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Do predators control prey species abundance? An experimental test with brown treesnakes on Guam

Earl W. Campbell III,[1,5] Amy A. Yackel Adams,[2,6] Sarah J. Converse,[3] Thomas H. Fritts,[4,7] and Gordon H. Rodda[2]

[1]*Ohio Cooperative Fish and Wildlife Research Unit, 1735 Neil Avenue, Columbus, Ohio 43210 USA*
[2]*U.S. Geological Survey Fort Collins Science Center, 2150 Centre Avenue, Building C, Fort Collins, Colorado 80526 USA*
[3]*U.S. Geological Survey Patuxent Wildlife Research Center, 12100 Beech Forest Road, Laurel, Maryland 20708 USA*
[4]*U.S. Geological Survey, National Museum of Natural History, MRC 11, Washington, D.C. 20560-0001 USA*

Abstract. The effect of predators on the abundance of prey species is a topic of ongoing debate in ecology; the effect of snake predators on their prey has been less debated, as there exists a general consensus that snakes do not negatively influence the abundance of their prey. However, this viewpoint has not been adequately tested. We quantified the effect of brown treesnake (*Boiga irregularis*) predation on the abundance and size of lizards on Guam by contrasting lizards in two 1-ha treatment plots of secondary forest from which snakes had been removed and excluded vs. two 1-ha control plots in which snakes were monitored but not removed or excluded. We removed resident snakes from the treatment plots with snake traps and hand capture, and snake immigration into these plots was precluded by electrified snake barriers. Lizards were sampled in all plots quarterly for a year following snake elimination in the treatment plots. Following the completion of this experiment, we used total removal sampling to census lizards on a 100-m^2 subsample of each plot. Results of systematic lizard population monitoring before and after snake removal suggest that the abundance of the skink, *Carlia ailanpalai*, increased substantially and the abundance of two species of gekkonids, *Lepidodactylus lugubris* and *Hemidactylus frenatus*, also increased on snake-free plots. No treatment effect was observed for the skink *Emoia caeruleocauda*. Mean snout–vent length of all lizard species only increased following snake removal in the treatment plots. The general increase in prey density and mean size was unexpected in light of the literature consensus that snakes do not control the abundance of their prey species. Our findings show that, at least where alternate predators are lacking, snakes may indeed affect prey populations.

Key words: abundance; Bayesian model selection; binomial mixture model; Boiga irregularis; Carlia ailanpalai; Emoia caeruleocauda; *geckos; Hemidactylus frenatus*; *Lepidodactylus lugubris*; *predation; removal experiment; skinks.*

Introduction

To what extent are terrestrial vertebrate populations depressed by their predators? A limited example is that exhibited by extinctions of prey, usually on islands, caused by invasive introduced predators. The brown treesnake's (*Boiga irregularis*) extirpation of the native forest birds of Guam (Savidge 1987) demonstrates that a predator can eliminate vulnerable prey, but what does that nonequilibrium outcome (extinction) suggest about the interactions of coexisting predator and prey populations? Perhaps coexistence reflects a prey species' relative insensitivity to predation pressure. Under what *sustainable* conditions, then, are prey populations appreciably depleted by their coexisting predators?

This classic question is most convincingly answered by experimental manipulation of predator presence, which is difficult to do. As noted by Sih et al. (1985:289), "... virtually no studies have manipulated predators of vertebrate prey." Salo et al. (2007) conducted a meta-analysis of replicated terrestrial studies and found only 45; however, none of these involved either ectothermic predators or ectothermic prey (but see Schoener et al. [2002] discussed below in the fourth paragraph of the *Introduction*).

Studies focused on endothermic predators and prey represent a subset of vertebrate predator–prey relationships that incorporate low energetic assimilation efficiencies and relatively high food intake requirements (Pough 1980). Nowak et al. (2008) argued that endo- and ectothermic predation energetics are fundamentally different; endothermic predators' food needs are much higher, and the incessant need for food drives a much higher level of activity among both predator and prey.

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[5] Present address: USFWS, Pacific Islands Fish and Wildlife Office, 300 Ala Moana Boulevard, Room 3-122, P.O. Box 50088, Honolulu, Hawaii 96850 USA.

[6] Corresponding author. E-mail: yackela@usgs.gov

[7] Present address: 24 Madrone Flyway, Belen, New Mexico 87002 USA.

Higher activity levels increase vulnerability of prey. Thus, one would expect similarly profound differences in the ability of prey populations of differing assimilation efficiencies to support and sustain predation.

Our literature search resulted in only two sets of experimental manipulations that shed light directly on either ectothermic predators or prey, and in one case both (Lindell and Forsman 1996 and Schoener et al. 2002 [see also Losos et al. 2004, Schoener et al. 2005]). In the first set of manipulations, Lindell and Forsman (1996) augmented viper densities on small Baltic islands, but found no significant effect on prey abundance. In the second set of manipulations, Schoener et al. (2002) introduced an exotic omnivorous lizard, *Leiocephalus carinatus*, to tiny islets in the Bahamas, where it preyed on both invertebrate prey (including various spiders, which themselves eat insects) and vertebrates (including the insectivorous lizard *Anolis sagrei*, which preys on both spiders and insects). Thus, this set of manipulations generated both predation and competition between the two lizard species. Unlike the brown treesnake, the introduced predator in this case, *L. carinatus*, was not inclined to climb vegetation, and thus allowed the semi-arboreal prey lizard species, *A. sagrei*, refuge above ground. The numerical response following predator introduction (~50% reduction in *A. sagrei*) was fairly rapid (<2 months), with little additional change over two years. Over the two-year time period, the prey lizard increased its mean height above ground from ~10 cm to 80 cm, and progressively spent more time towards the distal ends of branches (mean perch changed from ~3.5 cm to 2 cm diameter). The experiment ended when cyclonic storm overwash eliminated the tiny populations of introduced predators. The beauty of this manipulation was the vivid detail provided by Schoener et al. (2002) regarding the direct and indirect consequences throughout the food web (including impacts on leaf area, among others). However, understanding causation in this study was hindered because both direct (predation) and indirect (competition) effects impinged on each link in the food web, and because there is some question as to whether the outcome was sustainable (the islets may have been too small to sustain the predator indefinitely).

We present the results of an experimental manipulation that avoids limitations observed in Schoener et al. (2002) by having a much clearer separation between predation and competition. Snakes preyed on lizards, but did not compete with them, though competition probably existed among the lizard prey species. Predation by larger lizards on smaller ones may have played a minor role. In our study, we manipulated the system by removing rather than adding a predator. We removed the introduced brown treesnake from two 1-ha snake-proof exclosures on Guam and tracked population densities of the four prey lizard species over time both before and after snake removal, and between treatment plots from which snakes were removed and adjacent habitat-matched control plots. Our food web was not transient: studies of unmanipulated plots at our site from 1992 to 2011 (G. Rodda et al., *unpublished data*) indicate seasonal and short-term fluctuations, but no long-term trends in the abundance of the four lizards and snake.

The prevailing ecological dogma prior to the emergence of the brown treesnake problem on Guam (Savidge 1987) was that snakes do not influence the abundance of bird prey (Marshall 1985). Note that the present experiment did not involve bird prey, as all native endotherms had been lost from our study site prior to our manipulation (Savidge 1987, Rodda and Fritts 1992, Fritts and Rodda 1998, Rodda and Savidge 2007). The remaining vertebrates, all lizards, were presumably less vulnerable than birds to snake predation. Furthermore, prior to our study about half of the original saurofauna of Guam had been extirpated by the snake and other factors (Rodda and Fritts 1992); thus, the four lizard species available for study were present at our site because they had tolerated snake predation. This, presumably, is a conservative sample for the demonstration of predatory impacts.

The viewpoint that snakes have little numeric impact on their prey (whether ectothermal or endothermal) arose on empirical and theoretical grounds, and has been maintained in the absence of experimental evidence. Fitch (1949) surveyed snake populations in central California and judged them empirically incapable of appreciably influencing the abundance of rodents. On the basis of field studies in the continental United States, Fitch (1982), Reynolds and Scott (1982), and Reichenbach and Dalrymple (1986) reinforced the general conclusion that a variety of snake species did not influence prey densities. Lindell and Forsman (1996) reported a negative correlation between observed predator (viper) and prey (vole) densities on some Baltic islands, but failed to demonstrate a significant reduction in vole density following an experimental augmentation of viper density. Later studies have mostly reaffirmed these field conclusions (Lillywhite and Henderson 1993, Nowak et al. 2008, Beaupre and Douglas 2009).

On the basis of energetic computations, Porter and Tracy (1974) estimated that snakes would impact their prey only when the predator biomass approached that of the prey biomass. Nowak et al. (2008) focused specifically on the low-energy lifestyle of vipers, which is shared with many snakes including the brown treesnake, and concluded on theoretical grounds that vipers could influence the density of prey species only when the prey species densities were at the nadir of a population cycle. Although not addressing snakes specifically, Menge and Sutherland (1976) argued that the effects of predation should decrease at higher trophic levels (brown treesnakes are the top predator in the extant Guam ecosystem). With reference to mammalian predator–prey experiments, Newsome et al.'s (1989) predator-removal experiment supported Nowak et al.'s (2008)

reasoning that predators affect prey densities only when prey densities are exceptionally low. Thus, on the basis of the literature on snake predation or top predators, our expectation was that Guam's coexisting species of lizards would be little affected by the removal of brown treesnakes. The purpose of this work is to contribute to a broader understanding of vertebrate predation dynamics by evaluating whether this top ectothermic carnivore is capable of depleting coexisting lizard populations in this productive tropical forest ecosystem.

Materials and Methods

Study species, site, and data collection

The brown treesnake was accidentally introduced to Guam during the late 1940s (Savidge 1987, Rodda et al. 1992). Over the subsequent 60 years, this nocturnal, rear-fanged colubrid (typical length ~1 m) reached high population densities (Rodda et al. 1992, 1999*b*). Brown treesnakes forage both in the trees and on the ground (Rodda and Savidge 2007). The four coexisting species of lizards in this system were two geckos and two skinks. The two geckos (present prehistorically and possibly prehuman in the Marianas), both arboreal and nocturnal, were *Lepidodactylus lugubris* (hereafter *Lepidodactylus*), a parthenogenic species of ~1 g, and *Hemidactylus frenatus* (hereafter *Hemidactylus*), a sexual species of ~2 g. The two skinks, both diurnal and terrestrial, were *Emoia caeruleocauda* (hereafter *Emoia*), a native species of ~1.6 g, and *Carlia ailanpalai* (hereafter *Carlia*), an introduced species of ~3.1 g. Both the snake and *Carlia* were introduced to Guam from the Admiralty Islands shortly after WWII (Rodda et al. 1992, Austin et al. 2011). The native range of all four lizard species overlap with the native range of the brown treesnake. Introduced herbivorous rodents (primarily *Rattus* cf. *diardii*) were the only endotherms present in the study area, but were not monitored during this work. It should be noted that only the largest brown treesnakes regularly eat endotherms (Savidge 1988).

Two 1-ha brown treesnake exclosures and two 1-ha control plots (map provided in Appendix A) were established in early, second-growth tangantangan (*Leucaena leucocephala*) forest on Northwest Field, Andersen Air Force Base, Guam. The snake exclosures were bounded by an electrified barrier (1.15 m tall nylon mesh, impermeable to snakes but permeable to all prey but the largest *Carlia* individuals, with electro-shocking wires of alternating polarity at height increments of ~15 cm) designed to prohibit snake dispersal (Campbell 1999). We eradicated snakes from the exclosures using traps and hand capture during nocturnal visual snake surveys. Control plots had no barrier surrounding them.

Field crews monitored snake and lizard populations in treatment and control plots twice prior to the removal of snakes from exclosures. Prior to construction of the snake barrier we conducted pretreatment monitoring during February and March 1993 (monitoring period 1). Immediately following construction of the snake barrier but prior to its electrification, monitoring was conducted during July and August 1993 (monitoring period 2). In late January 1994 we initiated quarterly monitoring on all four plots (monitoring periods 3–6). This occurred three months after the mean date of snake removal from the exclosures. Following completion of monitoring period 6, a complete census of lizards was conducted in a 100-m^2 area within each of the four plots to further document prey densities in the plots.

Treatment (snake removal)

We estimated brown treesnake density on all plots prior to snake removal, with a 5×5 grid of 25 arboreal snake traps (Rodda et al. 1999*a*) placed along three equidistantly spaced (25-m) transects through the interior of each of the four plots. Each trap housed a caged mouse as an attractant and was modified from a commercially available crayfish (funnel) trap by incorporation of one-way flaps to prevent egress through the entrance holes. Traps were spaced 25 m apart and monitored for 16–60 days. During and after snake eradication, an augmented array (7×7) of 49 traps (14.3-m spacing between traps) was used for snake removal and subsequent quarterly verification that these plots remained snake-free. After snake removal, a 5×5 grid of 25 traps was used quarterly on the snake-present plots for 16–25 days to obtain mark–recapture estimates of snake density.

We kept records on individual snake capture histories through all trapping sessions. Each new snake was marked with a uniquely numbered passive integrated transponder (PIT) tag for identification (Lang 1992) prior to release. Brown treesnakes were also captured by hand during standardized nocturnal visual surveys for arboreal lizards. Methods of marking and data collection were the same for snakes captured by hand and in traps.

Following barrier construction and monitoring period 2, snake removal was continued on each removal plot until several days had elapsed without any captures. The required number of days without a capture, n, was determined in the following way. If a single snake was present on the plot during n days of trapping, then the probability it escaped capture was $(1 - \hat{p})^n$ where $\hat{p}$ is the capture probability per day (assumed constant). We estimated $\hat{p}$ using program SURGE using data from the trapping grid and visual surveys and calculated n so that $(1 - \hat{p})^n < 0.05$. At the end of n days of trapping (with no captures), the probability that we would have removed any snake initially present in the plot was greater than ~0.95.

Lizard abundance

Nocturnal headlamp surveys for arboreal lizards were conducted at the start of each monitoring period and occurred along five transects (three interior and two exterior edges; Appendix A). The survey protocol on each plot was as follows: On each of 10 nights (19:00–

24:00 hours) two surveyors working as a pair covered opposite sides of one-and-a-half of the interior transects (150 m) of each plot, and the pair split up every other night to survey the inside half of the two exterior transects (100 m) of each plot. Each transect was thereby visually searched five times during each monitoring period. To assure that each transect within each plot was surveyed equally by both observers, the sequence in which transects were surveyed was determined systematically. The same two surveyors made all observations, except during monitoring period 2, when one of the surveyors was replaced with another trained searcher.

Following the completion of nocturnal arboreal gecko surveys and snake trapping, we placed 12 adhesive traps (Bauer and Sadlier 1992) along the three interior transects of each plot to monitor terrestrial skink abundance (four traps per transect). Trapping lasted seven days during each monitoring period (except during monitoring period 3 which required nine days to complete trapping due to interruptions from rain), and traps were moved 3 m forward along each transect for each subsequent trapping session, thereby trapping each transect 7 times during each monitoring period. Trapping was conducted during fair weather in the morning (07:30–11:00 hours) during the period of peak skink activity and before the risk of mortality due to overheating on the traps became too great. We checked traps each half hour, and all lizards captured were released later in the day. Lizard age-class or size (snout–vent length), time, and trap locality, were recorded for each individual. *Carlia* were considered adults if they had a snout–vent length over 49 mm (M. McCoid, *unpublished data*). Data were insufficient to allow separate analyses for juvenile and adults of other species.

Census of lizards via removal sampling

Following the completion of our experiment, we used total removal sampling (Rodda et al. 2001) to census lizards on a 100-m^2 subsample of each plot. In this sampling we isolated the subsample area by canopy separation and construction of a ground-level lizard-proof fence, and disassembled and removed all vegetation, collecting all lizards as exposed.

Statistical analyses

We used a model for replicated binomial count data (the N-mixture model; Royle 2004, Royle and Dorazio 2008) with our spatially and temporally replicated lizard count data to estimate abundance for each transect in each plot during each monitoring period, corrected for detection, in a Bayesian mode of inference. Transects within plots were considered the appropriate scale of estimation because home ranges of these lizards are thought to be less than our transect spacing of 25 m. Direct measurements of home range size do not exist for our lizard species, but *Carlia*, the largest lizard in our study, is similar in size to congener C. *rubrigularis*, which has a recorded space use of only 15 m^2 (diameter of 4.77 m; C. Manicom and L. Schwarzkopf, *unpublished data*).

In the N-mixture model, count data are described by two generalized linear models. Each of the counts ($C_{i,t}$) from spatial replicate i at time t (where t is the day within each of the six monitoring periods) for a given species are modeled as arising from a binomial distribution with detection parameter $p_{i,t}$ and abundance parameter N_i. The detection parameter, $p_{i,t}$, was modeled with a logit-linear function, while the abundance parameter, N_i, is assumed to be Poisson distributed; the mean of the Poisson distribution, λ_i, was modeled with a log-linear function to develop inference about the biological processes influencing abundance. Our logit-linear model of detection probability, $p_{i,t}$, for each species included an intercept and normally distributed mean zero random effects to account for variation in detection over space (transect within plot effects) and time (survey within monitoring period effects). Our model of λ_i for each species included an intercept (*Carlia* had separate intercepts for adults and juveniles), fixed effects for space (plot) and time (period), and a treatment effect. Thus, though we estimated abundance at the transect-within-plot scale, we modeled mean abundance at the plot scale, in recognition that the plot is the experimental unit. Examination of the empirical data indicated that lizard abundance and trends were nearly identical between control plots and between treatment plots. A priori, we expected seasonal spikes in abundance in the juvenile group due to seasonal recruitment patterns, but relative population stability among adults, so we specified two independent log-linear Poisson models for *Carlia*. Treatment was modeled in two different ways: either as a linear time trend in treatment (trend treatment model; the treatment effect could increase or decrease with time since removal of snakes) or as a constant treatment effect, for monitoring periods 3–6.

We implemented Markov chain Monte Carlo methods to obtain a large sample of draws from the joint posterior distribution of the model parameters and used conventional vague priors for the standard deviation of random effects (uniform, minimum = 0, maximum = 5), and the intercept (normal, mean = 0, SD = 10) in the detection portion of the model. We conducted Bayesian model selection (details included in Appendix B) in order to analyze evidence in favor of each of the different treatment models (trend treatment and constant treatment) vs. a no-treatment model.

We used WinBUGS (Gilks et al. 1994, Spiegelhalter et al. 2003) executed from R (version 2.9.1; R Development Core Team 2009) with the R2WinBUGS interface (Sturtz et al. 2005) to fit our models. We ran three parallel chains with 15 000 iterations each and discarded the first 3000 iterations as burn-in for all models (however, for the *Carlia* constant treatment model, mixing was initially poor, so we ran 90 000 iterations, discarded the first 18 000 and thinned to retain each

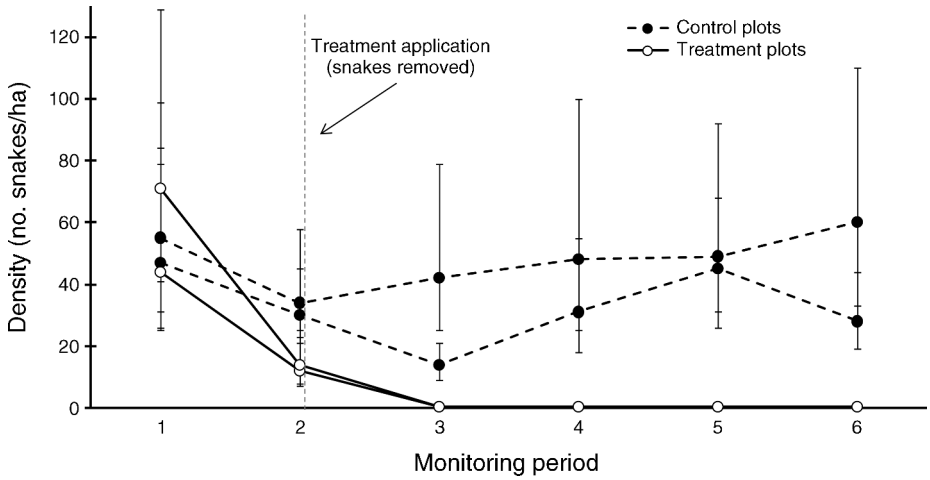

FIG. 1. Brown treesnake (*Boiga irregularis*) density estimates and 95% confidence intervals for two treatment and two control plots on Guam during each of the six monitoring periods. Period 1 was pretreatment, period 2 was also pretreatment (after barrier construction, but prior to electrification of the fence and removal of snakes), and periods 3–6 were all posttreatment. A low rate of leakage (0.06 incursions·day^{-1}·plot^{-1}) into the treatment plots was offset by immediate removal.

sixth sample from the chains). Output was visually examined to ensure that values were from a stationary distribution and $\hat{R} < 1.05$ for each variable in the chains (Gelman et al. 2004).

Snake capture histories were analyzed using the open population modeling program SURGE (Lebreton et al. 1992, Rodda et al. 1999*b*) for capture periods of 16–20 days during each trapping session. Abundance was estimated from the relationship

$$\hat{\bar{N}} = \frac{\bar{C}}{\hat{p}}$$

and density for these 1-ha plots was estimated as

$$\hat{\bar{D}} = \frac{\hat{\bar{N}}}{a}$$

where $\hat{\bar{N}}$ is abundance, $\bar{C}$ is mean number of captures per occasion, $\hat{p}$ is estimated detection probability per occasion, $\hat{\bar{D}}$ is mean density, and a is plot area.

RESULTS

Snake population monitoring and removal

Immediately prior to and during the posttreatment monitoring, we found an average of 34 snakes/ha on control (snake-present) plots (Fig. 1), ~2 kg/ha (treatment-specific estimates included in Appendix C). The snake exclosure fencing proved to be largely, but less than completely, successful: 47 snakes were captured and immediately removed on treatment (snake-free) plots during the 365 days of trapping following the completion of snake removal (0.06 incursions detected per day per plot). Thirty-eight incursions (81%) occurred during the last three months of the exclosure experiment. High rainfall occurred during this time period, and fence electrification was periodically drained by high fence conductivity. During this time period, we continuously conducted snake trapping to assure low snake densities for the predator-removal experiment.

Lizard abundance

All lizard species increased in abundance following brown treesnake removal except *Emoia*, but only *Carlia* and *Lepidodactylus* showed strong treatment effects. Predicted mean *Carlia* abundance was nearly equal in treatment and control plots during pretreatment (periods 1 and 2), but was, on average, 42% (95% credible interval [CRI]: 26–59%) larger on treatment plots following snake removal based on estimates from the constant treatment effect model (Fig. 2). The mean posterior treatment effect for adult and juvenile *Carlia* from the constant treatment effect model was 0.70 with a 95% credible interval that did not include 0 (Table 1). Bayes Factor estimates for both treatment models were much greater than 1 (and posterior inclusion probabilities were 0.999 and 0.996 for the constant and trend treatment models, respectively), which indicated decisive evidence for inclusion of a treatment effect in the model over a null model of no treatment effects (Table 1). Like adult *Carlia*, the abundance of juvenile *Carlia* was similar on treatment and control plots during pretreatment (periods 1 and 2), but their increase in abundance after snake removal was variable over time and less pronounced (Fig. 2). In a post hoc analysis where we modeled treatment effect by age, adults had a treatment effect two times that of juveniles.

An unsubstantial decrease in abundance (−4.6%, 95% CRI: −22.3 to 15.6) for the other skink, *Emoia*, was observed in treatment and control plots following snake removal (Fig. 2). There was no support for including either treatment effect in the model based on a small Bayes Factor (<1; Table 1). Additionally, the posterior

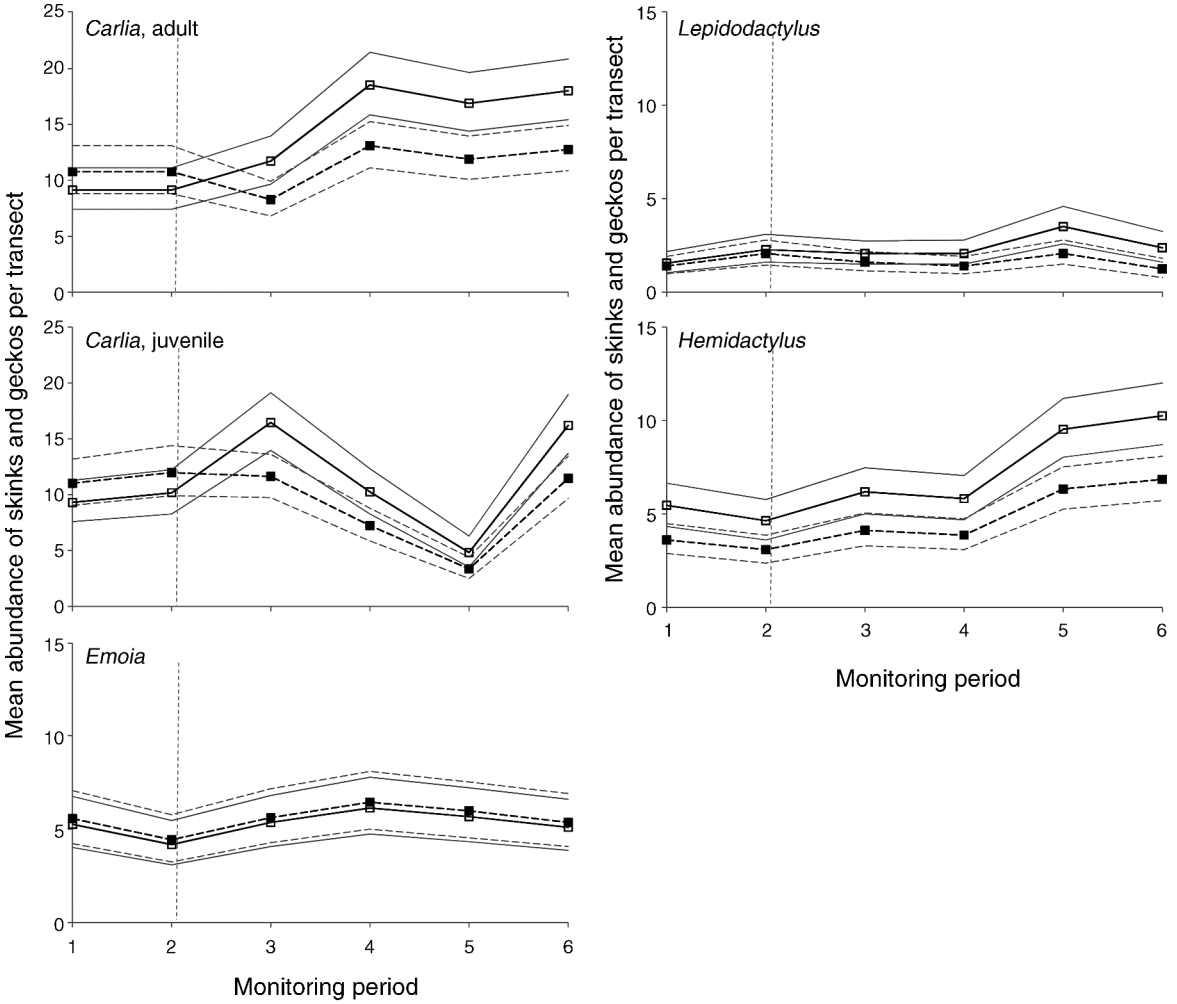

FIG. 2. Mean posterior abundance estimates per transect for skinks (adult *Carlia ailanpalai*, juvenile *Carlia ailanpalai*, and *Emoia caeruleocauda*) and geckos (*Lepidodactylus lugubris* and *Hemidactylus frenatus*) and 95% credible intervals (gray lines) for treatment (solid black line with open squares) and control (dashed black line with solid squares) plots combined during pretreatment (1–2) and posttreatment (3–6) monitoring periods. The dashed vertical line denotes snake removal from treatment plots. The scale was adjusted for *Carlia* to accommodate larger abundance values.

mean for the treatment effect for this species under the constant and trend treatment models had 95% credible intervals that overlapped zero.

Mean *Lepidodactylus* abundance was nearly equal on treatment and control plots during pretreatment (periods 1 and 2), but was on average 60% (95% CRI: 19–111%) higher on treatment plots following snake removal, based on the trend treatment model (Fig. 2). Of the three models considered, only a linear increase in abundance over time was supported (trend treatment model Bayes Factor = 2.4; Table 1). The posterior mean for the linear treatment effect for *Lepidodactylus* was 0.193 with a 95% credible interval that only marginally included zero (Table 1).

Mean abundance of *Hemidactylus* increased, on average, 50% (95% CRI: 29–74%) on treatment plots following the removal of snakes, based on the null model (Fig. 2; inclusion of either treatment model was not warranted over the null model (Bayes Factor < 0.50; Table 1). Additionally, the posterior mean for treatment effect for this species under the constant and trend treatment models had 95% credible intervals that overlapped zero.

Total removal census of lizards

Using total removal sampling following the completion of the last quarterly monitoring, we determined, on average, 19 650 and 13 210 lizards/ha in the treatment and control plots, respectively (Table 2). For all four lizard species, densities were higher on treatment plots compared to control (snake-present) plots. The percent difference was greater than 80% for all species except *Emoia* (9%). Skinks were more abundant than geckos in both treatment and control plots (about twofold by

TABLE 1. Comparison of constant and trend treatment models to the no-treatment (null) effect model for skinks and geckos in terms of Bayes Factor and posterior probability of a given model.

	Constant treatment				Trend treatment			
			Treatment effect				Treatment effect	
Species	BF†	Posterior Pr of model‡	Estimate	95% CRI	BF†	Posterior Pr of model‡	Estimate	95% CRI
Carlia	12 191.41	0.9999	0.703 ± 0.149	0.414, 0.996	326.46	0.9969	0.194 ± 0.046	0.104, 0.283
Emoia	0.53	0.3471	0.156 ± 0.272	−0.358, 0.707	0.29	0.2225	0.104 ± 0.092	−0.076, 0.286
Lepidodactylus	1.04	0.5105	0.209 ± 0.241	−0.231, 0.721	2.35	0.7016	0.193 ± 0.099	−0.001, 0.387
Hemidactylus	0.47	0.3198	0.163 ± 0.225	−0.284, 0.592	0.46	0.3135	0.119 ± 0.070	−0.016, 0.258

Note: Treatment effect (estimate ± SD) and 95% credible interval (95% CRI) are presented for each of the treatment models.
† The Bayes Factor (BF) is a measure of the strength of evidence in favor of a model. A Bayes Factor of 1.0 indicates that the evidence equally supports the null model (no treatment effect) and the treatment model, while larger Bayes Factors indicate increasing support for a treatment model.
‡ The probability, given the data, that the given treatment model is preferred over the no-treatment model.

density and fourfold by biomass (Table 2). The mean snout–vent length of all four lizard species captured during removal sampling was significantly greater on treatment plots compared to control plots (data summarized in Appendix D).

DISCUSSION

Snake predation response on lizards

The exclosure experiment validated our snake population monitoring techniques and verified that snake exclusion was possible though not absolute. Following snake removal, snakes were practically eliminated in treatment plots compared to control plots. Brown treesnake exclusion had variable effects on the different coexisting prey species, as documented by the quarterly monitoring (Table 1, Fig. 2) and total removal sampling (Table 2). Following snake removal, the abundance of *Carlia* increased significantly. Substantial, though not uniformly significant, increases were also observed in both gecko species. However, snake removal did not affect the abundance of the native skink, *Emoia*. One might have expected greater predatory impacts for species of lizards that have no evolutionary experience with snake predators. To the extent that present geographic distributions reflect their evolutionary coexistence, this hypothesis was not supported by our results. The lizard species with the least native range geographic overlap with snakes, *Emoia*, was the species that showed the greatest resistance to predation, whereas *Carlia*, the species with the most direct *Boiga* coevolutionary experience (*Carlia* and *Boiga* lived together in the Admiralty Islands as natives before their postwar introduction to Guam), was the least resistant. One might have also expected niche in the broad sense to play a role in the predatory impacts of this nocturnal treesnake but both nocturnal (geckos) and diurnal (*Carlia*) lizard species were affected as were both arboreal (geckos) and terrestrial (*Carlia*) species. Brown treesnake predation was not limited to one niche. Thus, neither evolutionary naiveté, nor niche in the broad sense explains the pattern of observed predatory impacts.

Adult *Carlia* abundance increased uniformly through time, while juvenile abundance appeared to spike seasonally (periods 3 and 6; Fig. 2). The juvenile fluctuations may indicate variation in recruitment between wet (May–Oct) and dry (Nov–Apr) seasons. The strong response of *Carlia* to brown treesnake removal was consistent with two contemporary studies of brown treesnake stomach contents. McCoid (1990) found that *Carlia* constituted 21–52% of ingested prey (n = 149 snakes) at four sites on Guam. E. Campbell (*unpublished manuscript*) found similar results for brown treesnakes ($n = 60$) captured in forest habitats on Guam during the summer of 1990, with skinks compromising 60% of snake diets. All four lizard species were found in

TABLE 2. Mean and actual density and biomass of lizards of four species captured during removal sampling (100-m^2 subplot) conducted on treatment and control plots following the final posttreatment monitoring period (period 6).

	Density (number/ha)					Biomass (kg/ha)				
	Treatment		Control			Treatment		Control		
Species	Mean	Actual	Mean	Actual	Difference (%)†	Mean	Actual	Mean	Actual	Difference (%)†
C. ailanpalai	9 100	8 300, 9 900	5 000	2 400, 7 600	82	33.9	29.1, 38.7	14.0	7.6, 20.4	142
E. caeruleocauda	4 100	1 900, 6 300	3 750	3 200, 4 300	9	8.2	3.9, 12.5	5.4	5.0, 5.8	52
L. lugubris	3 350	2 300, 4 400	1 750	700, 2 800	91	3.9	2.9, 4.8	1.4	0.7, 2.2	179
H. frenatus	3 100	2 400, 3 800	1 550	1 200, 1 900	100	7.6	5.8, 9.5	2.9	2.0, 3.8	162
Total	19 650		12 050		63	53.6		23.7		126

Note: Mean values are based on two plots. Plot values are shown as "actual."
† The point estimate of percentage difference in lizard density is [(treatment/control) − 1] × 100.

brown treesnake stomachs from this site (E. Campbell, *unpublished data*).

The results of the snake exclosure experiment suggest that brown treesnake predation has minimal, if any, net effect on *Emoia* abundance. This supports the statement by Rodda and Fritts (1992) suggesting that the scarcity of *Emoia* on Guam is not due to snake predation, but to ecological displacement by *Carlia*, introduced to the island of Guam sometime between the mid-1950s and the mid-1960s (Rodda and Fritts 1992, McCoid 1993, Austin et al. 2011). The continued persistence of *Emoia* in secondary forest habitats on Guam may be due to population suppression of *Carlia* by brown treesnakes. In this regard, it is noteworthy that on the two adjacent, but snake-free islands of Saipan and Tinian, four total removal plots in similar *Leucaena* habitat yielded a total of 60 *Carlia* and 0 *Emoia*, even though *Emoia* are present on both islands (G. Rodda et al., *unpublished data*). The removal of brown treesnakes from our exclosures may have locally created the conditions prevalent on Saipan and Tinian, where competition or predation on *Emoia* by *Carlia* is increased to the point where *Emoia* populations remained depressed despite the elimination of snake predation on *Emoia*. Nonetheless, we might have seen an effect of snake predation on *Emoia* if we had continued our experiment for longer than a year.

Lepidodactylus had the greatest proportional post-treatment increase of all species studied in this experiment (Fig. 2). Since *Lepidodactylus* is parthenogenetic, it may have had a twofold demographic advantage compared to a sexual lizard species such as *Hemidactylus* (Petren and Case 1996).

Other studies have suggested that brown treesnake abundance appears to be limited by food availability in both Guam and its native range (Rodda et al. 1999*b*). In forested areas of Guam, however, the food limitation appears to apply primarily to adult snakes, which require larger food items, such as mammals and birds, which had previously been severely suppressed or extirpated from forested areas (Fritts and Rodda 1998, Rodda et al. 1999*b*, Wiewel et al. 2009). We suspect that food availability for juvenile (saurophagous) brown treesnakes was not a limiting factor for the snake populations in this experiment. During this experiment, the mean density of snakes on control plots was 34 snakes/ha, and the lizard censuses conducted during total removal sampling on control plots indicated that there was a standing crop of ~12 000 lizards/ha, which equates to 259 skinks and 129 geckos as potential prey per snake. This is a substantial prey base for an individual brown treesnake and underscores the magnitude of any numerical response by lizards to predator removal.

Brown treesnake predation appeared to affect the size of all species of lizards found on our study site (Appendix D). Following brown treesnake removal, the relative increase in lizard size within snake exclosures suggested that lizards were more likely to survive or grow to reach larger size due to decreased snake predation. In general, both lizard numbers and sizes increased. Thus, the increases in prey biomass were starker than the numerical difference alone (Table 2). Prey biomass in the snake-free total removal plots was more than double (126% increase) that in the snake-present plots. The numerical increases following snake removal, in association with size increases, support the hypothesis that brown treesnake density, at the levels present during the removal experiment, was an important factor regulating lizard population levels and size structure.

Predator prey generalizations and snakes

This study contributes to the remarkably short list of replicated manipulative studies of predation on or by ectothermal terrestrial vertebrates. The strong influence exerted by snakes on prey density in our study was unexpected on the basis of the literature on population regulation by snakes. Furthermore, it is not consistent with the conclusion (e.g., Porter and Tracy 1974, Newsome et al. 1989, Nowak et al. 2008) that snake predators should exert their control only on prey species at the nadir of their abundance or when predator biomass approaches that of the prey. It is noteworthy that in the present study, the biomass of predators (~2 kg/ha) did not approach within an order of magnitude that of the prey populations (Table 2). Predator biomass was only ~8% that of prey biomass. Our results also do not comport well with the requirement that prey densities be absolutely low for predators to have a significant impact. Rodda and Dean-Bradley (2002) found that a typical terrestrial lizard assemblage biomass was ~0.6 kg/ha in mainland areas and 7.1 kg/ha on islands (most data from tropics, a mixture of species-poor, high-biomass and species-rich, low-biomass islands). This contrasts with the 19.4 kg/ha of terrestrial lizard biomass observed in our species-poor, high-biomass study area (Table 2). With 19.4 kg/ha, it is difficult to argue that the prevailing prey density on Guam was absolutely low.

At least two possibilities present themselves for the resolution of the apparent contradiction between the high prey biomass on Guam and the large predatory influence of a snake. First, it is possible that the generalization that snakes do not greatly influence prey abundance is overly broad, based as it is on sparse and weak correlational evidence largely from temperate mainland areas. The two experimental studies of predation impacts on lizards (Schoener et al. 2002 and the present work) show substantial prey population depression by predators. Second, perhaps the circumstances under which snake predators exert an appreciable influence on prey population densities and biomasses are limited to systems in which only a single major predator is present or food webs are simplified. When multiple predators exist, the impacts of each predator may be largely compensatory; removal or augmentation

of one predator is simply offset by the augmented or diminished impacts of the others (if the vipers don't prey on the voles, the raptors will). Either the presence of only a single predator or a simplified food web could account for the strong impacts associated with novel predator introductions to island ecosystems (e.g., Brockie et al. 1988, Ebenhard 1988, Atkinson 1989, Salo et al. 2007), as well as the strong impacts seen in the present study and Schoener et al. (2002). It would also account for the general lack of impacts associated with mainland sites such as those studied by Fitch (1949, 1982), Reynolds and Scott (1982), and Reichenbach and Dalrymple (1986). Perhaps, predator populations in complex ecosystems are constrained by other links in the food web, such that predators do not achieve densities high enough to appreciably impact their prey. The extraordinary abundance of lizard prey on very small islands (Rodda and Dean-Bradley 2002) is consistent with the notion that the addition of a single predator (present on slightly larger islands) has uniquely severe impacts on prey species densities in systems for which there are no alternate predators. Our Guam system had no alternate predator. Lizard densities on Guam, while high compared to large islands, are representative of ecologically simple islands (Rodda and Dean-Bradley 2002). Thus a strong influence of predation can occur despite a low predator : prey biomass ratio and a high absolute prey abundance. The need for additional experimental studies on the impacts of predation, with and without compensatory predation or complex food webs, is plain, and conspicuously acute for ectothermal vertebrates.

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Supplemental Material

Appendix A

Arrangement of the 1-ha treatment (snake-exclosure) and control (snake-present) plots with sampling transects on Guam (*Ecological Archives* E093-102-A1).

Appendix B

Bayesian model selection procedure used to analyze evidence in favor of each of the different treatment models (trend treatment and constant treatment) vs. a no-treatment model (*Ecological Archives* E093-102-A2).

Appendix C

Brown treesnake (*Boiga irregularis*) population estimates for 1-ha plots during monitoring period 2 (post-construction of barrier but prior to its electrification) and number of snakes removed from treatment exclosures (*Ecological Archives* E093-102-A3).

Appendix D

Mean snout–vent length (SVL), measured in millimeters, of four species of lizards captured during removal sampling (100-m^2 subplot) conducted on treatment and control plots following the final posttreatment monitoring period (period 6) (*Ecological Archives* E093-102-A4).