Research Article

Surface material and snout-vent length predict vertical scaling ability in brown treesnakes: an evaluation of multispecies barriers for invasive species control on Guam

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Abstract

The combination of snake-proof barriers and an aerial toxicant-delivery system for snake suppression may allow large-scale control of invasive brown treesnakes (*Boiga irregularis*) on Guam. However, suppression or local eradication of several other species (e.g., introduced ungulates, cats, rodents) may be required for successful restoration and recovery of forest habitat and reintroduction of native fauna. Island-wide eradication of invasive species is unlikely on Guam, and existing snake-proof barriers are largely ineffective against cats, rodents, shrews, or monitor lizards. Improved barrier technology and pest-control tools may together provide a viable solution to support localized restoration of species and habitats. We designed and tested prototype multispecies barriers using materials known to repel ungulates, cats, and rodents, with a focus on testing the ability of a rolled hood installed over three different mesh designs to repel brown treesnakes and black rats (*Rattus rattus*). Woven wire (4.9 × 12 mm aperture, 2.5 mm dia. wire) repelled 99.1% of all snakes, including ≥ 1031 breach attempts by 106 individuals and 2 successful breaches by 1 small individual. Woven wire (6 × 6 mm aperture, 2.7 mm dia. wire) repelled 100% of all snakes, including 611 breach attempts by 65 individuals. Mini chain link mesh (7 × 9 mm aperture, 1 mm dia. wire) repelled 100% of all snakes, including 1053 breach attempts by 97 individuals. Brown treesnakes were unable to climb either of the two woven wire designs (1642 breach attempts by 171 individuals), making the rolled hood serve as a redundant secondary snake barrier. The rolled hood repelled 100% of all snakes when individuals were provided a climbable surface to access the hood (94 breach attempts by 39 snakes). The probability of a snake being able to climb the mini chain link mesh was inversely related to snout-vent length. The rolled hood repelled 100% of all rats, with 5080 breach attempts by 21 individuals. Recommended next steps include consultation with engineers to address wind loading, structural integrity, material interactions, and integration of decision-support tools to optimize cost and efficacy of barrier designs on the landscape.

Key words: *Boiga irregularis*, conservation fences, control tools, island conservation, pest species, *Rattus rattus*

Introduction

Biological invasions are a global threat to native fauna and flora and a primary driver of extinctions on islands (Blackburn et al. 2004; Bellard et

al. 2016, 2017; Doherty et al. 2016). Due to isolation and small population sizes, island species are especially vulnerable to invasive mammals (Croll et al. 2005; Howald et al. 2007; Medina et al. 2011). On Guam, the threats posed by introduced mammals (rodents, shrews, feral cats and dogs, and ungulates) have been compounded by the accidental introduction of the brown treesnake (*Boiga irregularis* (Bechstein, 1802)) from the Admiralty Islands shortly after World War II (Rodda et al. 1992a; Richmond et al. 2015). The brown treesnake has since been causally linked to declines, extirpations, or extinctions of many of Guam's native bird, bat, and lizard species (Savidge 1987; Fritts and Rodda 1998; Rodda and Savidge 2007). Loss of vertebrate seed dispersers and pollinators has, in turn, negatively impacted Guam's native plant communities (Mortensen et al. 2008; Rogers et al. 2017; Fricke et al. 2018), including economically important species (Egerer et al. 2018). The extinctions on Guam represent significant losses and provide a case study of the cascading ecosystem effects that can result when invasive predators become established on an island.

Research into the control and containment of brown treesnakes has been ongoing since its role in the extirpation or extinction of nearly all of Guam's native avifauna was first recognized in the 1980s (Savidge 1987; Fritts 1988; Rodda and Savidge 2007). In 2003, the U.S. Geological Survey erected a two-way "double-bulge" barrier to prevent movement of snakes in or out of a 5-ha forested study area (hereafter, NWFN) on Northwest Field North of Andersen Air Force Base (Perry et al. 1998, 2001). Intensive capture-recapture efforts on both sides of the barrier since 2004 suggest minimal to no emigration or immigration, indicating efficacy of this barrier design (Tyrrell et al. 2009). More recently, several additional areas on Guam have been enclosed by one-way single-bulge barriers to prevent (Habitat Management Unit on Andersen Air Force Base) or impede (Guam National Wildlife Refuge) the ingress of snakes but allow the egress of snakes. With the development of snake-proof barriers (Perry et al. 1998, 2001) and, more recently, a novel aerial toxicant delivery system that deploys acetaminophen-laced baits to the landscape (Savarie et al. 2001; Clark and Savarie 2012; Siers et al. 2020), the first practical tools for large-scale control of brown treesnakes are now available.

Although large-scale control may be achievable, island-wide eradication of brown treesnakes and other invasive species on Guam is unlikely given its size (> 570 km^2) and extent of urbanization and karst terrain. When complete eradication of target pest species is impractical due to the size and characteristics of the landscape, multispecies barriers provide a more tenable focal area from which to eradicate pest species and impede their reentry (Saunders and Norton 2001; Burns et al. 2012; Young et al. 2013). Multispecies barriers can effectively exclude many invasive predators and browsers (Day and MacGibbon 2007; Speedy et al. 2007; Young et al. 2013). After multispecies barriers have been installed and pest species

removed from within the enclosed area, these barriers provide "safe zones" for native species and encourage localized recovery of native fauna and flora (Young et al. 2013; Tanentzap and Lloyd 2017).

Reintroduction of native species on Guam will require a multipronged approach of forest recovery that will likely include exclusion and suppression or eradication of the brown treesnake, Philippine deer (*Rusa marianna* Desmarest, 1822), feral pigs (*Sus scrofa* Linnaeus, 1758), dogs (*Canis lupus* Linnaeus, 1758), cats (*Felis catus* Linnaeus, 1758), rats (*Rattus* spp.), mice (*Mus musculus* Linnaeus, 1758), Indian musk shrews (*Suncus murinus* Linnaeus, 1766) and, at least initially, the native mangrove monitor (*Varanus tsukamotoi* Kishida, 1929) (Weijola et al. 2019, 2020). Although the current single- and double-bulge barrier designs used on Guam effectively repel snakes, they are ineffective against cats, rodents, shrews, and monitors. Additionally, the current fencing materials have experienced substantial rust and corrosion from wet conditions and salt spray, making barriers vulnerable to incursions by all species. Fortunately, developments in multispecies barrier technology (Day and MacGibbon 2007; Burns et al. 2012) and other control tools (Russell and Broome 2016; Murphy et al. 2019; Read et al. 2019) may provide additional avenues for pest control on Guam. For example, hood designs used atop multispecies barriers in New Zealand and Hawaii have substantially reduced incursion rates of cats and, to a lesser extent, rats (Day and MacGibbon 2007; Young et al. 2013). However, the effectiveness of these hoods at excluding brown treesnakes is unknown. Thus, additional research is still needed to achieve a barrier design that will meet Guam's needs for predator and ungulate-free areas suitable for reintroduction of native species. The objective of this study was to test barrier permeability of exclusion prototypes against brown treesnakes and rats (*Rattus* spp.) to inform the Department of Defense for construction of full-scale multispecies barrier fences on Guam.

Materials and methods

Arena design

To test barrier permeability to brown treesnakes and rats, we constructed a 3 × 3 m arena within a climate-controlled building at the U.S. Geological Survey Guam Magnetic Observatory (Figure 1). The arena included rounded corners constructed with a polyvinyl chloride composite, three 2.4 m sheer unclimbable formica walls, and one wall containing an experimental barrier that was interchangeable so that different mesh materials could be trialed independently. The experimental barrier wall consisted of a 2 × 2 m plywood frame to support the mesh and a single galvanized half-pipe design rolled hood atop the frame. The rolled hood was designed to repel animals that reached the top of the barrier, and a single prototype version was used in all trials (1.1 mm thick, inner to outer edge width ~ 24.8 cm,
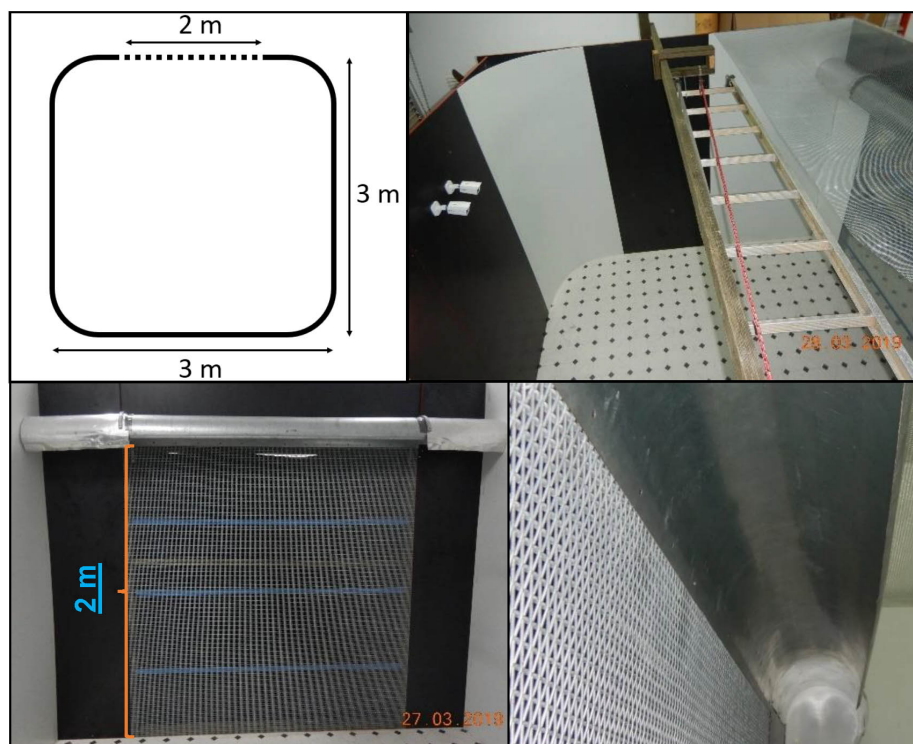
Figure 1. Clockwise from upper left: 1) arena design: three sheer walls and one interchangeable experimental barrier wall (dotted line), 2) overhead view of arena, IR cameras, and ladder for personnel entry/exit, 3) interior of rolled hood, 4) experimental 2 × 2 m exclusion prototype wall with external reflective tape indicating different barrier heights. Photographs by Eric T. Hileman.

arc length ~ 45.7 cm). We attached the hood to the mesh using rounded brackets mounted on the outside of the hood to reduce climbable surfaces on the interior of the mesh panel and hood. We placed each experimental barrier so that the hood faced the interior of the arena and trial animals within the arena would have to pass through the mesh or climb over the hood to escape (Figure 1).

We used a Lorex surveillance system with three infra-red, high-definition video cameras to monitor individuals during trials. We mounted two cameras inside the arena back wall and one camera above the arena to record breach attempts and other interactions with the experimental barrier (Figure 1). We placed blue reflective tape on the outside of the experimental wall to demarcate heights of 0.5, 1, and 1.5 m to tally heights climbed by individuals. The bottom edge of the hood was at a height of 2 m (Figure 1).

Collection of trial subjects

Brown treesnakes

We captured snakes via visual surveys or trapping using standard brown treesnake traps, which are modified minnow traps baited with live mice (Rodda et al. 1999). We recorded snout-vent length (SVL) by stretching individuals over a cloth measuring tape, mass using Pesola scales, and sex via cloacal probing and palpation to evert hemipenes. Brown treesnakes have known differences in arboreality based on size (Rodda and Reed

2007). Therefore, we collected snakes from four size classes, to account for size-related differences in climbing ability and barrier permeability. The four size classes included small (< 800 mm SVL), medium (800–950 mm SVL), medium-large (951–1100 mm SVL), and large (> 1100 mm SVL) snakes. In general, we trialed snakes within two weeks of capture, excluding eight snakes held long-term for educational purposes and two snakes initially held for other research. We trialed the long-term captive snakes because snakes of their size (range = 1505–1931 mm SVL) are infrequently encountered in the wild on Guam. Snakes awaiting trial were housed individually and provided refuge and water *ad libitum* in well-ventilated 5-gallon plastic buckets with indirect exposure to natural lighting.

Rats

We captured rats using Haguruma traps baited with a mixture of peanut butter, oats, and food-grade paraffin. We identified species and recorded body length by measuring from the tip of the snout to the anus using a ruler, mass using a digital or Pesola scale, and sex via external reproductive characteristics. All rats were trialed within two weeks of capture. Rats awaiting trial were housed individually in metal wire cages with indirect exposure to natural lighting and provided a PVC tube refuge, a substrate of wood shavings, a seed mixture, and potato for water.

Arena trials

Both rats and brown treesnakes are generally nocturnal species. Therefore, we ran all trials for 12 consecutive hours, beginning at ca. 1830 and concluding at ca. 0630 the next day to capture nocturnal activity. Rat trials began 28 April 2019 and concluded 26 June 2019. To avoid aggression between conspecifics, only a single rat was trialed per night. Snake trials began 2 April 2019 and concluded 11 March 2020. We trialed up to 8 snakes per night because aggression between conspecifics is undocumented in this species and believed to be uncommon, which we confirmed during trials. To individually identify snakes on video recordings, we uniquely marked individuals using non-toxic surgical glue and high index reflective powder. The reflective powder is made of non-toxic smooth, rounded (virgin) glass beads 35–45 microns in size (https://colesafetyinternational.com/High-Index-Reflective-Beads-Type-3-HiInd1pd.htm). Beginning on 18 April 2019, we added a caged live mouse placed over the hood as lure to encourage breach attempts by snakes.

We viewed infrared videos at up to 16X speed using the open source multimedia player VLC (version 3.0.8, https://www.videolan.org/vlc/download-windows.html) and transcribed detailed accounts of individual breach attempts to quantify the success of a given experimental barrier wall at preventing breaches, classified as an escape from the trial arena. We considered
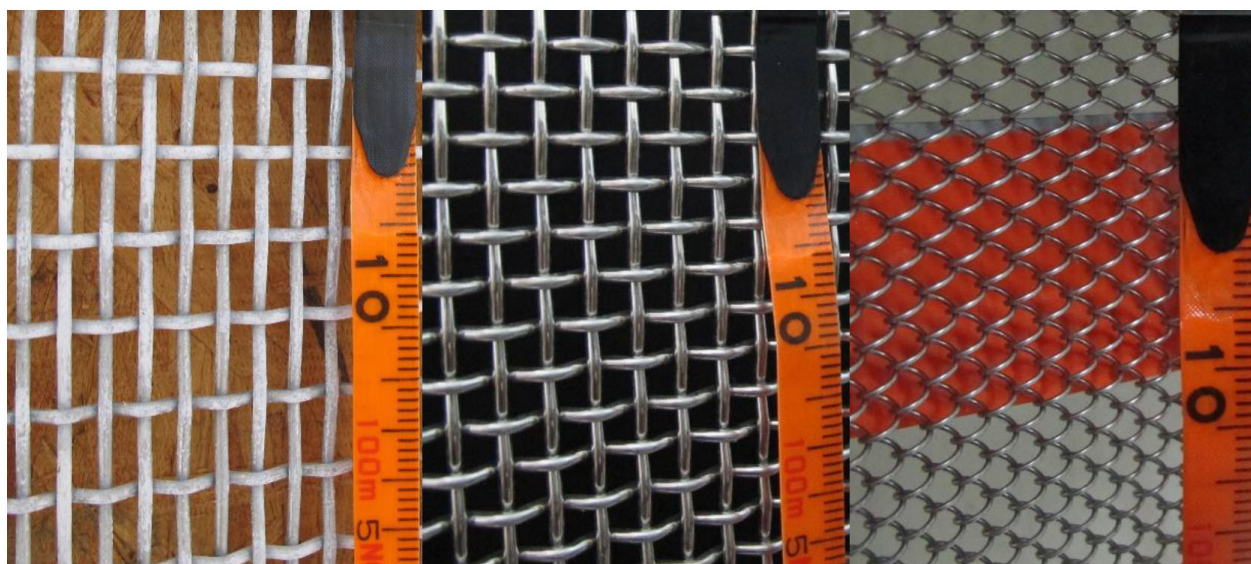
Figure 2. Three mesh designs used in trials (left to right): 1) galvanized woven wire, 4.9 × 12 mm aperture, 2.5 mm diameter wire (prototype #1), 2) T-304 stainless steel woven wire 6 × 6 mm aperture, 2.7 mm diameter wire (prototype #2) and, 3) T-304 stainless steel mini chain link 7 × 9 mm aperture, 1 mm diameter wire (prototype #3). Photographs by Patrick D. Barnhart.

a breach attempt to have occurred when any part of the animal's body reached a height ≥ 0.5 m on the experimental barrier wall. For each attempt, we recorded the maximum height achieved (i.e., 0.5, 1, 1.5, or 2 m) and whether the animal breached the experimental barrier. Each breach attempt was considered concluded when all four limbs (rat) or both the head and > 50% of the body (snake) returned to the ground. We also recorded the number of times an animal reached ≥ 2 m and considered each observation at this height an attempt to defeat the hood.

Materials tested

In selecting mesh types for evaluation, our aim was to test materials that brown treesnakes, shrews, rodents, cats, dogs, and monitors could not pass through and that were sufficiently durable to withstand repeated impact by ungulates (Perry et al. 2001; Day and MacGibbon 2007; Siers and Savidge 2017). All mesh designs consisted of small aperture woven wire or mini chain link mesh with a rolled hood affixed at the top (Figures 1 and 2). The first mesh type we trialed was prototype # 1 (woven wire mesh with an aperture of 4.9 × 12 mm; Kapiti Fencing and Gate Services Ltd., 1 Kaitawa Crescent Paraparaumu 5032, NZ). Both rats and snakes were trialed (separately) using this mesh. Subsequent mesh types were trialed only with snakes because rats can climb all mesh types, and we were only assessing the ability of rats to breach the hood, which was identical on all prototypes.

To increase motivation of small snakes to attempt to pass through openings of this mesh, we also constructed a second, fully enclosed shoebox-sized arena (~ 27.9 × 18.2 × 19.6 cm) to trial snakes < 800 mm SVL. This small arena was designed to evaluate mesh aperture and consisted of wooden walls on all sides except one, which was a 15.2 × 17.8 cm panel of

the same woven wire used in the full-scale arena trial of prototype #1. The small arena was housed within a larger Neodesha reptile cage to contain any snakes able to breach via the mesh apertures. Trial duration ranged from ~ 15 to ~ 24 consecutive hours, with all trials encompassing the hours of 1830–0630 to capture nocturnal activity. We trialed up to two snakes per trial from 10 April–19 July 2019. In 30 of 35 trials, 1–2 live lizards were placed outside the arena, but within the Neodesha, as a lure to encourage snakes to penetrate the mesh aperture. We documented any snake that was outside the arena at the conclusion of a trial as a successful breach of the mesh. After observing penetration of this aperture by a neonate brown treesnake (details reported in Results), we trialed two additional prototypes: prototype #2 (woven wire prototype with a smaller 6 × 6 mm aperture; Edward J. Darby & Son Inc., 2200 N 8th St, Philadelphia, PA 19133, USA) and prototype #3 (mini chain link mesh 7 × 9 mm aperture; Conservation Fencing LLC., 3030 Oahu Ave, Honolulu, HI 96822, USA; Figure 2). Prototype #3 was lighter (~ 305g/304.8 mm^2), has lower wind loading, and conforms to the landscape better than prototype #1 (~ 743g/304.8 mm^2) or #2 (~ 1017g/304.8 mm^2).

Because brown treesnakes were unable to scale > 1 m on the prototype walls in woven wire mesh trials (i.e., prototypes #1 and #2), these snakes never reached the barrier hood. Therefore, to test permeability of the hood in the event of mesh deterioration (e.g., rust accumulation) that may allow snakes to climb after weathering, we added climbable features to this mesh type and conducted additional trials of snakes (hereafter, hood trials), otherwise using the same methods previously described. These added features were small "steps" made of packing foam and attached to the mesh using zip ties, with the highest step approximately 0.5 m below the hood (Figure 3).

Statistical analyses

We used program R (R Core Team 2019) for all statistical analyses. To test if mesh type influenced the probability that a snake could reach ≥ 1 m on the prototype wall, given that it made a breach attempt (i.e., reached a height ≥ 0.5 m as defined above), we used data from all trials conducted in the full-scale arena, except for hood trials. We used the lme4 package (Bates et al. 2015) to fit a generalized linear mixed-effects model with a binary response variable indicating if an individual breach attempt reached a maximum height ≥1 m (1) or < 1 m (0). Our explanatory variables included an interaction between SVL (standardized) and mesh type (i.e., woven wire *vs* mini chain link), an additive effect of sex, and a random intercept for individual ID to account for multiple breach attempts per individual. For the sex effect, we used a numeric code to classify individuals as unknowns (0) that were too small to reliably sex, males (−1), and females (1). This coding allowed us to obtain estimates for cohorts by adding the beta value
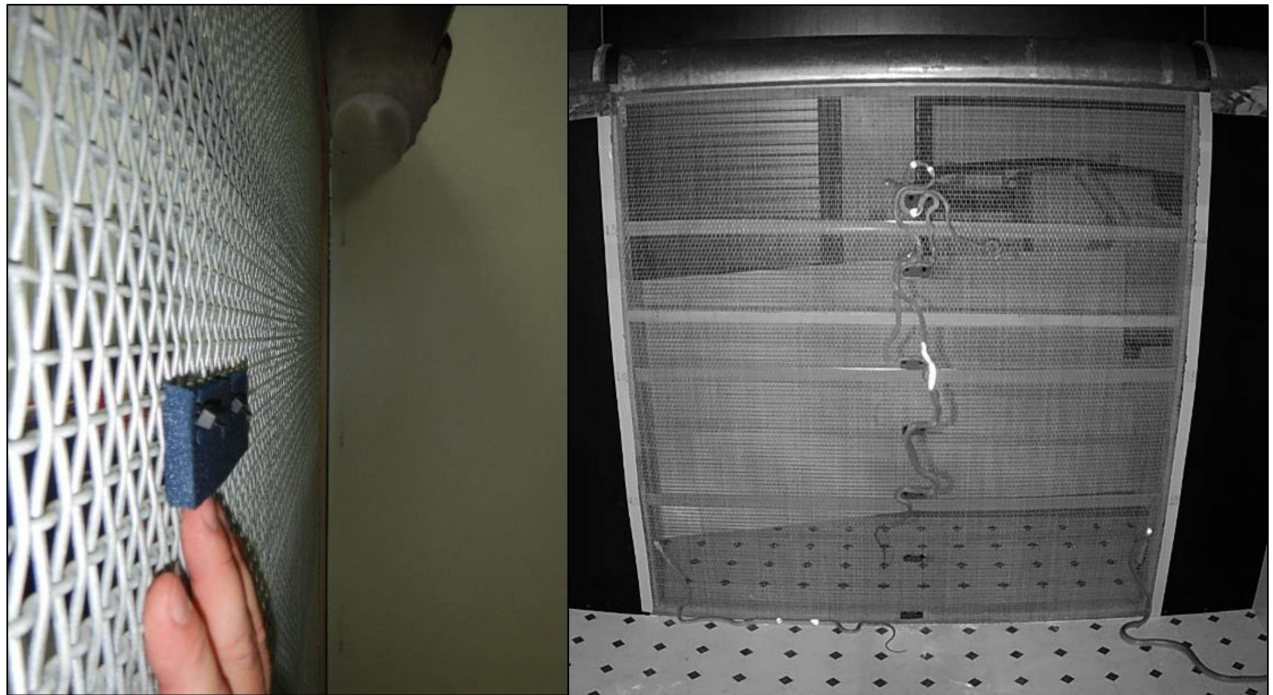
Figure 3. Climbable features added to mesh to allow snakes to reach the hood and attempt to breach it (left) and infra-red video camera image of snakes using the climbable features to get within range of the hood (right). Photograph by Eric T. Hileman.

for females, subtracting it for males, and leaving it out for individuals that were not assigned a sex. We used a likelihood ratio test and set α = 0.05 to compare this model to a reduced model that omitted the effect of mesh type.

Because no snakes in woven wire mesh trials scaled the prototype walls higher than 1 m, but some snakes in mini chain link mesh trials were able to climb to the top, we also conducted separate analyses for each mesh type so we could use different response variables by mesh type and make more meaningful inferences. For each analysis, we constructed a candidate set of five models that included a null model and all possible combinations of the explanatory variables SVL (standardized) and sex, with all models including the random intercept effect for individual ID. For trials of woven wire mesh, the response variable was identical to our first analysis, indicating if a breach attempt reached a maximum height ≥1 m (1) or < 1 m (0). However, for trials of mini chain link mesh, the response variable indicated if a breach attempt reached a maximum height ≥ 2 m (1) or < 2 m (0). We used Akaike's information criterion adjusted for small sample size (AIC$_c$) for model selection within each candidate set (Akaike 1973). To calculate and plot marginal effects, we used the ggeffects (Lüdecke 2018) and ggplot2 (Wickham 2016) packages.

Results

Brown treesnakes

In total, we conducted 350 trials of 291 individuals (Tables 1 and 2). No snakes breached the prototype walls, including the hood, of the full-scale arena; however, one neonate (SVL = 392 mm) penetrated the 4.9 × 12 mm

Table 1. Summary of arena and hood trials for small, S (< 800 mm SVL), medium, M (800–950 mm SVL), medium-large, ML (951–1100 mm SVL), and large, L (> 1100 mm SVL) brown treesnakes.

Trial type	Size class	No. individuals	No. trials	No. breaches	No. breach attempts and height (m) achieved			
					0.5	1.0	1.5	2.0
Prototype 1: woven wire 4.9 × 12 mm aperture 2.5 mm diameter wire	L	19	25	0	309	38	0	0
	ML	25	25	0	363	0	0	0
	M	26	26	0	260	0	0	0
	S	25	25	0	61	0	0	0
Prototype 1: (small arena)	S	17	35	2[†]	NA	NA	NA	NA
Prototype 2: woven wire 6 × 6 mm aperture 2.7 mm diameter wire	L	23	23	0	313	51	0	0
	ML	13	14	0	122	0	0	0
	M	14	14	0	116	0	0	0
	S	15	15	0	9	0	0	0
Prototype 3: mini chain link 7 × 9 mm aperture 1 mm diameter wire	L	21	21	0	303	102	0	0
	ML	29	30	0	240	0	0	0
	M	29	29	0	258	3	1	0
	S	18	29	0	82	21	21	22
Hood trial	L	30	30	0	NA	NA	NA	75
	ML	9	9	0	NA	NA	NA	19

[†] Both breaches were by the same individual.

Table 2. Summary of brown treesnake snout-vent lengths (mean, $\bar{X}$, standard deviation, SD; range) by mesh type and size class (small, S; medium, M; medium-large, ML; large, L).

Mesh type	N	Size class	$\bar{X}$	SD	Range
Prototype 1: woven wire[†] 4.9 × 12 mm aperture 2.5 mm diameter wire	19	L	1384	304	1103–1931
	25	ML	1012	42	951–1090
	26	M	876	44	800–938
	36	S	638	111	392–795
Prototype 2: woven wire 6 × 6 mm aperture 2.7 mm diameter wire	23	L	1264	161	1100–1678
	13	ML	1020	46	952–1080
	14	M	895	47	815–947
	15	S	575	131	378–769
Prototype 3: mini chain link 7 × 9 mm aperture 1 mm diameter wire	21	L	1211	117	1100–1460
	29	ML	999	32	952–1090
	29	M	890	35	829–950
	18	S	590	69	446–727
Hood trial	30	L	1262	163	1100–1678
	9	ML	1030	21	1000–1065

[†] Includes trials within full-scale and small arena.

aperture woven wire mesh in two separate trials within the small-scale arena (Table 1). None of the snakes trialed on the woven wire prototypes were able to fully lift themselves off the ground onto the mesh wall unless aided by climbable features for hood trials. Instead, these snakes relied on "tail-standing" behavior to reach ≤ 1 m height. However, 13 small individuals (range = 530–727 mm SVL) in the mini-chain-link prototype trials were able to climb to the top of the mesh.

Given an attempt was made, the probability that a snake could climb the mini chain link mesh (defined as reaching a height ≥ 1 m) was higher than the probability that a snake could climb the woven wire mesh (likelihood ratio test, $\chi_2^2 = 72.789, P = 2.2e - 16$). Controlling for SVL, sex, and the random effect of ID, snakes trialed on mini chain link mesh had a mean

Table 3. Candidate generalized mixed effects models for woven wire and mini chain link mesh trials. A random intercept effect for individual ID contributes one parameter (K) to each model.

Model	K	AIC_c[†]	ΔAIC_c[‡]	w_i[§]	$-2\text{Log}(\mathscr{L})$[#]
Woven wire					
SVL * Sex	5	455.85	0.00	0.470	−222.91
SVL + Sex	4	456.92	1.07	0.275	−224.45
SVL	3	457.08	1.23	0.255	−225.53
Sex	3	500.87	45.01	0.000	−247.43
Intercept	2	516.27	60.42	0.000	−256.13
Mini chain link					
SVL	3	133.01	0.00	0.660	−63.49
SVL + Sex	4	134.98	1.97	0.247	−63.47
SVL * Sex	5	136.92	3.91	0.093	−63.43
Intercept	2	188.03	55.02	0.000	−92.01
Sex	3	190.00	56.99	0.000	−91.99

[†] Akaike's Information Criterion adjusted for small sample size.
[‡] Difference between the AIC_c of model i and the top-ranked model.
[§] Probability model i is the best model given the data and alternative models in the candidate set.
[#] Model fit.

probability of 0.03 (95% CI = 0.01–0.06) of reaching ≥ 1 m. Snakes trialed on woven wire mesh had a mean probability of 0.00 (95% CI = 0.00–0.00) of reaching ≥ 1 m.

For the woven-wire analysis, the model including an interaction between SVL and sex garnered the most support for explaining the probability of a snake reaching ≥ 1m (AIC$_c$ weight = 0.47, Table 3). However, comparing this model to one that included only SVL and a random intercept effect indicated that sex and the interaction term were uninformative as they did not improve model fit sufficiently to overcome the four-unit penalty imposed on the global model for having two additional parameters (Table 3). Similarly, the model including the additive effect of SVL and sex was ranked second, but it did not improve model fit sufficiently to overcome the two-unit penalty imposed by having one additional parameter (Arnold 2010, Table 3). Therefore, we selected the SVL and random intercept model as our most parsimonious model, which included a positive effect of SVL on the probability of a snake reaching ≥ 1 m (Figure 4). For the minichain-link-mesh analysis, our most supported model was also the SVL and random intercept model (AIC$_c$ weight = 0.66). However, in this case there was a negative effect of SVL on the probability of a snake climbing to the top of the prototype wall (≥ 2 m; Table 3, Figure 5).

Rats

We conducted 31 trials of 21 individuals, including 11 females and 10 males, all identified as black rats (*Rattus rattus* Linnaeus, 1758, mean body length = 166 mm ± 26 SD, range = 103–215 mm; mean mass = 105 g ± 38 SD, range = 54–189 g). In total, we recorded 4351 breach attempts and 5080 attempts to defeat the hood. No individuals successfully breached the experimental barrier. However, we documented five attempts by three rats
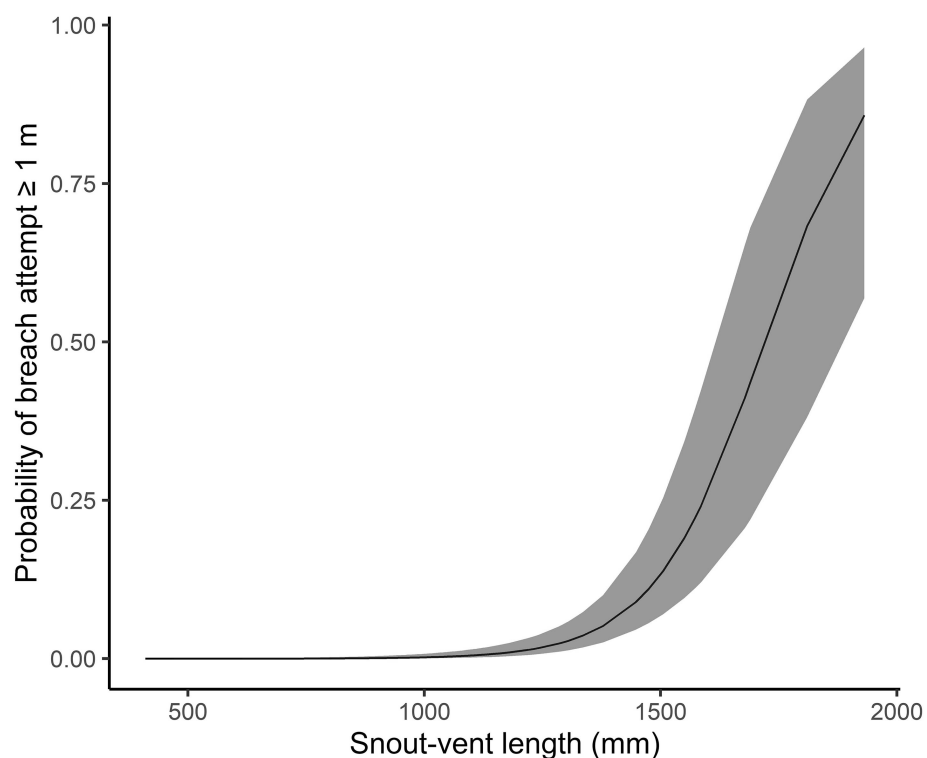
Figure 4. The effect of snout-vent length on the probability of a snake reaching a height of 1m using "tail-standing," given that a breach was attempted.
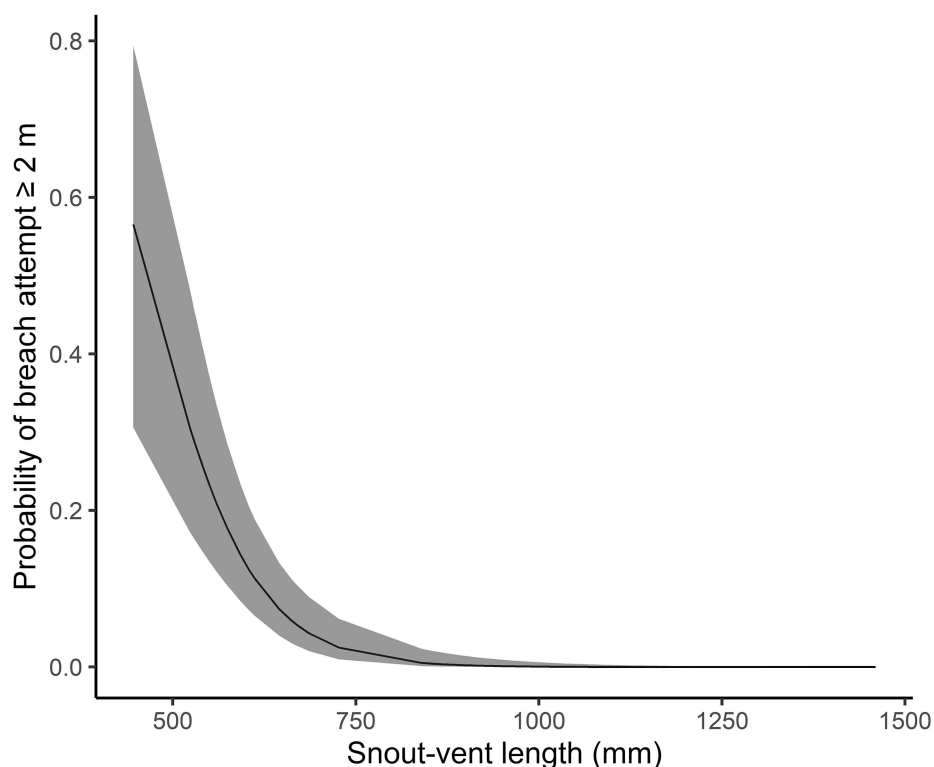
Figure 5. The effect of snout-vent length on the probability of a snake being able to climb mini chain link mesh (defined as reaching a height of ≥ 2 m), given that a breach was attempted.

(2 females, 1 male) where individuals were able to leap to the underside of the hood and cling to it for a maximum of ~ 22 s before falling to the ground.

Discussion

When island-wide invasive-species eradication is not possible, multispecies barriers may provide a viable alternative by creating smaller areas in which eradication of pest species and restoration of native species may occur with reduced risk of re-invasion (Innes et al. 2019). Our arena trials demonstrate that a multispecies barrier with a rolled hood design similar to those used in New Zealand, Hawaii, and elsewhere to repel invasive mammals (Day and MacGibbon 2007; Young et al. 2013) also repels brown treesnakes. Of the 350 brown treesnake trials and three different mesh designs, only the woven wire 4.9 × 12 mm mesh was breached, and that was by a single individual (SVL = 392 mm, Table 1). We observed no breaches using woven wire 6 × 6 mm or mini chain link 7 × 9 mm mesh types (Table 1). In addition, none of the hood trials for snakes or rats resulted in breaches, supporting earlier findings for rats (Table 1, Day and MacGibbon 2007). Polynesian and Norway rats (*R. norvegicus* and *R. exulans*) are also present on Guam but were not detected during our trapping efforts. We do not expect that either of these species would be able to breach the hood as their jumping abilities are comparable to *R. rattus* (Pitt et al. 2011). Similarly, mice (*Mus musculus*) and Indian musk shrews (*Suncus murinus*) have lower jumping abilities than rats, making them unlikely to breach the hood unless it has been compromised (Day and MacGibbon 2007). However, juvenile mice may be able to penetrate the 7 × 9 mm mesh (Day and MacGibbon 2007).

An unanticipated benefit of the two woven wire mesh prototypes was that snakes were unable to free climb either design (Table 1, Figure 4), making the rolled hood serve as a redundant secondary feature for repelling snakes. However, the tail-standing behavior we observed on all mesh types allowed snakes to gain access to larger areas of the experimental barrier wall. This behavior, known as gap-bridging, allows arboreal snakes to cross distances by extending unsupported portions of their body. Snakes can span larger unsupported vertical gaps than horizontal gaps (Byrnes and Jayne 2012; Hoefer and Janyne 2013). This is in part because gap-bridging vertically (90°) requires less muscle activity than gap-bridging horizontally (0°) or at a 45° angle (Jorgensen and Jayne 2017). Brown treesnakes can bridge gap distances upward almost as well as they can downward (Byrnes and Jayne 2012). Still, having their venter in contact with the mesh likely permitted snakes to reach higher vertical heights than if their bodies were unsupported (Figure 4, Perry et al. 1998). In a real-world scenario (i.e., a multispecies barrier on the landscape), this behavior would increase the likelihood of a snake finding barrier weaknesses (e.g., holes, rust, snagged branches, lichen growth) if fences were inadequately maintained and managed. For the mini chain link mesh, we found an inverse relationship between SVL and the probability of a snake being able to climb (Table 1, Figure 5), suggesting that as snakes increase in length they lose the ability to scale this mesh. A consequence of small snakes being able to scale the mini chain link mesh is

that the rolled hood serves as the sole feature to repel individuals that can climb the barrier.

Creating fenced areas that are predator-free or predator-suppressed for the purpose of reintroducing native species to the landscape presents many challenges on Guam. Guam has a tropical climate that experiences high heat and humidity, a pronounced wet season, salt spray, typhoons and tropical storms—which are sources of major wind loading—and earthquakes. An important limitation to the barrier designs we tested is that they all used a rolled hood, which is not expected to withstand typhoons. Designing sectional fences with designated breakpoints may mitigate damage and cost of replacing fence panels and hoods damaged or lost during typhoons. Alternatively, adding a track so hoods can slide may decrease hood loss by reducing wind loading (C. Laxon *pers. comm.*). Integrated remote alarm systems that notify managers of potential breaches via a tripwire atop the barrier have been successfully used elsewhere to reduce response time for fence repairs (e.g., Connolly et al. 2009). Spare hood sections should be maintained in storage to allow for rapid repair of typhoon-related damage and to minimize potential breaches. A non-textured (smooth) concrete barrier wall of sufficient height (≥ 2 m) is another option and would not require a rolled hood. Of the available options, concrete barriers undoubtedly have the highest initial cost but would likely provide the greatest durability against typhoons and salt spray and the lowest long-term maintenance costs. A hybrid design that incorporates a concrete barrier at the bottom and an upper portion constructed with stainless steel (woven wire or chain link mesh) may provide a more economical medium-term solution, while still providing higher durability and requiring lower maintenance than a fence constructed primarily of stainless steel. Existing concrete and hybrid concrete/stainless steel barriers on Guam do not exclude rodents, cats, or monitors. Retrofitting existing solid concrete barriers by increasing the height of unclimbable surface to ≥ 2 m or by extending their height with fencing to obtain a height of ≥ 2 m and attaching a rolled hood element atop the barrier would address this deficiency. Alternatively, barriers constructed of fly ash (Wondertec™ International; Loxahatchee, Florida, USA; www.wondertecinternational.com) could be constructed. A barrier made of this material effectively repelled brown treesnakes, cost approximately 20% less than previously tested pre-stressed concrete barrier designs, and can purportedly withstand a class 5 typhoon (Perry et al. 2001; Rodda et al. 2007a). Where use of opaque barriers such as concrete and Wondertec™ may have some restrictions (e.g., military base), our transparent mesh prototype barriers may provide a viable alternative, assuming the barrier is adequately maintained.

The landscape on Guam presents additional challenges to erecting barriers and excluding introduced species. For example, a concrete footer 83.8 cm deep has been used on Guam to prevent animals from burrowing

underneath the barrier (Perry et al. 2001). However, unexploded ordinance, cultural resources, and uneven terrain and karst complicate digging below the surface on Guam. Additionally, work is needed to demonstrate how these prototype multispecies barrier panels will connect to each other on the landscape and still effectively repel target pest species. The greatest source of incursions are culverts, waterways, and pedestrian and vehicle gates. Water gates and fish passages will need to be installed for waterways and drains that abut fences. Consultation with certified structural design engineers and relevant taxa specialists is recommended to minimize incursion risk when adding openings, gateways, or other access points.

Eradication of rodent populations has proven more challenging on tropical islands than in temperate systems (Harper et al. 2015; Holmes et al. 2015), and eradication of brown treesnakes has not yet been achieved at a scale larger than 1 ha (Campbell et al. 2012). Research conducted in NWFN has demonstrated that mesh barrier fences can effectively exclude brown treesnakes (Tyrrell et al. 2009; Christy et al. 2010), with the caveat that these fences require substantial maintenance and upkeep. Those same barrier designs built upon a concrete footer have been demonstrated to exclude ungulates and yield forest regeneration (Nafus et al. 2018). Pigs only require a short (≥ 0.91 m) durable fence to prevent access (Siers and Savidge 2017). Conversely, deer are excellent jumpers and require taller fencing to be excluded. Given that rolled hoods are effective barriers against cats (Day and MacGibbon 2007), which are agile climbers and jumpers, the experimental barriers we trialed should also be able to prevent mangrove monitor incursions. Still, little research has been conducted to promote creation of predator-free areas suitable for reintroduction or recovery of Guam's native fauna and flora.

Undoubtedly, the three biggest direct threats to bird reintroductions on Guam are brown treesnakes, cats, and rodents. Suppression of snake populations is expected to increase rodent abundance, which in turn may cause increases in cat abundance, given that rats are a primary prey source (Parkes et al. 2014). Mesopredator release effects of non-target invasive species are a known consideration for control or eradication programs (Courchamp et al. 1999). Consequently, the trophic interactions among species occurring on Guam will have to be considered in any eradication or suppression program so that interactive threats from introduced species are mitigated (Bergstrom et al. 2009; Dowding et al. 2009; Parkes et al. 2014). Moreover, little is known about what habitat conditions are necessary for reintroductions because widespread extirpations or extinctions of native vertebrates occurred prior to studies of their ecology on Guam.

Some researchers have been critical of the use of multispecies barriers, citing limited evidence of efficacy at improving species conservation and high cost (Scofield et al. 2011; but see also Innes et al. 2012). However, there is now ample evidence that these barriers are effective in the conservation

of native species for a variety of taxa and in a multitude of ways, including increasing abundance of avifauna and reptiles (Reardon et al. 2012; Bombaci et al. 2018; Miskelly 2018), improving nesting success (Fea and Hartley 2018), and restoring vegetation (Tanentzap and Lloyd 2017). The substantial costs associated with construction and maintenance of conservation fences are well documented and have led to the development of several decision-support tools. For example, Bode and Wintle (2010) used a return-on-investment framework to optimize fence length and design by providing a quantitative tool to balance maintenance costs with construction costs and maximize the benefit-to-cost ratio. To make the investment more cost-effective, Norbury et al. (2014) determined the appropriate level of fence impermeability based on the size of the focal area. Based on predictive modeling research conducted in New Zealand, conservation fences that are 100% effective at excluding predators are the most economical for focal areas smaller than 1 ha (Norbury et al. 2014). As the size of the exclusion area increases, exclusion efficacy requirement decreases. For example, fences with 90% repulsion rates were most cost-effective for areas 1–219 ha. For areas > 219 ha, trapping alone (i.e., no fence) was most cost-effective based on a 60% efficacy rate using 0.2 traps/ha and a 1500-m buffer to reduce the chances of reinvasion (Norbury et al. 2014). However, locality specific predictive modeling is needed to determine guidelines and rates applicable to Guam. Other researchers have used holistic approaches to identify locations for conservation fences by sequentially factoring in economic, cultural, ecological, and political constraints into the decision process (Bode et al. 2012).

Despite the challenging climate and landscape on Guam, there are also many factors that can contribute to the success of using multispecies barriers to achieve reintroduction goals. Typhoons are generally less severe on Guam than elsewhere in the region (e.g., Saipan). In addition, tropical cyclone projection models predict that climate change will decrease the frequency of typhoons on Guam in the future, although their maximum intensity may increase slightly (Widlansky et al. 2019). Fenced environments on military bases provide added security (e.g., protection from vandalism and poaching) that may be unavailable elsewhere. In addition, research into the control and eradication of the brown treesnake has been ongoing since the 1980s (Fritts and Scott 1985; Fritts 1988; Rodda et al.1992b). This long history of research on the island has and continues to provide innovative ways to combat the brown treesnake and other invasive species (Savarie et al. 2001; Rodda et al. 2007b; Siers et al. 2018). Considerable progress has been made toward landscape-suppression of brown treesnakes on Guam (Clark and Savarie 2012; Nafus et al. 2020; Siers et al. 2020). Past research on barriers provides a sound baseline to improve upon designs, and existing fence structures on the landscape offer opportunities to retrofit fences to repel a larger group of invasive species at lower initial costs (Perry

et al. 1998; Rodda et al. 2007a). In addition, recent developments in multispecies barrier technology (Day and MacGibbon 2007; Burns et al. 2012), traps (Russell and Broome 2016), and toxicant-delivery systems (Read et al. 2019) offer promising additional tools for eradication and control of invasive species. We recommend the next steps include consultation with engineers to address wind loading, structural integrity, material interactions, and integration of decision-support tools to optimize cost and efficacy of barrier designs on the landscape. To be successful, future work must further leverage historic and contemporary knowledge and expertise and continue to foster and support cooperation among military, state and federal agencies, universities, nonprofit organizations, and the community.

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Ethics and permits

All capture and handling methods used in this study were in accordance with protocols approved by the Institutional Animal Care and Use Committee and within guidelines of the USGS Fort Collins Science Center. FORT IACUC Approval of Study Plan (FORT IACUC 2018-16), entitled "Multispecies Barrier Development (Phase I)."

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