

Research Article

Experimental landscape reduction of wild rodents increases movements in the invasive brown treesnake (*Boiga irregularis*)

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Abstract

Experimental studies evaluating the effects of food availability on the movement of free-ranging animals generally involve food supplementation rather than suppression. Both approaches can yield similar insights, but we were interested in the potential for using food suppression for the management and control of invasive predators, in particular, the brown treesnake (*Boiga irregularis*) on Guam. However, understanding a species' response to food resources is critical before employing such a strategy. We studied the movements of 24 radio-tagged *B. irregularis* initially caught within four 4-ha unfenced plots in rodent-abundant (control) and rodent-suppressed (treatment) grassland habitats over a 40-day period. Because monitoring duration differed among snakes, we also analyzed short-term (16-day) activity areas. Over the 16 days, snakes associated with rodent-suppressed plots had 86% larger activity areas (ha), 94% greater dispersal distances (m), and 43% greater movement rates (m/h) than snakes associated with control plots. *Boiga irregularis* moved extensively, but these movements were not always reflected in the size of the snake's total activity area. Movement rates did not differ between sexes, but snakes in above-average body condition moved greater distances per hour than those in below-average condition irrespective of treatment. Our study indicates that a relatively small prey suppression effort can cause almost immediate and significant changes in *B. irregularis* movement. On Guam, prey suppression might enhance control efforts by either increasing trap capture success or discouraging snakes from entering areas of conservation or management concern. However, the outcome of using prey suppression as a control tool in areas threatened with the accidental introduction of the brown treesnake is more difficult to predict and might have negative consequences such as elevated dispersal rates.

Key words: management, invasive species, prey reduction, radio-telemetry, snake, Guam

Introduction

Understanding the motivation for animal movement is an important aspect of invasive-species management. This information is useful when protecting high-risk locales, identifying search areas after an incursion has been discovered, or predicting range expansion. Animal movement is driven primarily by the distribution and density of critical resources such as food, shelter, and mates (Greenwood 1980;

Hansson 1991; Croft et al. 2003; Ebrahimi and Bull 2015). Prey abundance and foraging behavior play important roles in determining when, where, and why many animals move at both organismal and population levels. Much of our knowledge on how food availability impacts movements and activity of terrestrial vertebrates has come from food-supplementation experiments. Many species alter their foraging patterns, home-range or core-area size, and onset of dispersal when supplemental food is provided

(e.g., Boutin 1990; Eifler 1996; Hubbs and Boonstra 1998; Kennedy and Ward 2003; Ewen et al. 2015). Most food supplementation studies have focused on mammals—particularly herbivores—and birds. With the exception of several studies on lizards, experiments with amphibians and other reptiles have been less common (e.g., Boutin 1990; Ebrahimi and Bull 2015). Failure to consider ectotherms in food manipulation studies would leave the expectation that prey suppression would have little short-term impact on their movement as a result of the reduced energetic demands, untested.

Studies on snake movement in relation to prey abundance have produced mixed results. In one of the few prey-supplementation studies, no differences were found in surface-activity levels or home-range size between fed and control western diamond-backed rattlesnakes (*Crotalus atrox* Baird and Girard, 1853), a sit-and-wait predator with low energy demands (Taylor et al. 2005). Similarly, Wasko and Sasa (2012) reported no difference in mean home range between naturally foraging and food-supplemented terciopelos (*Bothrops asper* Garman, 1883). However, fed snakes exhibited shorter and less-frequent movements, increased body mass, and less time spent foraging (Wasko and Sasa 2012). Natural fluctuations in prey influenced growth rates, body condition, and survival of adders (*Vipera berus* Linnaeus, 1758), but inter-island movement rates, which ranged up to 29% of the known population, were not correlated with prey density differences between islands (Forsman and Lindell 1997). An observational study of adult and subadult garter snakes (*Thamnophis cyrtopsis* Kennicott, 1860) documented a habitat shift from streambanks to upland pools where frogs and toads were more abundant (Jones 1990). Radio-transmitted water pythons (*Liasis fuscus* Peters, 1873) migrated seasonally in response to migratory dusky rats (*Rattus colletti* Thomas, 1904) (Madsen and Shine 1996), and brown snakes (*Pseudonaja textilis* Duméril, Bibron and Duméril, 1854) showed a tendency to move to sites where mice were more abundant (Whitaker and Shine 2002).

Most experimental manipulations of food involve supplementation; rarely is food suppressed (Boutin 1990). Both approaches can provide insight on animal movement. We studied an invasive predator, the brown treesnake (*Boiga irregularis* Merrem, 1802) on Guam, and wanted to evaluate the utility of suppressing prey resources via rodenticide for its management and control. For example, suppressing prey in or around a transportation hub could motivate a predator to move away from these high-risk export areas, reducing the chance of it entering the transport route and hitch-hiking to a new location.

Boiga irregularis, a nocturnal predator accidentally introduced to Guam shortly after World War II (Savidge 1987; Rodda et al. 1999), achieved high densities island-wide within 25 years of introduction (Savidge 1987). Rodda and Savidge (2007) estimated the species' linear rate of dispersal to be around 2 km/yr and speculated that such rapid spread was possible because of an abundance of available prey. Native avian prey have since been decimated on Guam, and available prey in grassland habitat now consist predominantly of introduced rodents (Savidge 1987).

Here we analyze radio-telemetry data collected within a 40-day period. We examine activity areas, distance from plot centers, and movement rates in relation to the rodenticide treatments. Because adult snakes in this habitat feed largely on rodents, we predicted that decreased rodent availability would increase *B. irregularis* activity areas, distances from plot centers, and movement rates. However, as an ectotherm needing to eat infrequently, we anticipated differences in *B. irregularis* movements might not transpire immediately following prey suppression, although we did expect an impact within our experimental time frame. Our data are the first for *B. irregularis* movement in grassland and the first quantifying free-ranging reptile movement in response to an experimental suppression of prey. We discuss the implications of our results for management of this invasive predator.

Study area

We conducted radio-telemetry between 18 July and 27 August 2003 on a 300-ha grassland in southern Guam (13°N; 144°E). Guam's climate is tropical; daytime temperatures ranged from 26 to 32 °C. A moderate drought occurred before and during the study. The area was principally uncultivated and surrounded by residential, agricultural and fallow land. Vegetation consisted of dense heterogeneous grassland dominated by *Dimeria chloridiformis* (Gaudich.) K.Schum. and Lauterb., *Miscanthus floridulus* (Labill.) Warb. ex K.Schum. and Lauterb., and *Pennisetum* spp. in addition to various sedges, rushes, and ferns. *Phragmites karka* (Retz.) Trin. ex Steud. was present in moist areas. The height of grass clumps was influenced by soil type and recent fire history (Gragg 2004), ranging from ground level to >3 m. Small, isolated patches of remnant forest, steep ravines, and eroding scarps and gullies were also present. Canopy height of forest patches was typically 3 to 5 m, with emergent *Cocos nucifera* L., *Areca catechu* L. and *Pandanus tectorius* Parkinson ex Zucc. to 10 m. Topography was undulating, with elevation ranging from 40 to 100 m. Permanent

surface water, usually in rivers and streams, was available on and adjacent to the study area (Gragg 2004). This grassland/forest mosaic is typical for southern Guam (Mueller-Dombois and Fosberg 1998).

Methods

Study area design

Within the study area, four 4-ha plots were subjectively delineated and used for a *B. irregularis* and rodent-trapping experiment published elsewhere (Gragg 2004; Gragg et al. 2007). The plots were located at least 300 m apart and were selected for similarity and uniformity of habitat. On each plot, a 9 × 9 grid of transects was set up with snake traps placed at 25-m intervals. Traps were open between 30 June and 18 August 2003 and were the source of our study subjects. Although trapping took place concurrently to our project, there was no evidence that it influenced movements; only one telemetered snake was trapped (and released the subsequent morning) a month after it was initially caught, and no telemetered snakes were caught during the 16-day periods we report. Two days before our radio-telemetry study (16 July 2003), we began reducing densities of small mammals on plots 1 and 4 (henceforth treatment plots) using diphacinone (0.005% active ingredient), a first-generation anticoagulant rodenticide (J.T. Eaton and Co., Twinsburg, OH), placed in labeled tamper-resistant bait stations (Protecta, Bell Laboratories Inc., Madison, WI; see Gragg (2004) and Gragg et al. (2007) for further details). Plots 2 and 3 were not treated with rodenticide (henceforth control plots). Rodenticide was applied continuously from 16 July 2003 until the final day of telemetry (27 August 2003) and effectively depleted rodents on treated plots, with an estimated decrease of more than 80% (Gragg 2004). There was no evidence of secondary poisoning of *B. irregularis* (Gragg 2004).

Transmitter implantation

We transported trapped *B. irregularis* adults exceeding 1000 mm snout-vent length (SVL) and 100 g to the laboratory, where we implanted an intracoelomic transmitter within 24 hrs of initial capture. Implanted females were without mature follicles or eggs at the time of transmitter implantation. We modified radio-transmitters (AVM Instrument Co. Ltd. model G3-IV, 7 × 8 × 5 mm, 2.0 g, 85-day battery life) by encasing the antenna in silicon tubing and dipping the transmitter in flowable silicon sealant (Dow Corning 734) to prevent adhesion to the surrounding tissue once implanted. Encased transmitters weighed 2.3 g

(\bar{x} = 1.29% of body weight, range = 0.75–2.15%). Radio-transmitter implantation followed methods in Reinert and Cundall (1982) and Hardy and Greene (1999), except we used inhalation isoflurane to anaesthetize snakes. We determined sex by probing or everting hemipenes, and we measured SVL while snakes were anesthetized. We extended captive recovery to three days in compliance with Animal Care and Use Committee requirements, after which we released snakes at the initial capture site.

Field data collection

We located snakes in the field using a LA12-Q portable telemetry receiver (AVM Instrument Company, Ltd.) fitted with a hand-held three-element Yagi-Uda antenna. Individuals were located once per day following release for a period of two days, after which we located snakes three times in each 24-h tracking session, scheduled every other day. We monitored half of the study population during any given session, with equal numbers of control and treatment snakes monitored each day.

We partitioned data collection into three periods of activity per session based on previous studies by Rodda et al. (1991), Santana-Bendix (1994), Tobin et al. (1999), and Anderson et al. (2005): 0600–1800 h (day; when snakes typically remain inactive in a refuge), 1800–2400 h (PM; when most foraging occurs) and 2400–0600 h (AM; when snakes seek refuge). To decrease disturbance to telemetered snakes and account for limited personnel, we monitored nocturnal locations by triangulation (Mech and Barber 2002). To reduce the size of the error polygon (White and Garrott 1990), we typically obtained four to five bearings per snake for each PM and AM session from 37 pre-established telemetry stations set up on or surrounding the four study plots. We recorded coordinates using a global positioning system receiver (GPS: Garmin III Plus; ± 1–5 m accuracy). We took all bearings for each estimated location within one hour (usually within 30 minutes) to reduce the error produced by snake movement. During the day, we tracked and visually located snake refuge sites and recorded their position using GPS. We caught and inspected the health of an individual within the first five days of release, including the surgical incision. Thereafter, we visually observed snakes every five to seven days without capture in all but one case.

To test triangulation accuracy, we used blind placement of 16 transmitters (four per study plot) in trees, grass clumps and hollow logs and took bearings from the pre-established telemetry stations (Zimmerman and Powell 1995).

Data analysis

Due to small sample sizes (between and within plots), and no differences in habitat (Gragg 2004) or movement patterns, we pooled data from similarly-treated plots. We assigned Universal Transverse Mercator (UTM) coordinates for each location using Location of a Signal software (LOAS 4.0; Ecological Software Solutions). Each estimated location used the combination of ≥ 3 bearings that resulted in the smallest 95% error ellipse. We tracked snakes for 16 to 40 days and calculated activity area, distance from the plot center (“displacement”) and movement rate (m/h) using BIOTAS 2.0 (Ecological Software Solutions). Snakes temporarily removed from the study site for transmitter implantation were returned to the site of capture over the first 14 days of the study, and thus implant dates, tracking dates, and number of fixes varied among individuals. Since snakes were returned to each of the four plots over time, any effect of time since initialization of prey reduction was reduced. We accounted for autocorrelation by tracking snakes on alternate days and variation in sample size by restricting most analyses to initial datasets of the first 16 days from initial release for each snake (Samuel and Garton 1985; Samuel et al. 1985; White and Garrott 1990).

For comparison to earlier studies on *B. irregularis*, we used the minimum convex polygon (MCP) method for our analyses. We report total activity area (TAA) for each snake using 100% MCP on the complete data set (up to 40 days of tracking). However, observed home-range size increases with duration of monitoring (Jennrich and Turner 1969), and duration of monitoring differed among snakes; thus, for comparison among snakes we also calculated activity area (AA), in which 100% MCPs were calculated for the first 16 days.

To determine the degree of displacement of individuals from the potential food vacuum induced by application of rodenticide, we calculated the distance between the center of the plot on which the snake was caught to the 16-day activity area centroid. We calculated a modified harmonic mean center of activity (Dixon and Chapman 1980) using program BIOTAS, which estimates the probability of use at any location within the AA (Samuel et al. 1985).

Movement rates were estimated from straight-line distances between the three nightly fixes and corrected for time differences (Gregory et al. 1987). We assumed that snakes remained inactive during the day and assigned 1800 h as the time at which all snakes started moving, based on previous studies (Fritts and Chiszar 1999; Rodda et al. 1999; Tobin et al. 1999). Local sunset ranged from 18:36–18:52

during our study (Astronomical Applications Department, U.S. Naval Observatory).

In separate analyses, we modeled each of four dependent variables (natural log of 16-day AA (ha), mean displacement distance (m), PM mean movement rate, and AM mean movement rate) as a function of three independent variables (treatment, body condition index, and sex) and their interactions. We calculated body condition index as the ratio of the individual mass to its expected mass given its length (Christy et al. 2010). Thus, all condition index values were positive, and a snake of precisely its expected mass had a condition index of 1. Expected mass was estimated by linear regression on a logarithmic scale, based on snakes in this study ($x = \ln \text{SVL}$, $y = \ln \text{mass}$) and used the returned slope and intercept in the following equation: expected mass = $\exp([4.126 \times \text{SVL}] - 24.008)$.

Unless otherwise stated, values expressed are mean \pm standard error along with 95% confidence limits (CL). We report untransformed values when listing summary statistics and back-transformed values when presenting results from analyses.

We evaluated models using Akaike’s Information Criterion (AIC) corrected for small sample size (AIC_c ; Burnham and Anderson 2002). By comparing the relative differences (ΔAIC_c) between each model to the model with the minimum AIC_c value, all candidate models can be ranked. As a balanced model set was used for each analysis (i.e., in our set of 18 models, each variable and interaction appeared in 13 and 5 models, respectively), we computed a relative importance value for each variable and interaction by summing Akaike weights over every model in which that variable or interaction appeared (Burnham and Anderson 2002: 168). Covariates with 95% CLs not overlapping zero were considered influential.

Results

We captured and implanted transmitters in 26 snakes; however, two snakes produced fewer than 16 days of movement data and were removed from analysis. In total, we located the 24 snakes 885 times at 285 locations and tracked individuals from 16–40 days between 18 July and 27 August 2003 (Table 1).

Triangulation accuracy

We estimated locations of 16 planted transmitters on the four plots and assessed accuracy between the two trackers (8 planted transmitters per tracker). The overall mean distance between the actual location of the transmitter and the location estimated using triangulation

Table 1. Summary statistics for 24 brown treesnakes (*Boiga irregularis*) implanted with radio transmitters and tracked in southern Guam in 2003. “Treatment” refers to the application of rodenticide on the plot; “Control” indicates rodenticide was not applied. SVL = snout-vent length, Wt = weight, TAA = total activity area calculated as 100% Minimum Convex Polygon (MCP) on the complete data set of 40 days, and AA = 16-day activity area as 100% MCP on the first 16 days of data. All values are based on non-transformed data.

	Plot no.	1 st track date	Days monitored	No. of fixes	Sex	SVL (mm)	Wt (g)	TAA (ha)	AA (ha)	
Control	2	20-Jul	36	41	F	1206	246	94.9	26.9	
	2	21-Jul	34	48	M	1275	217	106.7	18.0	
	2	29-Jul	26	35	M	1245	237	95.8	50.6	
	2	30-Jul	26	35	M	1205	175	97.7	51.0	
	3	18-Jul	40	46	M	1128	127	106.1	22.0	
	3	19-Jul	37	51	M	1297	310	94.7	38.0	
	3	20-Jul	18	23	M	1135	139	81.2	55.4	
	3	20-Jul	35	44	F	1057	120	123.1	66.9	
	3	22-Jul	35	44	M	1098	137	98.4	14.5	
	3	22-Jul	35	43	F	1201	199	106.8	12.8	
	3	24-Jul	32	43	F	1190	219	93.3	10.1	
	3	24-Jul	26	29	F	1190	154	92.2	49.5	
	Treatment	1	18-Jul	17	26	F	1095	149	47.9	24.3
		1	21-Jul	34	44	M	1175	142	81.4	27.7
1		22-Jul	34	46	M	1157	145	103.5	92.8	
1		29-Jul	24	33	M	1175	103	94.1	33.8	
1		30-Jul	22	33	F	1039	112	98.1	65.8	
1		31-Jul	26	35	M	1105	122	83.1	65.6	
4		18-Jul	40	42	M	1274	266	115.4	69.8	
4		18-Jul	38	27	F	1193	218	82.3	58.3	
4		18-Jul	34	28	M	1080	120	105.6	73.0	
4		20-Jul	16	12	F	1107	156	73.1	65.7	
4		23-Jul	32	41	M	1062	115	89.4	66.5	
4		30-Jul	26	36	M	1117	167	105.2	56.8	

was 19.5 ± 11.8 m SD (95% CL = 13.7, 25.3, $n = 16$); this distance was not influenced by plot (treatment: 23.0 ± 14.7 m SD [95% CL = 12.8, 33.2, $n = 8$]; control: 16.0 ± 7.5 m SD [95% CL = 10.8, 21.2, $n = 8$]) or tracker (tracker_{day}: 17.3 ± 14.6 m SD [95% CL = 7.1, 27.4, $n = 8$]; tracker_{night}: 21.8 ± 8.6 m SD [95% CL = 15.8, 27.7, $n = 8$]). Likewise, neither the plot nor tracker had an effect on error-area ellipse.

Morphometrics

The average mass of *B. irregularis* males (168 ± 15.9 g, $n = 15$) and females (175 ± 15.7 g, $n = 9$) implanted with transmitters was comparable as were average SVLs (males: 1169 ± 19.5 mm, $n = 15$; females: 1142 ± 22.4 mm, $n = 9$). We did not obtain equal sample sizes per plot; however, sample sizes of snakes were equal between treatment and control ($n = 12$ treatment and 12 control; Table 1). At initial capture, snakes from treatment plots were moderately lighter (treatment: 151 ± 13.8 g, 95% CL = 124, 178 g; control: 190 ± 19.4 g, 95% CL = 152, 228 g) and shorter (treatment: 1132 mm SVL ± 19.0 , 95%

CL = 1090, 1172 mm; control: 1186 mm SVL ± 20.4 , 95% CL = 1146, 1226 mm) than control-plot snakes although not significantly so (note confidence interval overlap). The body condition index for snakes on treatment and control plots at initial capture was similar between plots (treatment: 1.00 ± 0.05 , 95% CL = 0.90, 1.10; control: 1.03 ± 0.04 , 95% CL = 0.95, 1.11 g).

Activity area

Estimates of TAA of *B. irregularis* were relatively large (Table 1) and progressively increased over the 40-day tracking period (Figure 1). TAA did not differ between sexes or between treatment and control plots (Table 2). Sixteen-day AA ranged from 10.1 ha (snake from a control plot) to 92.8 ha (snake from a treatment plot; Table 1, Figure 2); the 95% CLs for treatments and controls did not overlap.

The top model for 16-day AA incorporated treatment alone ($w_i = 0.49$). The next closest models ($\Delta AIC_c = 2.32$ and 2.89; $\Sigma w_i = 0.27$) included [treatment and sex] and [treatment and condition index],

Figure 1. Cumulative mean activity area (ha) \pm SE (untransformed) for 12 *B. irregularis* initially caught on treatment plots (dashed line) and 12 *B. irregularis* on control plots (solid line). Data were collected for 16 to 40 days per snake (summing to 885 fixes at 285 locations) and are presented in 5-day increments. The vertical line indicates 16 days from the first day of tracking ($n = 150$ locations); all snakes are represented in the first 16 days.

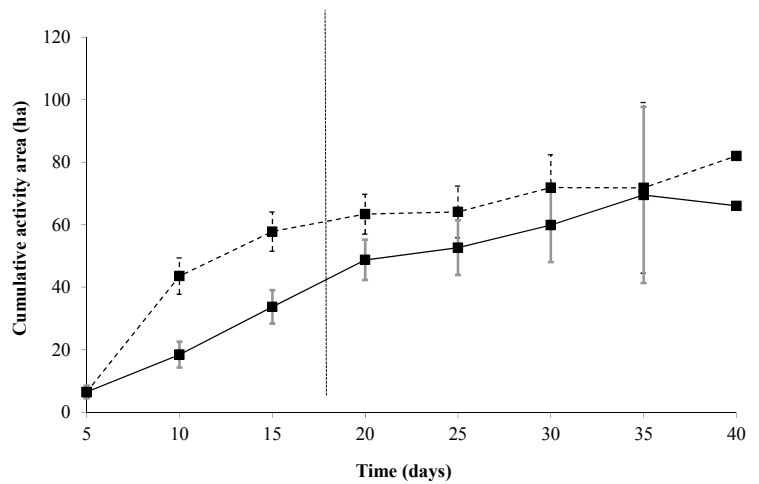


Table 2. Median, mean and 95% confidence limits (CL) for total activity area (ha), 16-day activity area (ha), distance moved per hour from dusk to midnight (PM) and midnight to dawn (AM) for 24 *B. irregularis* on Guam. n = number of snakes. All values are based on non-transformed data.

	Female	Male	Treatment	Control
Number of Snakes	9	15	12	12
Total Activity Area				
Median	93.3	97.7	91.8	96.8
Mean \pm SE	90.2 \pm 7.1	97.2 \pm 2.6	89.9 \pm 5.2	99.2 \pm 3.0
95% CI	76.3–104.0	92.0–102.4	79.7–100.2	93.4–105.1
16-day Activity Area				
Median	49.5	51.0	65.7	32.4
Mean \pm SE	42.3 \pm 7.9	49.0 \pm 5.9	58.3 \pm 5.8	34.6 \pm 5.6
95% CI	26.8–57.7	37.5–60.6	46.9–69.7	23.6–45.7
PM Distance (m/h)				
Median	33.9	22.3	34.8	20.4
Mean \pm SE	29.3 \pm 4.7	24.8 \pm 2.6	30.2 \pm 3.8	21.5 \pm 2.2
95% CI	20.1–38.6	19.7–30.0	22.7–37.7	17.2–25.8
AM Distance (m/h)				
Median	9.9	7.1	6.2	9.6
Mean \pm SE	9.4 \pm 1.4	6.8 \pm 0.7	6.4 \pm 0.8	9.2 \pm 1.09
95% CI	7.1–11.6	5.5–8.2	4.8–8.1	7.2–11.1

respectively (Table 3). Snakes on control plots had smaller AA, as indicated by a negative coefficient ($\hat{\beta}$) for treatment in the best model ($\hat{\beta}_{\text{tr}} = -0.63 \pm 0.22$, 95% CL = $-1.06, -0.19$). Based on back-transformed data, *B. irregularis* had mean 16-day AA of 54 ha (95% CL = 41.8, 70.7) and 29 ha (95% CL = 19.3, 43.8) for treatment and control plots, respectively. The order of relative importance values (Σw_i) confirmed strong support for treatment (0.94) and less support for sex (0.32) and condition index (0.31). Additionally, effect sizes for the variables of sex and condition index in these models had 95% CLs that included zero. The global model had an $R^2 = 0.39$.

Displacement

The average net distance of snakes from the capture plot centroid to the snake's mean harmonic centroid fluctuated over time, but snakes were consistently located farther away from treatment than from control plots. Data pooled into 5-day periods showed *B. irregularis* associated with treatment plots were located a mean distance of 717 ± 43.9 m 6–10 days post release and 662 ± 56.7 m 26–30 days post release from their associated plot centroid. In contrast, snakes on control plots were located a mean distance from their associated plot centroid of 631 ± 37.4 m 6–10 days and 613 ± 39.6 m 26–30 days after release.

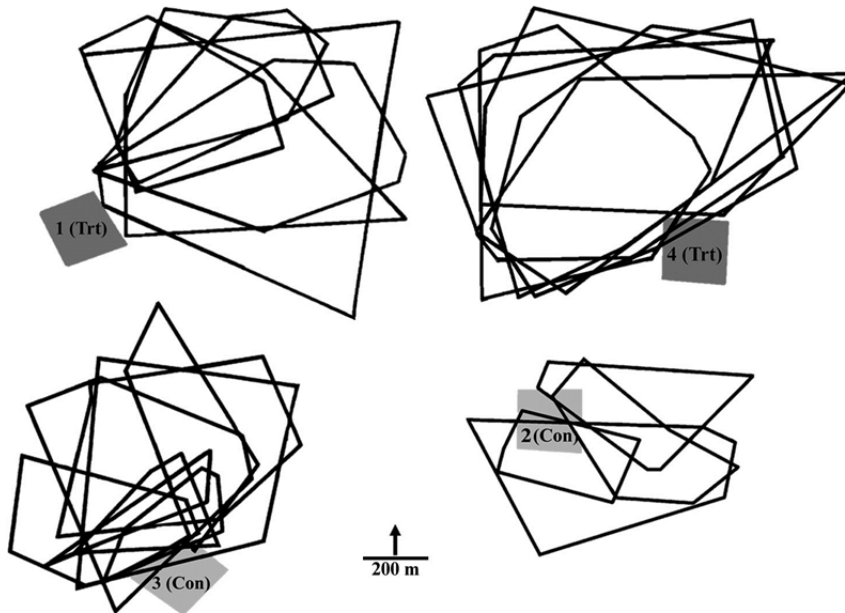


Figure 2. The 16-day activity area (ha) for *B. irregularis* initially caught on treatment (Trt: dark grey shaded areas) and control plots (Con: light grey shaded areas). Data represent 100% MCP on the first 16 days from the initial day of tracking. Panel (A) depicts activity areas of snakes originating from rodenticide treated plots 1 ($n = 6$ snakes) and 4 ($n = 6$ snakes). Panel (B) depicts activity areas of snakes originating from control plots 2 ($n = 4$ snakes) and 3 ($n = 8$ snakes). All 24 snakes are represented in this time period ($n = 150$ locations). Snakes originally trapped on treatment plots (A) had activity areas that generally did not include treated areas. Snakes originally trapped on control plots (B) continued to have activity areas that included those plots. Study plots were similar habitats, at least 300 m apart, and small in contrast to snake movements.

The 16-day displacement distance from the plot centroid to the 16-day AA centroid was best explained by a model that incorporated treatment alone ($w_i = 0.56$; Table 3). Snakes on control plots dispersed over a shorter distance, as indicated by a negative coefficient ($\hat{\beta}$) for this variable in the best model ($\hat{\beta}_{\text{trt}} = -0.67 \pm 0.18$, 95% CL = $-1.02, -0.32$). Based on back-transformed data, *B. irregularis* were displaced on average 719 m (95% CL = 537.4, 962.0) and 368 m (95% CL = 284.6, 476.0) over a 16-day period from the treatment and control plot centers, respectively. Ordered relative importance values (Σw_i) indicated strong support for treatment (0.99) and less support for sex (0.27) and condition index (0.22). Additionally, effect sizes for the variables of sex and condition index in the next closest models had 95% CLs that included zero. The global model for the displacement analysis had an $R^2 = 0.42$.

Movement rates

The time of night (PM versus AM) strongly influenced movement rates of *B. irregularis* in the first 16 days of tracking (Table 2). On average, snakes traveled more than three times farther per hour

before midnight (back transformed: 25.6 m/h, 95% CL = 21.4, 30.6) than after midnight (back transformed: 8.2 m/h, 95% CL = 6.9, 9.6). Assuming a snake moved consistently over the 6-hr time period before midnight (up to 154 m if maintaining mean PM speed) and after midnight (up to 49 m if maintaining mean AM speed), but did not move appreciably during the day, we estimate that adult *B. irregularis* moved an average of 203 m per 24 h in grassland habitat.

PM movement rates over a 16-day period were a function of both treatment and body condition index ($w_i = 0.44$; Table 3). *Boiga irregularis* associated with control plots moved fewer meters per hour than snakes associated with treatment plots, as indicated by a negative coefficient ($\hat{\beta}$) for this variable in the best model ($\hat{\beta}_{\text{trt}} = -0.16 \pm 0.12$, 95% CL = $-0.63, -0.12$). Based on back-transformed data from the best model, *B. irregularis* moved an average of 30 m/h (95% CL = 23.0, 40.4) and 21 m/h (95% CL = 17.6, 26.3) for treatment and control plots, respectively. Irrespective of plot treatment, snakes with an above-average condition index moved greater distances per hour than those with a lower

Table 3. Summary of model selection results from the general linear models for activity area (ha), displacement (m) from the center of the plot to harmonic mean centroids for each of 24 *B. irregularis*, and distance moved per hour (m/h) between dusk and midnight (PM). All regressions use the first 16 days of data. Models with the lowest ΔAIC_c and the greatest Akaike weights (w_i) have the most support and are in bold. K = number of parameters in each model.

Model	K	Activity Area		Displacement		PM Distance m/h	
		AIC_c	w_i	ΔAIC_c	w_i	ΔAIC_c	w_i
Sex ^a	3	6.59	0.02	11.79	0.00	12.82	0.00
Trt ^b	3	0.00	0.49	0.00	0.56	8.75	0.01
CI ^c	3	7.26	0.02	11.83	0.00	5.32	0.03
Sex + CI	4	9.49	0.01	14.50	0.00	7.95	0.01
Trt + Sex	4	2.32	0.15	2.35	0.17	10.36	0.00
Trt + CI	4	2.89	0.12	2.91	0.13	0.00	0.44
Sex + Trt + CI	5	5.47	0.03	5.43	0.04	3.06	0.10
Sex + CI + (Sex × CI)	5	11.48	0.01	16.63	0.00	11.17	0.00
Sex + Trt + (Sex × Trt)	5	5.53	0.03	5.42	0.04	9.21	0.00
Trt + CI + (Trt × CI)	5	4.72	0.05	6.09	0.03	1.53	0.20
Sex + Trt + CI + (Sex × Trt)	6	9.07	0.01	8.81	0.01	2.68	0.12
Sex + Trt + CI + (Sex × CI)	6	5.37	0.04	8.68	0.01	6.31	0.02
Sex + Trt + CI + (Trt × CI)	6	7.55	0.01	8.98	0.01	4.90	0.04
Sex + Trt + CI + (Sex × Trt) + (Sex × CI)	7	9.34	0.01	12.56	0.00	5.91	0.03
Sex + Trt + CI + (Sex × Trt) + (Trt × CI)	7	11.31	0.00	12.58	0.00	6.47	0.02
Sex + Trt + CI + (Sex × CI) + (Trt × CI)	7	9.27	0.00	12.74	0.00	8.96	0.00
Sex + Trt + CI + (Sex × Trt) + (Sex × CI) + (Trt × CI)	8	13.86	0.00	17.09	0.00	10.51	0.00
Intercept only	2	4.72	0.05	9.26	0.01	10.90	0.00

^aSex: male or female.

^bTrt: effect of ambient prey abundance versus prey reduction through the application of rodenticide.

^cCI: body condition index of snakes (defined in Methods section).

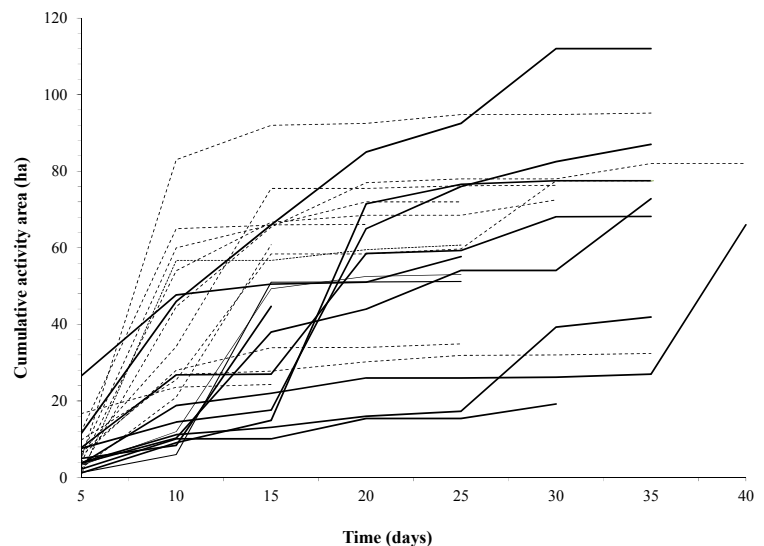


Figure 3. Cumulative activity area (ha), presented in 5-day increments, for each of 12 *B. irregularis* initially caught on treatment plots (dashed lines) and 12 *B. irregularis* on control plots (solid lines). Data were collected for 16 to 40 days per snake; all snakes are represented in the first 16 days.

condition index, as indicated by a positive coefficient in the best model ($\hat{\beta}_{ci} = 0.66 \pm 0.19$, 95% CL = 0.70, 2.37). Relative importance values ($\sum w_i$) indicated strong support for condition index (0.99) and treatment (0.96). The variable sex had less support (0.32), and its slope estimate had a 95% CL that included zero in all models. The global model for PM distance moved per hour had an $R^2 = 0.59$.

As with PM, the mean AM distance moved per hour was best explained by the model that incorporated effects of treatment and condition index ($w_i = 0.33$). The coefficients for treatment and condition index from the top model were $\hat{\beta}_{trt} = 0.10 \pm 0.05$ (95% CL = 0.05, 0.56) and $\hat{\beta}_{ci} = 0.32 \pm 0.18$ (95% CL = 0.11, 1.82), respectively. The R^2 value for the AM global model was 0.38. Whereas PM

movements for snakes on treatment plots were greater than those associated with control plots, there was slight evidence that the reverse was seen for AM movements (control: 10 m/h, 95% CL = 7.9, 11.6 and treatment: 7 m/h, 95% CL = 5.4, 8.9). Irrespective of plot treatment, snakes with an above-average condition index moved greater distances per hour than those with a lower condition index.

Discussion

Prey depletion

By far the most important effect on *B. irregularis* movements was the reduction of rodent densities. The effect size of treatment was large and consistently important. Snakes initially captured on prey-depleted plots had an 86% increase in 16-day AA, over 94% increase in displacement distances, and a 43% increase in movement rates when compared with snakes initially captured on non-depleted plots. Gragg et al. (2007) assessed the effects of prey suppression on *B. irregularis* trappability on the same site and found that *B. irregularis* capture probabilities increased by up to 65%; the authors hypothesized this result was due to increased snake movement in search of food and/or once ambient prey odors declined, snakes were able to better detect and locate bait mice used in traps.

Food abundance can motivate snake movement (e.g., Duvall et al. 1985; Gregory et al. 1987; Whitaker and Shine 2003; Wasko and Sasa 2012), and at least some foraging snakes move in response to seasonal shifts in prey abundance (Plummer and Congdon 1994; Madsen and Shine 1996, 1999; Whitaker and Shine 2002; Whitaker and Shine 2003). Madsen and Shine (1996) tracked water pythons that moved up to 12 km away from their dry-season home ranges following migrating prey. *Boiga irregularis* is an opportunistic predator that is not limited to foraging in any specific habitat (Rodda et al. 1997) and appears to shift between ambush predation and active foraging, depending on the type of prey available (Rodda 1992). Radio-tracked snakes in this study were adults. Accordingly we presume the ontogenetic shift in diet from ectotherms to endotherms (Savidge 1988; Siers 2015) had previously taken place and individuals were foraging primarily on mammalian prey. Thus, it is likely that movements by *B. irregularis* could be influenced by rodent density. However, many terrestrial ectotherms are thought to wait out periods of scarce prey, rather than actively tracking prey, either due to their small size, thermal constraints, and/or territoriality (Madsen and Shine 1996). Additionally, snakes have low

energy demands and are adapted to food shortage (Pough 1980). Nonetheless, our results indicate *B. irregularis* may actually respond relatively quickly, via increased movements, to a decline in prey.

That rodent reduction on only 4 ha could affect movement of snakes with relatively large AA is remarkable. We can only hypothesize the underlying causes for the observed responses. Based on field observations during tracking and examination of changes in AA for individual snakes (Figure 3), it appeared that control snakes generally foraged within an area for approximately 5–15 days before shifting to a new location and repeating the pattern; this is reflected in their relatively constant increase in mean cumulative AA seen in Figure 1. Individual cumulative AA for snakes tracked by Santana-Bendix (1994) reveal a similar pattern. In our study, snakes placed back into treatment plots, showed larger movements, translating into larger cumulative mean AA, than did control snakes in the initial days after release, with most movements starting to stabilize by day 15 (Figures 1 and 3). One hypothesis, and in our opinion the best supported by this and other studies (e.g., Santana-Bendix 1994; Gragg 2004), is that these behaviors (for both treatment and control snakes) are consistent with optimal foraging – once a food reward is reduced beyond a certain threshold in a patch, an animal should leave and seek alternative foraging patches (Charnov 1976); being returned to a prey vacuum, and sensing a lack of ambient prey odor, may have triggered more rapid and larger movement responses by the treatment snakes.

We do not know the extent to which rodents were suppressed outside of our plots; our continual poisoning could have caused an influx of rodents into the treatment plots (Nelson et al. 2002), potentially decreasing prey densities for an unknown distance beyond. There is no evidence to support diphacinone as an attractant, repellent, or causing non-target poisoning of *B. irregularis*. The low concentration of the active ingredient, diphacinone, in the bait (50 ppm) would render detectability by *B. irregularis* unlikely (R. Sugihara, USDA APHIS, personal communication). Non-target poisoning by diphacinone is also unlikely since the half-life in the liver is short (1–2 days) (Daniels 2013), and the toxicity level for *B. irregularis* of 80mg kg⁻¹ is substantially above the threshold concentration required to kill rodents (32mg kg⁻¹) (Brooks et al. 1998). Further, the ability of first generation rodenticides to bioaccumulate in target and non-target animals is considered low (Townsend et al. 1984), and requires rodents to consume bait over a number of days (Daniels 2013). Although dead and

dying rats were observed (Gragg 2004), no dead and dying snakes were detected.

At present, we do not know what effect the initial influx of carrion (dead rodents) following rodenticide diphacinone application had on snake movements. In some instances the effectiveness of *B. irregularis* capture using 2–3 day-old mouse carrion as bait is almost equivalent to that of live mice (Shivik et al. 2000; Jojola-Elverum et al. 2001). Based on rodent bait take, Gragg et al. (2007) estimated that rodent reduction began on the treatment plots within a week of application. Presumably, the rapid effect of treatment resulted in a spike of carrion availability for *B. irregularis* in the study area, at least for a short time period.

Condition index

Irrespective of treatment, snakes with above-average body condition moved farther per hour during the PM time period (1800–2400 h) than those with below-average condition with the difference more pronounced in prey-depleted areas. This reinforces the findings of Gragg et al. (2007), who found that underweight *B. irregularis* trapped at the same study area exhibited higher site fidelity than their heavier conspecifics. The authors surmised that either dispersal is less motivated by hunger or prey availability than by other needs, or that sub-optimum body condition does not give a snake the energetic resources to disperse to new foraging areas and forces them instead to remain in prey-depleted environments, at least under the prevailing circumstances. Moreover, larger, better-conditioned snakes may have better success than their poorer-conditioned conspecifics at discovering prey-rich foraging sites. Plummer and Congdon (1994) reported a similar finding for racers (*Coluber constrictor* Linnaeus, 1758) in South Carolina where snakes with small size and mass exhibited the smallest home ranges and slowest movement rates. These *Coluber* movements may, however, be related to age-specific foraging modes rather than snake condition. We tracked only adult *B. irregularis* and extend the results of Gragg et al. (2007) to include greater PM movements as among the attributes positively correlated with improved body condition.

Sex

Differences in movement patterns between sexes have been reported for some snakes (Brown and Weatherhead 2000; Jenkins et al. 2001; Anderson et al. 2005; Wilson et al. 2006; Linehan et al. 2010; Plummer 2010), and not in others (Wasko and Sasa 2009; Linehan et al. 2010; Wasko and Sasa 2012).

Most authors speculated that movement differences were motivated by reproduction or thermoregulation. As in previous studies (e.g., Santana-Bendix et al. 1994; Tobin et al. 1999), sex of *B. irregularis* did not appear to influence movement patterns. Reproduction occurs year round in *B. irregularis* on Guam (Savidge 1987), although we observed no indication that any of our snakes reproduced during our experiment. Had we chosen snakes with fully matured eggs, we may have detected differences.

Time of day

Boiga irregularis moved over three times farther between dusk and midnight (PM) than between midnight and dawn (AM) on any given night. This result is consistent with other studies of *B. irregularis* (e.g., Fritts et al. 1987; Santana-Bendix et al. 1994; Tobin et al. 1999). That *B. irregularis* are most active (and presumably more detectable) before midnight has practical implications for management including increased capture probability given availability and motivation of human searchers is higher in the evening than late night to early morning (Henke 1998).

Comparison to other studies of *B. irregularis*

Snakes in our study used variable and relatively large areas. AA for the first 16 days of tracking in our study varied among snakes almost 10-fold (10 to 92 ha). This variation is consistent with Santana-Bendix et al. (1994) who also reported large variation in AA (up to 99 ha over 80 days). Although the author reported smaller AA in some of the 11 *B. irregularis* tracked, longer movements to new areas continued to increase the cumulative AA, leading to speculation that spatial variability in available prey forced some snakes to forage more widely.

We cautiously compare displacement distances and movement rates we found to those reported in other studies, noting differences in data collection, habitat and treatment effects. Displacement of our control-plot snakes from the original capture location 30–40 days post release averaged 118 ± 17 m. *Boiga irregularis* in a northern forest of Guam were located an average of 93 m from their original release points 30–50 days post release (Tobin et al. 1999). Santana-Bendix (1994) reported displacement from original capture site of 142.8–1809.4 m 35–102 days post release. Clark (1998) followed snakes overnight using radio-telemetry and thread-trailing and found average meandering movements of 96 m (11m/h); an almost identical rate was reported by Rodda (1992). In a recent study, Siers et al. (2014) found displacement distances in northern Guam

ranged from 1.2–253.7 m (mean = 38.4 m) over 1–17 days (mean = 7.2 days) along road corridors. However, the ability to detect a signal perpendicular to the road decreased more rapidly than along the road because of forest density, a constraint that may impact our ability to compare results. The methods of Tobin et al. (1999) were most consistent with ours and their estimated movement rate of 182 m/day (7.6 m/h) during the wet season was very close to the 203 m/day (8.5 m/h) average movement rate during the wet season documented by our study. Santana-Bendix (1994) recorded a slower average rate of 54.5 m/day (4.5 m/h).

Prey suppression as a management tool

The present work further adds to our understanding of *B. irregularis* behavior and indicates that a relatively modest area of rodent (i.e., snake prey) reduction can affect snake movement. Repercussions of this phenomenon could be applied to two different scenarios: 1) areas where the snake is established (e.g., Guam), and 2) areas threatened with introduction (e.g., Hawaii, Saipan, U.S. mainland). Where snakes are established, the lack of prey (or prey odor) in a prey-suppressed area could serve as an environmental cue influencing habitat selection away from the prey-reduced area. Thus, if prey were reduced in or around cargo storage/handling facilities, ports of exit and transportation vehicles (i.e., aircraft or sea vessels), the probability of *B. irregularis* entering the transportation network and being inadvertently transported to a new locale may be significantly reduced. Greater movement (both spatial and temporal) associated with prey depletion may also increase the probability of a snake encountering a trap or oral toxicant, thereby increasing the likelihood of removal from the population (Gragg et al. 2007). If *B. irregularis* can sense the general density of rodent prey in an area, then amplifying detection of the exit port traps (by reducing ambient prey odors) could be an effective strategy. If traps or oral toxicants were positioned in concentric rings outside the prey-suppressed area, migrating snakes could potentially be more successfully intercepted and prevented from entering the transportation network.

The outcome of prey reduction at reciprocal locales threatened with *B. irregularis* introduction is difficult to predict. Although prey reduction would decrease food availability for exiting stowaway snakes, it could also increase the chance and rate of dispersal away from the port of entry. Once in the surrounding habitat, detection could become problematic. Moreover, if prey densities in surrounding

habitats are high enough to increase a snake's body condition, movement rates and survival may increase and in turn possibly improve the probability of population establishment. To mitigate increased movements away from prey-depleted areas, traps or toxicants could be deployed within the treatment area. Without extraneous prey and prey odor, snakes may more readily intercept mice-baited traps and toxicants (e.g., Gragg et al. 2007). Frequent visual searching in the trap/toxicant areas could further facilitate the detection and capture of small snakes not likely to be trapped (Tyrrell et al. 2009; Christy et al. 2010).

In conclusion, prey suppression on a relatively small area produced immediate and significant changes in movement of *B. irregularis*. Although this study is specific to one invasive species, our results could be relevant to the management of other introduced predators. However, suppression of non-native prey could lead to increased predation on native prey by introduced predators (Murphy and Bradfield 1992; Zavaleta et al. 2001), a risk not applicable to our study area with no native rodents. Nevertheless, prey suppression is a potential tool for invasive species management but should be used with caution and might best be applied on a local spatial scale.

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