bare ground, but did not otherwise exhibit strong preferences for the other microhabitat components. Mouse population demography and behavior is thought to depend on microhabitat components such as dense ground cover, especially in the presence of black rats (Moller 1978; Brown et al. 1996). Our study did not find a significant association with mouse RA and number of stems (Table 3). Additionally, mice were

TABLE 2. Multiple linear regression of microhabitat components on black rat relative abundance on St. Eustatius. Significance levels (P -values) are shown. Bold typeface indicates significance. Model $\alpha < 0.001$.

	t	P
Grass cover	-2.42	0.02
Bare ground	-2.48	0.02
Leaf litter cover	-0.29	0.77
No. of stems	-1.44	0.15
Live trees	5.15	<0.001
Logs	-1.97	0.05

less (though not significantly) likely to occur in microhabitats with greater tree densities, in stark contrast to rats (Table 2). Grass cover in our regression model was identified as a marginally significant predictor of mouse occurrence, whereas bare ground was identified as the most important predictor. This is contrary to a number of other studies that suggest that mice are more likely to occur in sheltered microhabitats, which offer greater refuge from predation. For example, Arthur et al. (2005) determined that house mouse abundances were greater in microhabitats (outdoor enclosures) with increased habitat cover (grass and logs), which reduced their exposure to predators. Similarly, Dickman (1992) revealed that house mouse abundance roughly correlates with vegetation density in Western Australia.

At a macrohabitat scale, mouse RA did not differ significantly between vegetation type. However, mouse RA was higher than rat RA in vegetation types L1 and L2 (lowland areas characterized by scattered trees, shrubs, and extensive grass cover; de Freitas et

TABLE 3. Multiple linear regression of microhabitat components on house mouse relative abundance on St. Eustatius. Significance levels (P -values) are shown. Bold typeface indicates significance. Model $\alpha = 0.05$.

	t	P
Grass cover	1.94	0.06
Bare ground	2.01	0.05
Leaf litter cover	0.90	0.37
No. of stems	0.79	0.43
Live trees	-1.79	0.08
Logs	-0.93	0.36

al. 2012; Fig. 3). Similarly, mouse RA was higher than rat RA in vegetation types M4 and M9 (lower elevation areas characterized by low tree diversity, shrubs, grasses, and herbs; de Freitas et al. 2012; Fig. 3). We were surprised to detect mouse tracks inside the Quill crater during the second, third, fourth, and sixth assessments, especially since mice were not detected in any of the nearby vegetation types (Fig. 3). Unlike rats, mice are neophilic (Crowcroft 1973), therefore it is unlikely that they initially avoided the tracking tunnels. It is possible that the denser ground cover inside the Quill crater compared with the surrounding forest could account for the presence of a population of mice within this vegetation type (see Brown et al. 1996; Pocock et al. 2014; Shiels et al. 2018). We also note that a study on Hawai'i documented house mice at elevations from sea level to >3,500 meters (Cole et al. 2000).

We did not test whether the presence of rats affected mouse occurrence and distribution (e.g., through predation or exclusion through scent marking). In the majority of macrohabitats sampled, however, there was an inverse relationship between rat and mouse RA (Figs. 2 and 3). Our results are similar to Shiels et al. (2017), who found that black rats dominated forest habitat on Maui, whereas house mice dominated the adjacent grassland. If our data represent true population densities, house mice do not occur in any forest macrohabitats of the Quill except the crater (Fig. 3), whereas rats occur in all vegetation types at differing densities. However, if behavioral interference from rats is stronger in microhabitats with lower percentages of bare ground, then comparison of rat and mouse RA from tracking tunnel data could be confounded. If interference does occur, it may have affected comparisons of mouse and rat RA between assessments and habitats.

Rat RA differed significantly between assessments two and three (May to August 2018) and four and five (Nov 2018 to February 2019; Fig. 2; Table 2). Such differences might be explained by fluctuations in rainfall, especially since monthly rainfall on St. Eustatius is irregular (Van den Burg et al. 2012). The main flowering season of tree species in dry forest habitats is May (pers. obs.), with subsequent fruit availability in July/August. This could in part account for the differences in rat RA, however as mentioned earlier rodent populations on tropical islands are known to fluctuate and do not necessarily infer a decrease or increase in abundance (Russell et al. 2011). Mouse RA did not differ significantly over the study period except between as-

sessments one and two (July 2017 to May 2018; Fig. 3; Table 2), suggesting that food or other resources were either not limiting mouse populations, or were equally limiting, in the macrohabitats where mice occurred (Banks and Dickman 2000). Mouse RA was highest in November 2018 and lowest in May 2019, coinciding with the wet and dry seasons respectively.

This paper presents results that warrant further research. As stated earlier, rodent populations on tropical islands are generally denser than their temperate counterparts. When planning conservation efforts related to invasive rodents in the tropics, therefore, it is essential to understand temporal and spatial patterns in populations (Samaniego Herrera et al. 2017). Overall, the paucity of significant temporal differences in rat and mouse RA indicates that populations are relatively stable throughout the year. This is expected given the island's tropical climate. Our results are consistent with other studies (Harper and Carrion 2011; Harper et al. 2015; Russell and Holmes 2015) that document stable rodent populations year-round, but cite the dry period as most optimal for eradication purposes. We hope that the results of this study will be useful for local government and protected area managers to develop policies and conservation strategies to manage invasive rodents in rural areas, especially TPAs.

Acknowledgements—This work was funded by the Netherlands Ministry of Agriculture, Nature and Food Quality under the Nature Fund (Natuurgeld), grant number 1300023642. Permission to conduct fieldwork in the terrestrial protected areas was granted by St. Eustatius National Parks Foundation. We extend our gratitude to Elizabeth Bell of Wildlife Management International Ltd. for her expert advice throughout the duration of this project. We thank Jeremy Miller of Naturalis Biodiversity Center for his assistance with the map.

LITERATURE CITED

- Arthur, A. D., R. P. Pech, and C. R. Dickman. 2005. Effects of predation and habitat structure on population dynamics of House Mice in large outdoor enclosures. *Oikos* 108: 562–572.
- Banks, P. B. and C. R. Dickman. 2000. Effects of winter food supplementation on reproduction, body mass, and numbers of small mammals in montane Australia. *Canadian Journal of Zoology* 78: 1775–83.
- Barun, A., D. Simberloff, N. Tvrtkovic, and M. Pascal. 2011. Impact of the introduced small Indian mongoose (*Herpestes auro-punctatus*) on abundance and

- activity time of the introduced ship rat (*Rattus rattus*) and the small mammal community on Adriatic islands, Croatia. *NeoBiota* 11: 51.
- Brace, S., S. T. Turvey, M. Weksler, M. L. Hoogland, and I. Barnes. 2015. Unexpected evolutionary diversity in a recently extinct Caribbean mammal radiation. *Proceedings of the Royal Society B: Biological Sciences* 282: 20142371.
- Brown, K. P., H. Moller, J. Innes, and N. Alterio. 1996. Short communication - calibration of tunnel tracking rates to estimate relative abundance of ship rats (*Rattus rattus*) and mice (*Mus musculus*) in a New Zealand forest. *New Zealand Journal of Ecology* 20: 271–75.
- Brown, J. H. and E. J. Heske, 1990. Temporal changes in a Chihuahuan desert rodent community. *Oikos* 59: 290–302.
- Christie, J. E., P. R. Wilson, R. H. Taylor, and G. Elliott. 2017. How elevation affects ship rat (*Rattus rattus*) capture patterns, Mt Misery, New Zealand. *New Zealand Journal of Ecology* 41: 113–19.
- Clark, D. B. 1980. Population ecology of *Rattus rattus* across a desert montane forest gradient in the Galapagos islands. *Ecology* 61: 1422–33.
- Cole, F. R., L. L. Loope, A. C. Medeiros, C. E. Howe, and L. J. Anderson. 2000. Food habits of introduced rodents in high-elevation shrubland of Haleakala National Park, Maui, Hawai'i. *Pacific Science* 54: 313–29.
- Collier, N. and A. Brown. 2008. St. Eustatius. Pp. 268–271 in *Important bird areas in the Caribbean: key sites for conservation*, D. C. Wege and V. Anadon- Irizarry (eds.). BirdLife International.
- Cox, M. P. G., C. R. Dickman, and W. G. Cox. 2000. Use of habitat by the black rat (*Rattus rattus*) at North Head, New South Wales: an observational and experimental study. *Austral Ecology* 25: 375–85.
- Crowcroft, P. 1973. *Mice all over*. The Chicago Zoological Society.
- De Freitas, J. A., A. C. Rojer, B. S. J. Nijhof, and A. O. Debrot. 2012. A landscape ecological vegetation map of Sint Eustatius (Lesser Antilles). IMARES. CARMABI and Royal Netherlands Academy of Arts and Sciences.
- Dickman, C. R. 1992. Predation and habitat shift in the house mouse, *Mus domesticus*. *Ecology* 73: 313–322.
- Ernest, S. K. M., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. *Oikos* 88: 470–82.
- Hansson, L. and H. Henttonen. 1985. Gradients in density variations of small rodents: the importance of latitude and snow cover. *Oecologia* 67: 394–402.
- Harper, G. A., K. J. M. Dickinson, and P. J. Seddon. 2005. Habitat use by three rat species (*Rattus* spp.) on Stewart Island/Rakiura, New Zealand. *New Zealand Journal of Ecology* 29: 251–60.
- Harper, G. A. and V. Carrion. 2011. Introduced rodents in the Galápagos: colonisation, removal and the future. Pp. 63–66 in *Island invasives: eradication and management*, C. R. Veitch, M. N. Clout, and D. R. Towns (eds.). IUCN.
- Harper, G. A., M. van Dinther, J. C. Russell, and N. Bunbury. 2015. The response of black rats (*Rattus rattus*) to evergreen and seasonally arid habitats: informing eradication planning on a tropical island. *Biological Conservation* 185: 66–74.
- Harper, G. A. and N. Bunbury. 2015. Invasive rats on tropical islands: their population biology and impacts on native species. *Global Ecology and Conservation* 3: 607–627.
- Henttonen, H. 1985. Predation causing extended low densities in microtine cycles: further evidence from shrew dynamics. *Oikos* 45: 156–157.
- Kairo, M., B. Ali, O. Cheesman, K. Haysom, and S. Murphy. 2003. *Invasive species threats in the Caribbean Region*. Report to the Nature Conservancy. CAB International.
- Kot, M. and W. M. Schaffer. 1984. The effects of seasonality on discrete models of population growth. *Theoretical Population Biology* 26: 340–360.
- Madden, H., T. Van An del, J. Miller, M. Stech, K. Verdel, and E. Eggermont. 2019. Vegetation associations and relative abundance of rodents on St. Eustatius, Caribbean Netherlands. *Global Ecology and Conservation* 20: e00743.
- Madsen, T. and R. Shine. 1999. Rainfall and rats: climatically-driven dynamics of a tropical rodent population. *Austral Ecology* 24: 80–89.
- Moller, H. 1978. A weta and rodent study on Arapawa Island. Self-published file report, Ecology Division, DSIR, Nelson, N.Z.
- Pocock, M. J. O., J. B. Searle, and P. C. L. White. 2004. Adaptations of animals to commensal habitats: population dynamics of house mice *Mus musculus domesticus* on farms. *Journal of Animal Ecology* 73: 878–88.

- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roobol, M. J. and A. L. Smith. 2004. *Volcanology of Saba and St. Eustatius, Northern Lesser Antilles*. Koninklijke Nederlandse Akademie van Wetenschappen.
- Russell, J. C., D. Ringler, A. Trombini, and M. Le Corre. 2011. The island syndrome and population dynamics of introduced rats. *Oecologia* 167: 667–676.
- Russell, J. C. and L. Ruffino. 2012. The influence of spatio-temporal resource fluctuations on insular rat population dynamics. *Proceedings of the Royal Society B* 279: 767–74.
- Russell, J. C. and N. D. Holmes. 2015. Tropical island conservation: rat eradication for species recovery. *Biological Conservation* 185: 1–7.
- Salibay, C. C. and H. A. V. Luyon. 2008. Distribution of native and non-native rats (*Rattus* sp) along an elevational gradient in the tropical rainforest of Southern Luzon, Philippines. *Ecotropica* 14: 129–36.
- Samaniego Herrera, A. 2014. Ecology and impacts of invasive rodents on tropical islands, in relation to eradication operations: Science-based restoration. Doctoral dissertation, The University of Auckland.
- Samaniego Herrera, A., M. N. Clout, A. Aguirre-Muñoz, and J. C. Russell. 2017. Rodent eradications as ecosystem experiments: a case study from the Mexican tropics. *Biological Invasions* 19: 1761–79.
- Schaffer, W. M. 1985. Order and chaos in ecological systems. *Ecology* 66: 93–106.
- Schaffer, W. M., S. Ellner, and M. Kot. 1986. Effects of noise on some dynamical models in ecology. *Journal of Mathematical Biology* 24: 479–523.
- Shapiro, S. S. and M. B. Wilk. 1965. An analysis of variance test for normality (complete samples). *Biometrika* 52: 591–611.
- Shiels, A. B., C. A. Flores, A. Khamsing, P. D. Krushelnycky, S. M. Mosher, and D. R. Drake. 2013. Dietary niche differentiation among three species of invasive rodents (*Rattus rattus*, *R. exulans*, *Mus musculus*). *Biological Invasions* 15: 1037–48.
- Shiels, A. B., W. C. Pitt, R. T. Sugihara, and G. W. Witmer. 2014. Biology and impacts of Pacific island invasive species. 11. *Rattus rattus*, the black rat (rodentia: muridae). *Pacific Science* 68: 145–184.
- Shiels, A. B., A. C. Medeiros, and E. I. von Allmen. 2017. Shifts in an invasive rodent community favoring black rats (*Rattus rattus*) following restoration of native forest. *Restoration ecology* 25: 759–767.
- Shiels, A. B. and G. R. de Arellano. 2018. Invasive rats (*Rattus* sp.), but not always mice (*Mus musculus*), are ubiquitous at all elevations and habitats within the Caribbean National Forest, Puerto Rico. *Caribbean Naturalist* 48: 1–14.
- Statistics Netherlands. 2018. Trends in the Caribbean Netherlands 2018.
- Sokal, R. R. and F. J. Rohlf. 1995. Biometry: The principles and practice of statistics in biological research, 3rd Ed. W. H. Freeman.
- Taitt, M. J. and C. J. Krebs. 1985. Population dynamics and cycles. Pp. 567–620 in Biology of New World *Microtus*, R. H. Tamarin (ed.). *Special Publication, The American Society of Mammalogists* 8: 1–893.
- Van Andel, T., B. van der Hoorn, M. Stech, S. Bantjes, S. B. Arostegui, and J. Miller. 2016. A quantitative assessment of the vegetation types on the island of St. Eustatius, Dutch Caribbean. *Global Ecology and Conservation* 7: 59–69.
- Van der Burg, W. J., J. De Freitas, A. O. Debrot, and L. A. P. Lotz. 2012. Naturalised and invasive alien plant species in the Caribbean Netherlands: status, distribution, threats, priorities and recommendations: report of a joint Imares/Carmabi/PRI project financed by the Dutch Ministry of Economic Affairs, Agriculture & Innovation (No. C185/11). Plant Research International, Business Unit Agrosystems Research.
- Wanless, R. M., A. Angel, R. J. Cuthbert, G. M. Hilton, and P. G. Ryan. 2007. Can predation by invasive mice drive seabird extinctions? *Biology Letters* 3: 241–44.