Use of Visual Surveys and Radiotelemetry Reveals Sources of Detection Bias for a Cryptic Snake at Low Densities

Scott M. Boback  
*Dickinson College*

Melia G. Nafus

Amy A. Yackel Adams

Robert N. Reed

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Use of visual surveys and radiotelemetry reveals sources of detection bias for a cryptic snake at low densities

SCOTT M. BOBACK,1,† MELIA G. NAFLUS,2 AMY A. YACKEL ADAMS,2 AND ROBERT N. REED2

1Department of Biology, Dickinson College, Carlisle, Pennsylvania, USA
2Fort Collins Science Center, U.S. Geological Survey, Fort Collins, Colorado, USA


Abstract. Transect surveys are frequently used to estimate distribution and abundance of species across a landscape, yet a proportion of individuals present will be missed because either they were out of view and unavailable for detection or they were available but not detected because the surveyors missed them. These situations lead to availability and perception bias, respectively, and can result in misleading estimates of abundance and habitat use. In this study, we examined potential biases of visual surveys used for the brown tree snake (Boiga irregularis), a cryptic invasive snake responsible for the extirpation of at least 15 vertebrates on Guam. We simultaneously executed visual surveys and radiotelemetry in a low-density population of brown tree snakes with two goals in mind: to assess the efficacy of visual surveys in detecting subjects at low densities and to identify sources of perception and availability bias in such surveys. Results indicated that with considerable effort, visual surveys can predict the presence of this cryptic reptile even at low densities (0.4 animals/ha) but perform poorly at predicting areas of high use resulting in inaccurate estimates of relative habitat importance. Telemetered snakes used densely foliated plants including Pandanus tectorius and ferns (epiphytic and terrestrial species) for nearly half of their time, yet <9% of visual survey observations occurred in these microhabitats. Visibility of snakes decreased as they perched higher in the canopy mirroring the disparity between visual survey and telemetry detections but was also surprisingly low near the forest floor (0–1 m). Microhabitats identified in this study are likely to disproportionally affect visual surveys and would be appropriate resources to target for management purposes. When there is critical need to prevent false negatives, such as during an incipient invasion elsewhere, targeted searches of high-use resources could augment other detection tools to improve detection probabilities of this and other cryptic species.

Key words: availability bias; detection probability; habitat use; invasive species; perception bias; radiotelemetry; species management; visual surveys.

Received 25 June 2019; revised 6 October 2019; accepted 15 October 2019; final version received 23 November 2019.

Corresponding Editor: Debra P. C. Peters.

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† E-mail: bobacks@dickinson.edu

INTRODUCTION

Transect surveys that rely on visual encounters (hereafter referred to as visual surveys) are commonly used to estimate the distribution of organisms within a landscape (Foster 2012). With relatively low cost and effort, such surveys allow sampling over geographically extensive...
areas and enable scientists to model population characteristics at large spatial scales (MacKenzie et al. 2006, Glisson et al. 2017). Yet, estimates generated from visual surveys are sensitive to detection probabilities and many animals possess suites of behavioral and morphological characters that enable them to blend into their environment and circumvent detection by other animals. Organisms with such characteristics pose a major problem for visual surveys. Reptiles and amphibians can be particularly challenging in this regard due to their small body sizes, habitat preferences, and secretive nature (Turner 1977, Pough 1983, Siers et al. 2018). Further, our ability to detect some of these species may be lowest in high-quality rather than low-quality habitat (Bailey et al. 2004a, Nafus et al. 2017), which can result in biased abundance and habitat-use estimates. Therefore, estimating detection probabilities for species in a variety of habitats is necessary to account for such biases. Additionally, understanding where and how the detection fraction is obtained may be equally important not only to correct for habitat-specific detection effects, but also to improve survey designs for cryptic species.

Failure to detect the target species when present during visual surveys results in imperfect detection and leads to underestimating distribution or abundance (Buckland et al. 2001, Gu and Swihart 2004, Ruiz-Gutierrez and Zipkin 2011). However, the detection process can be broken into two distinct components and failures in either of these can yield imperfect detection. First, the subject must be physically available for detection. For visual surveys, this means the subject is not hidden, for example, in vegetation, underground, or underwater. Failure to account for the fraction of subjects physically unavailable for detection results in availability biases (Marsh and Sinclair 1989). Availability bias should be tightly associated with an organism’s activity patterns, habitat use, and antipredator strategies among others (Bailey et al. 2004b, Smolensky and Fitzgerald 2010). Second, once available, the subject must be seen (or heard) by the observer. Failure to observe subjects that are available for detection results in perception or visibility biases (Marsh and Sinclair 1989). For species with secretive habits, such as reptiles and amphibians, availability biases may be especially variable (Smolensky and Fitzgerald 2010), but both perception and availability biases are likely quite common.

Researchers have dealt with potential biases in visual surveys by adjusting detection probabilities with correction factors generated from such methods as occupancy, mark-recapture, and double-observer counts (e.g., Nichols et al. 2000, Nolte et al. 2016). However, more often these methods address perception and not availability biases (Pollock and Kendall 1987, Marsh and Sinclair 1989, Smolensky and Fitzgerald 2010). Correction factors based on radiotelemetry or direct, continuous observations of animal behavior have been used to address availability bias by accounting for subjects that are inactive during surveys (Laake et al. 1997, Hounsome et al. 2005, Thomson et al. 2012, Sucunza et al. 2018). This method might be most suitable for species with large physiological demands that must be met with regular activity, such as endotherms (Schmidt-Nielsen 1990) and air-breathing aquatic animals that must surface for air (Thomson et al. 2012, Heide-Jorgensen and Laidre 2015). In contrast, reptiles and amphibians have low energetic demands (Pough 1983), exhibit unpredictable activity patterns (Turner 1977, Dunham 1981), and frequently forgo activity to avoid predation, referred to as submergent behavior (Maiorana 1976, Siers et al. 2018). Therefore, to account for detection bias in cryptic species we must validate visual surveys using independent methods (e.g., total removal plots: Rodda et al. 2001, Rodda and Campbell 2002) and we must obtain direct knowledge of where and when subjects become unavailable for detection.

The brown tree snake (Boiga irregularis, hereafter BTS) is a rear-fanged, semiarboreal colubrid snake native to the AustraloPapuan region that preys upon a variety of vertebrates including frogs, lizards, birds, and mammals (Savidge 1988, Rodda et al. 1999b). BTS were accidentally introduced to the U.S. territory of Guam around the time of WWII, with profound ecological and economic consequences including extirpation of least 15 vertebrates, millions of dollars of infrastructure damage, and human envenomations (Fritts et al. 1987, Savidge 1987, Wiles 1987a, Fritts and Rodda 1998, Fritts and McCoid 1999). The primary management objectives for BTS on Guam include minimizing the likelihood of
accidental transport of BTS to other islands in the Pacific (Stanford and Rodda 2007) as well as suppression of BTS populations at landscape scales to facilitate restoration of native species and ecosystem function (Siers et al. 2014, Bts 2015).

Visual surveys (Guyer and Donnelly 2012) are frequently used methods to control and manage BTS on Guam and have been used to reliably estimate BTS presence, relative abundance, and, in combination with mark–recapture, population sizes (Rodda et al. 1999c, 2007). In contrast to snake trapping, the other major control tool used to manage this species, visual surveys have been shown to effectively sample BTS of all sizes (Rodda et al. 2007) and progress has been made to identify potential perception biases (Lardner et al. 2007, 2009, Christy et al. 2010). Availability bias affecting visual surveys has been relatively unexplored in part due to the difficulty in obtaining such data; however, both have been shown to be an important source of bias for another cryptic reptile (Allison and McLuckie 2018).

The primary aim of this study was to identify factors that drive BTS detection availability during visual surveys, specifically focusing on perch heights and microhabitats used. Secondarily, previous visual surveys for BTS on Guam were conducted on high-density populations; yet, early detection of incipient populations on islands other than Guam will undoubtedly occur in low-density populations. Because low-density populations generally have reduced detection probabilities (Royle and Nichols 2003, Tanadini and Schmidt 2011), we also aimed to determine the efficacy of visual surveys in a low-density BTS population. To accomplish these goals, we simultaneously conducted radiotelemetry and visual surveys in a suppressed population of BTS on Guam. This population was suppressed with a series of aerially delivered snake toxicants over the course of 16 months prior to our study (Dorr et al. 2016). By conducting visual surveys and radiotelemetry concurrently, our experimental design allowed us to test for both perception and availability bias in visual surveys for BTS. Knowledge of the precise location of a subset of telemetered and visually detected snakes, we identify microhabitats that could be targeted during BTS management activities and suggest ways to improve visual surveys for this and other cryptic species.

**METHODS**

**Study site**

We conducted our study between 22 March 2010 and 28 September 2015 in the 55-hectare Habitat Management Unit (HMU), located on Andersen Air Force Base on the northern end of the island of Guam (13.596 N, 144.865 E). The HMU consists of a disturbed limestone forest completely enclosed with a 1.8 m high chain-link style fence covered with 6-mm galvanized steel mesh. An overhang (aka bulge) in the mesh was created at a height of 1.2 m on the outside surface of the fence preventing snake immigration but allowing emigration from the HMU (Perry et al. 1998). Ten forest interior transects (forest present on both sides of the transect) and eight forest edge transects (forest on one side and fence on the other side) were established inside the fence to provide ease in navigating during nighttime surveys and radio tracking (Fig. 1). Interior transects were approximately 125 m apart.

Recently, the U.S. Department of Agriculture developed a system to aerially deliver toxic baits to BTS. The selected toxicant, acetaminophen, is delivered attached to a dead juvenile mouse, with an attached paper streamer to increase the likelihood that baits will become entangled in the tree canopy and available to foraging snakes (Clark et al. 2018). Aerial toxicant delivery has the objective of suppressing or eradicating snake populations at landscape scales on Guam, which has not been achievable using previous control tools. The HMU was subjected to aerial application of toxic baits between 3 September 2013 and 19 December 2014. During each of eight applications, 1,980 baits were dropped, for a total of 15,840 baits dropped over 16 months (Dorr et al. 2016).

**Visual surveys**

We conducted nocturnal visual surveys (one to four times per week) from 19:00 to 24:00 h before (May 2010–October 2010 and March 2013–August 2013) and during (April 2014–June 2014
and November 2014–December 2014) toxicant applications within the HMU. After toxicant deliveries had been completed, we performed nocturnal visual surveys from 01 June to 06 August 2015, four times per week (39 total search nights; see Table 1 for summary of search effort). Using headlamps and working in teams of two, four biologists conducted nightly searches along the 18 transects (total of 5.28 km/night [11.7 h/night] across both teams). Surveys began no earlier than 30 min after civil twilight. Each crew of four biologists searched randomly assigned transects with equal time devoted to interior and edge transects. Each biologist searched one side of each transect.

We captured all snakes within reach during visual surveys and recorded capture locations using handheld GPS units (Garmin 60CSx, ±5 m accuracy). We recorded snout–vent length (SVL; mm) by gently stretching snakes along an outstretched tape measure, mass (g) using Pesola spring scales, and sex by probing for hemipenes. We uniquely marked each snake via scale clipping and injection of a passive integrated transponder tag and palpated to check for the presence of prey in the gut. We calculated the catch per unit effort (CPUE) for our visual surveys before, during, and after toxicant delivery. Catch per unit effort is defined as the total number of BTS captured per person-hour of survey effort.

At each snake capture, we recorded perch type, vertical height, and relevant behaviors. Perch type included the plant species on which the snake was found as well as other substrates such as ground, rocks, or dead logs. Vertical height was visually estimated to the nearest 0.5 m. Snakes detected on the ground received a vertical height score of zero. After processing, all snakes were released at their point of capture.

**Radiotelemetry**

Radiotelemetry was initiated approximately 5 months after the last toxicant drop, with sampling occurring for four months (31 May–28 September 2015). Snakes large enough for transmitter implantation (>76 g) were trapped in the
HMU using standard USGS BTS traps baited with live mice (Rodda et al. 1999a). We deployed 150 traps for 27 d; this resulted in 1861 interior and 1849 edge transect trap nights after accounting for some trapping interruptions due to typhoons and tropical storms. Traps were checked daily, and mouse food and water were replenished as necessary. Due to low population density of BTS in the HMU after toxicant application, we supplemented trapping with nocturnal visual surveys conducted both inside and outside the HMU between 20 May and 28 May 2015 to attain our desired sample size for radiotelemetry (N = 20).

Snakes selected for transmitter implantation were transported to a climate-controlled facility at the Guam National Wildlife Refuge and held in individual cages with water provided ad libitum. Snakes held for more than five days were offered a small, pre-killed mouse equivalent to 10% of the snake’s body mass every 5 d. No snake was fed in the seven days prior to or after transmitter implantation. Surgical implantation of 3.8 g Holohil PD-2 transmitters (Holohil Systems, Canada) was performed by a local veterinarian and generally followed the procedures of Reinert and Cundall (1982). All snakes were >900 mm in SVL, and transmitters were <5% of the snake’s body mass. Snakes were released 2–3 d post-surgery. Habitat Management Unit-resident snakes were released at their point of capture, and translocated snakes were released near the center of the HMU.

Using radio receivers (Communications Specialists, R-1000) and directional antennas (Telonics, 2-element H-style), a crew of four biologists worked in pairs to locate each telemetered snake at least once during each night. Snakes were tracked between 1900 and 24:00 h, 4 times per week (31 May–06 August 2015; 648 relocations) and then 2 times per week for an additional 7 weeks (10 August–28 September 2015; an additional 322 relocations). We attempted to locate snakes visually (active snakes) or obtain locations within two meters (inactive snakes) of their actual position, taking care to avoid disturbing animals. At each snake location, we recorded the same environmental and behavioral data that were recorded during visual surveys (above). In contrast to visual surveys, radiotelemetry allowed us to locate snakes that were not visible. For not visible snakes, both biologists independently estimated the snake’s position using triangulation and all snakes detected belowground were assigned a vertical height of ~1 m.

At the end of the study, we removed and euthanized telemetered snakes. We calculated body condition for telemetered snakes at the time of transmitter implantation and then again for those recovered at the end of the study (16 of 20). We followed previous authors in calculating a condition index (CI) as the ratio of snake mass to the snake's expected mass given its length; expected mass was estimated from mass × SVL regression based on more than 10,000 snakes sampled throughout Guam (Christy et al. 2010).

Table 1. Summary of brown tree snake (Boiga irregularis) capture data from the Habitat Management Unit (HMU) during visual surveys conducted before, during, and after aerial toxicant delivery.

<table>
<thead>
<tr>
<th>Time period</th>
<th>Edge/interior</th>
<th>Searcher nights</th>
<th>Searcher distance (km)</th>
<th>Searcher hours</th>
<th>Total snakes captured</th>
<th>Total snakes captured &gt;900 mm</th>
<th>CPUE all snakes</th>
<th>CPUE snakes &gt;900 mm</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pre-toxicant drop†</td>
<td>Edge</td>
<td>132</td>
<td>138.83</td>
<td>284.8</td>
<td>258</td>
<td>72</td>
<td>0.906</td>
<td>0.253</td>
</tr>
<tr>
<td></td>
<td>Interior</td>
<td>119</td>
<td>116.04</td>
<td>290.5</td>
<td>144</td>
<td>70</td>
<td>0.496</td>
<td>0.241</td>
</tr>
<tr>
<td>During toxicant drop‡</td>
<td>Edge</td>
<td>81</td>
<td>117.14</td>
<td>293.0</td>
<td>168</td>
<td>13</td>
<td>0.573</td>
<td>0.044</td>
</tr>
<tr>
<td></td>
<td>Interior</td>
<td>124</td>
<td>175.59</td>
<td>439.7</td>
<td>70</td>
<td>25</td>
<td>0.159</td>
<td>0.057</td>
</tr>
<tr>
<td>Post-toxicant drop§</td>
<td>Edge</td>
<td>80</td>
<td>67.035</td>
<td>152.4</td>
<td>65</td>
<td>9</td>
<td>0.427</td>
<td>0.059</td>
</tr>
<tr>
<td></td>
<td>Interior</td>
<td>154</td>
<td>133.662</td>
<td>303.8</td>
<td>48</td>
<td>15</td>
<td>0.158</td>
<td>0.049</td>
</tr>
</tbody>
</table>

Notes: Total snakes captured include previously marked plus unmarked snakes. Catch per unit effort (CPUE) is defined as the number of BTS captured (marked and unmarked)/survey-person hour.
† 18 May 10–28 October 10 and 26 March 13–13 August 13 (visual survey data collected under the direction of S.R. Siers and P.E. Klug, respectively).
‡ 21 April 14–10 June 14 and 18 November 14–05 February 15.
§ 01 June 15–06 August 15.
Data analysis

To assess the ability of visual searchers to detect snakes at low population densities (20 telemetered snakes in a 55-ha area or 0.4 BTS/ha), we calculated an encounter rate for our telemetered snakes. For each evening on which both visual surveys and radiotelemetry were conducted, we defined a detection buffer around surveyed transects. In staged surveys using dead snakes, detection rates were 10% or less at distances of 5 m perpendicular to the transect (Lardner et al. 2007). Therefore, we defined the detection buffer as a rectangular cuboid, centered on the transect, with a width of 12.5 m (5 m on either side + 2.5 m for transect width). We chose a maximum vertical limit of 15 m, which was the maximum height of any observed telemetered snakes.

To explore the effectiveness of visual surveys to predict areas of high use, we used kernel density estimation (KDE) to estimate utilization distributions for radiotelemetered or visually detected animals (Kernohan et al. 2001). Kernel density estimation is a nonparametric neighborhood-based smoothing function that can be used to identify hot spots or areas with high use, biomass, or abundance for wildlife (Nelson and Boots 2008). Hot spots were based on BTS coordinates in the Universal Transverse Mercator projected coordinate system, North American Datum 1983 Zone 55 from telemetry and visual survey data. We used a quadratic kernel density function to fit a smooth curve over each data point in ArcGIS 10.3.1 (ESRI 2017), using the default values for the Kernel Density Tool. The output raster was constrained to calculating cells in which a BTS could occur based on detections within the HMU barriers. Once the output raster was produced, we used natural breaks (Jenks) to divide the telemetry-based KDE into five density levels/thresholds. The calculation was repeated for each of the five thresholds: 0 = absent/unused, 1 = low probability of use, 2 = low-to-moderate probability of use, 3 = moderate-to-high probability of use, and 4 = high probability of use. Visual survey KDE was manually classified into five density thresholds based on values decided by natural breaks identified from telemetry. We used the KDE categories to calculate spatial overlap between telemetry and visual survey hot spots to identify extent of spatial overlap.

To understand how vertical height may have affected our ability to detect snakes, we first generated three-dimensional scatterplots of vertical height for visually detected snakes of all sizes and for telemetered snakes within the HMU (x = northing, y = easting, z = vertical height). However, because we detected so few of our telemetered snakes during visual surveys, we were prevented from modeling encounter rates as a function of snake height to test the role of vertical height in generating perception bias during visual surveys. Rather, we compared the frequency distributions of vertical heights for snakes detected during visual surveys and only those telemetered snakes that were visible. Rodda and Reed (2007) found that the tendency to use arboreal habitats was related to snake body size, with smaller BTS (<1000 mm TL) overwhelmingly found in trees. However, all our telemetered snakes were larger than 900 mm SVL due to transmitter size constraints. Thus, for this analysis and some of the direct comparisons of habitat use below, we ran comparisons using snakes >900 mm SVL from our visual survey dataset to ensure vertical height differences were not an artifact of body size differences between telemetered and visually surveyed snakes. We tested distributions for normality with a Shapiro-Wilk test and calculated skewness coefficients. We considered distributions significantly skewed if the absolute value of skewness divided by its standard error was >2 (sensu Reed and Boback 2002). To explore the role of vertical height in generating availability bias, we compared frequency distributions for visible and not visible telemetered snakes. Finally, we compared mean vertical heights between our groups using a linear mixed-effect model (using lme in the nlme package in R) and accounted for repeated measures by incorporating subject as a random effect. Because underground snakes were arbitrarily assigned vertical heights of −1 and were not considered available to sample on a visual survey, we eliminated these locations from our radiotelemetry data for the mixed-effect model.
To understand the influence of perch type on detection frequency, we compared perch type between visually detected snakes and telemetry snake locations. We analyzed the seven most frequently used perch types with Fisher’s exact test. The large number of comparisons prevented us from calculating an exact P-value; instead, we estimated a P-value using Monte Carlo estimation with 1000 replicates (Senchaudhuri et al. 1995). Lastly, to test how these microhabitats might have contributed to availability bias during visual surveys, we examined the effect of perch type and vertical height on visibility of telemetered snakes. Visibility was modeled as a binomial response variable (visible or not visible) in a generalized linear mixed model (using the glmer function in R). The main fixed effect was perch type with three levels: broad-leaved plants (Aglaia mariannensis, Ficus sp., Guamia mariannae, Hibiscus tiliaceus, Morinda citrifolia, Neisosperma oppositifolia, and Vitex parviflora), ferns (terrestrial and epiphytic ferns, e.g., Asplenium sp.), and Pandanus tectorius (a midstory tree with long [90–150 cm], spiny leaves spirally arranged in dense clusters at the ends of branches). Although a small proportion of snakes also used several vine species as perches (<2% of telemetered snakes, <1% of visual survey snakes), these data were omitted due to problems with model convergence resulting from small sample sizes. Vertical height was added to the model first as an interactive effect with perch type and then as an additive effect. Subject was included as a random term to account for repeated measures, and we employed the nonlinear optimizer bobyqa.

All statistical tests were performed in R (version 3.4.0; R Development Core Team 2017) using the following packages: moments, dplyr, lme4, magick, nlme, plot3D, plot3Drgl, and rgl. Additional spatial analyses were performed in ArcGIS 10.3.1 (ESRI 2017) and included kernel density estimation (KDE) within the Spatial Analyst Toolbox. Dispersion about means is indicated with ± 1 SD unless otherwise indicated, and α was set at 0.05 for all tests.

**RESULTS**

**Telemetry summary**

We radiotracked 20 BTS (seven males: 1274 ± 306 mm SVL and 388.5 ± 367 g, 13 females: 1051 ± 97 mm SVL and 168.5 ± 87 g) during the study. Due to variation in battery life and occasional snake mortality, periods of tracking ranged from 52 to 142 d per individual (mean = 107 ± 24 d) and 25 to 61 relocations (mean = 48 ± 9) resulting in 970 total relocations. We lumped translocated (n = 7) and resident (n = 13) snakes together in subsequent analyses because preliminary comparisons indicated no major differences in space use or detection probabilities between these groups. Additionally, the body condition of telemetered snakes did not deteriorate during the study. Rather, the condition of telemetered snakes was greater at the end of the study relative to that at implantation (mean CIstart = 1.4 ± 0.3, mean CIend = 1.9 ± 0.5, T = −4.2, P < 0.001).

**Changes in BTS abundance pre- and post-toxicant application**

Visual survey results showed that CPUE for BTS of all sizes dropped by 58% after initiation of toxicant applications in late 2013 and dropped an additional 15% after completion of all eight toxicant drops (Table 1). For medium to large snakes (>900 mm), CPUE dropped by 82% after initiating toxicant applications and stayed at similarly low levels during the current study (Table 1). We conclude that low rates of visual detections in the HMU during this study were the result of the aerial toxicant applications.

**Detection of BTS at low densities**

Twenty telemetered snakes provided a known BTS population equating to 0.4 marked BTS/ha. Telemetered snakes were visible to telemetry teams on roughly 45% (431/966) of relocations (Table 2). Of the 648 relocations that occurred concurrent with our visual surveys, 87 (13%) were within our defined detection buffer on the same night a visual survey was conducted. Of those 87 potential encounters, visual survey teams detected a single telemetered snake and required 323 survey hours before that detection was achieved. If encounter rates remained consistent across time, and visual survey teams used the same transect spacing, approximately 6,460 survey hours would have been required to detect all 20 telemetered snakes.
Space use predicted by visual surveys and radiotelemetry

Visual surveys and radiotelemetry predicted divergent patterns of snake hot spots across the study site. During visual surveys, edge transects yielded higher CPUE relative to interior transects throughout the toxicant application (pre-toxicant, during, and post-toxicant) and for all size classes of snakes (Fig. 1; Table 1). The exception was for large snakes during the toxicant application period, during which CPUE tended to be higher for interior compared with edge transects based on raw numbers (Table 1). As a result, KDE from visually detected snakes predicted that the majority (if not entirety) of the HMU should be occupied and that hot spots occur primarily along the forest edge (Fig. 2A). In contrast, KDE thresholds based on telemetry relocations suggested that tracked snakes had the greatest activity near, but not on, forest edges (Fig. 2B).

Kernel density estimation results based on visual survey positions predicted larger areas for all density thresholds than did KDE based on telemetry relocations (Table 3). KDE thresholds based on visual survey data also encompassed the bulk of the area predicted to be used by telemetered snakes (Fig. 2). However, overlap of high-use regions based on telemetry and visual surveys was relatively low (Fig. 2C). For instance, density thresholds with moderate-to-high probability of use (3) and high probability of use (4) overlapped by <1 ha each (Table 3) between telemetry and visual survey positions indicating predicted areas of high use differed between methods.

Three-dimensional plots of snake locations

Relative to locations of visually detected snakes, telemetered snake locations encompassed a greater range of vertical space within the forest (Fig. 3 and supplemental Video S1). Telemetered snakes had standard deviations for vertical height that were twice those of visually detected snakes (Table 2). Using a mixed-effect model, we found that average vertical height was greater for telemetered (mean = 2.9 ± 2.6 m) than visually detected snakes (mean = 2.0 ± 1.2 m; df = 44, t = −2.59, P = 0.013).

Effect of vertical height on snake visibility

The frequency distribution of vertical heights for snakes visible during telemetry was nonnormal (W = 0.890; P < 0.001) and significantly right-skewed (skewness = 1.40375, SE = 0.111; Fig. 4A). The frequency distribution of vertical height for snakes captured during visual surveys, restricted to those with body lengths comparable to telemetered snakes (>900 mm), was similar in shape: nonnormal (W = 0.928; P < 0.001) and right-skewed but skewness was nonsignificant for visual survey data (skewness = 0.795, SE = 0.155; Fig. 4A). The difference between the two distributions was the location of the primary and secondary modes. The primary mode for the visual survey vertical heights was between 2 and 3 m with a secondary mode between 0 and 1 m. In contrast, the primary mode for visible telemetered snakes was between 0 and 1 m and a secondary mode between 2 and 3 m (Fig. 4A). A comparison of vertical height distributions using a larger dataset of visual surveys (pre-toxicant, during, and post-toxicant combined) revealed nearly identical shapes between telemetry and visual surveys (Fig. 4B) suggesting that the differences in mode location could in part be due to the smaller sample of our post-toxicant visual survey.

The effect of vertical height on snake visibility was also evident from the telemetry dataset. Vertical height distributions for visible and all telemetry relocations (visible plus not visible) were similarly right-skewed, but the proportion of telemetered snakes visible to biologists varied by height. About half (48%, 119/250 observations) of telemetered snakes detected at or near ground level (0–1 m) were visible to biologists.

Table 2. Comparison of vertical heights (means ± SD) and microhabitat use (% of observations) for radiotelemetered and visually encountered brown tree snakes (Boiga irregularis) in the Habitat Management Unit (HMU).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Telemetry</th>
<th>Visual surveys (only snakes &gt;900 mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vertical height (m)</td>
<td>2.9 ± 2.6</td>
<td>2.0 ± 1.2</td>
</tr>
<tr>
<td>% underground</td>
<td>9% (91/966)</td>
<td>0 (0/25)</td>
</tr>
<tr>
<td>% on ground</td>
<td>14% (134/966)</td>
<td>4% (1/25)</td>
</tr>
<tr>
<td>% arboreal</td>
<td>77% (741/966)</td>
<td>96% (24/25)</td>
</tr>
<tr>
<td>Percent visible</td>
<td>45% (431/966)</td>
<td></td>
</tr>
</tbody>
</table>
The highest proportion of snakes were visible in the 1–2 m height range (1–2 m: 90%), but visibility declined with increasing height (2–3 m: 65%, 3–4 m: 54%, 4–5 m: 41%, 5–6 m: 34%, 6–7 m: 17%; Fig. 5). The highest proportion of snakes were visible in the 1–2 m height range (1–2 m: 90%), but visibility declined with increasing height (2–3 m: 65%, 3–4 m: 54%, 4–5 m: 41%, 5–6 m: 34%, 6–7 m: 17%; Fig. 5).

**Effect of perch type on snake visibility**

We found a strong influence of perch type on the proportion of snakes detected using telemetry (visible and not visible) and those found during visual surveys (Fisher’s exact test; $P < 0.001$). Telemetered snakes were detected most frequently in *Guamia* trees followed by epiphytic plants, *Pandanus* trees, terrestrial ferns, underground, on the ground, and in *Vitex* trees (Table 4). Snakes encountered during visual surveys were also frequently found in *Guamia* trees, on the ground, and in *Vitex* trees. However, during visual surveys, snakes were infrequently found (<5% of the time) in *Pandanus* trees and terrestrial ferns, and snakes were never visually detected in epiphytes or underground despite these two perch types accounting for more than 27% of all telemetered snake locations.

An examination of telemetered snake data revealed that BTS were frequently visible to biologists in *Guamia* (83% of observations) and in *Vitex* (57% of observations) trees even though these perch types were relatively high in the forest canopy (average vertical height of snakes in *Guamia* = 3.3 m, in *Vitex* = 5.0 m; Table 4). Comparatively, snakes seeking refuge in another canopy microhabitat, epiphytic ferns (mean = 4.9 m; Table 4), were rarely visible (14% of snakes in epiphytic ferns were visible). Visibility of snakes using lower strata of the forest structure also varied with perch type. Telemetered BTS on the ground were visible 64% of the
time, yet those detected underground and in terrestrial ferns were visible less frequently (underground = 4%, terrestrial ferns = 32%). Therefore, although BTS became less visible when perched higher in the canopy or underground, visibility was also influenced by perch type.

Using generalized linear mixed models, we found a significant effect of perch type on visibility ($Z = 9.2$, $P < 0.001$) and that visibility was greater when snakes were located on broad-leaf plants (e.g., *Guamia mariannae*, *Neisosperma oppositifolia*, and *Vitex parviflora*) relative to ferns ($Z = -12.2$, $P < 0.001$) and *Pandanus* trees ($Z = -6.6$, $P < 0.001$). Lastly, there was an additive effect of vertical height on snake visibility ($Z = -5.8$, $P < 0.001$). Thus, although the statistical model did not support a significant interactive effect of perch type and height, both height and perch type had significant effects on visibility.

**DISCUSSION**

This study demonstrated that visual surveys could detect BTS presence at low densities after toxicant application and could detect BTS presence even at a simulated lower density of 0.4 snakes/ha with sufficient search effort. However, our results also demonstrate the limits of such surveys. By documenting the precise locations of a subset of snakes using radiotelemetry, we showed that visual surveys inaccurately predicted areas of high use and how such surveys suffer from both perception and availability biases. Importantly, we identified the relative influence of vertical position and refuge type used by snakes in creating such biases. Thus, our results clarify where our detection fraction is obtained during BTS visual surveys and identifies fruitful areas for improving visual survey design.

Complete eradication of invasive species is challenging regardless of the target, but has unique challenges for cryptic, secretive species. For many, if not all species, removal of the very last female from the population is necessary for successful eradication, a challenging and expensive endeavor (Kendrot 2004, Russell et al. 2005). Prior research on behavioral and environmental factors affecting visual detection of BTS on Guam was conducted at densities of 23–33 snakes per hectare (Rodda et al. 1999c, Christy et al. 2010). Thus, the current study was designed, in part, to address visual survey efficacy at lower densities. Although we did not attempt to directly estimate snake density, CPUE of BTS decreased by 79% for medium to large (>900 mm) individuals after toxicant applications, indicating suppression of snakes in the HMU. Visual survey teams were successful in detecting BTS at this lower density and, with extensive effort, detected a snake at a
Fig. 4. Frequency distribution of vertical heights for (A) all visually detected brown tree snakes (*Boiga irregularis*) >900 mm snout–vent length captured after aerial toxicant delivery (gray bars; see Table 1) as compared to radiotelemetered brown tree snakes (black bars). Visually detected snakes >900 mm captured during the same time as the radiotelemetry are inset (white bars) within the gray bars. Distributions of vertical heights using (B) a larger dataset of visually detected brown tree snakes (>900 mm, pre-, during, and post-toxicant combined; gray bars; see Table 1) compared with radiotelemetry brown tree snakes (black bars).
simulated density of 0.4 snakes/ha. The intensive sampling effort required to detect BTS at the simulated low density of 0.4 snakes/ha is commensurate with recent modeling exercises. For example, our visual survey team detected the first and only telemetered snake on 15 July 2015 after completing 142 km of transects. Using recent models developed to infer the amount of search effort required to detect BTS at varying densities, and assuming a hypothetical population of BTS at a density of 0.5 snakes/ha with a detection probability of 0.07, visual survey teams should have a 93.5% chance of detecting any snake after visually surveying 95.04 km of transects and a 99.6% chance after surveying 190.08 km of transects (Yackel Adams et al. 2018). Thus, our results are the first to confirm these modeling estimates and support the effectiveness of visual surveys to obtain information on population demographics, occupancy, rate of expansion, and general habitat use.

Table 4. Height (means ± SD) and frequency (% of observations) of perch types used by brown tree snakes (Boiga irregularis) during radiotelemetry (visible + not visible) and visual surveys (only snakes >900 mm snout–vent length) conducted within the Habitat Management Unit (HMU).

<table>
<thead>
<tr>
<th>Perch type</th>
<th>Telemetry (all)</th>
<th>Visual surveys</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Height (m)</td>
<td>Frequency</td>
</tr>
<tr>
<td>Guamia mariannae</td>
<td>3.3 ± 1.5</td>
<td>0.183</td>
</tr>
<tr>
<td>Epiphytes</td>
<td>4.9 ± 2.2</td>
<td>0.178</td>
</tr>
<tr>
<td>Pandanus tectorius</td>
<td>4.4 ± 2.3</td>
<td>0.166</td>
</tr>
<tr>
<td>Terrestrial ferns</td>
<td>0.4 ± 0.4</td>
<td>0.144</td>
</tr>
<tr>
<td>Underground</td>
<td>–1</td>
<td>0.096</td>
</tr>
<tr>
<td>Ground</td>
<td>0.01 ± 0.3</td>
<td>0.089</td>
</tr>
<tr>
<td>Vitex parviflora</td>
<td>5.0 ± 3.5</td>
<td>0.051</td>
</tr>
<tr>
<td>Log</td>
<td>0.5 ± 0.4</td>
<td>0.032</td>
</tr>
<tr>
<td>Vine</td>
<td>1.8 ± 1.0</td>
<td>0.018</td>
</tr>
<tr>
<td>Other</td>
<td>0.043</td>
<td></td>
</tr>
</tbody>
</table>

*Note:* Ellipses indicate no snakes were encountered in these microhabitats using visual surveys.
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helped to reveal where and when our visual surveyors missed snakes. Telemetry data are requisite for ensuring detection of individuals irrespective of their visibility or activity, yet smaller numbers of sampled individuals and temporal autocorrelation between detections create separate challenges in interpreting such data. Thus, although our methods have some limitations, including the assumption that telemetered snakes are representative of population-level behaviors (Millspaugh et al. 2012), our data suggest that snake behavior and microhabitat use introduce important sources of detection error during visual surveys. We found that visual surveyors detected snakes in a much narrower vertical space range than used by our telemetered snakes, likely because visibility decreased with height of the snakes’ perch. Visual confirmations were similarly less frequent for telemetered snakes when perched higher in the canopy and the greatest number of snakes encountered during both telemetry and visual surveys were in the lowest forest strata, between 0 and 1 m; the latter is consistent with previous findings (Rodda and Reed 2007). However, less than half of our telemetered snakes in this zone were visible compared with 90% of snakes located at the next higher zone: 1–2 m. Thus, while vertical height is likely contributing to perception bias, the low proportion of telemetered snakes visible in terrestrial ferns suggests snakes ensconced in this vegetation type may be largely unavailable to visual survey teams and explains the low visibility of all telemetered snakes below 1 m. For cryptic arboreal species, estimating the fraction of the population that is too high to detect is likely as important as estimating the fraction of the population that is inactive and therefore unavailable to sample. BTS using other vegetative cover (epiphytic ferns and Pandanus tectorius trees) may also be unavailable during visual surveys. For instance, more than 30% of all telemetered snake relocations were in Pandanus and ferns combined, yet these two perch types accounted for just over 8% of snakes encountered during visual surveys. While distance and vegetative interference likely combine to influence our ability to visually detect BTS, reduced activity of snakes in these microhabitats could have contributed to low snake sightings. For instance, recently fed BTS dramatically reduce their activity and tend to perch higher in the canopy for up to a week following consumption of large prey (Siers et al. 2018). Therefore, snakes located high in the canopy may have sought refuge within microhabitats conducive to digestion or periods of reduced activity (Peterson et al. 1993, Hetherington et al. 2008). Thus, for this and other cryptic species with extended periods of dormancy, estimating the fraction of individuals available for detection during a given survey is critical for reducing bias (Allison and McLuckie 2018).

The tendency for telemetered BTS to make extensive use of densely foliated, thin-leaved plants such as Pandanus has been previously noted (Santana-Bendix 1994, Tobin et al. 1999, Hetherington et al. 2008), despite the fact that Pandanus often represents a small fraction of Guam’s forests (Hetherington et al. 2008). Pandanus crowns may be a preferred microhabitat for a variety of reasons including protection from predators, thermoregulation (Hetherington et al. 2008), water balance due to accumulation of water in leaf axils (Lillywhite and Henderson 1993), and elevated basking opportunities within the forest (Anderson et al. 2005). Pandanus sp. (in combination with banana leaves) is also a preferred habitat for some gecko species on other Pacific islands (Wiles et al. 1990); thus, these perch types may also represent high-quality foraging habitat for BTS. When a false negative carries a high cost, destructive sampling of high-use resources such as Pandanus that also have relatively low occurrence on the landscape may increase the confidence that failure to detect individuals is indicative of true absence.

Our visual surveys failed to detect snakes underground, yet 9% of our telemetered snake relocations were underground, a finding consistent with other radiotelemetry studies of BTS (Santana-Bendix 1994: 7, % underground; Hetherington et al. 2008: 3.2, % underground). Even more concerning, our surveys occurred during the transition between dry and wet seasons and evidence from other studies indicates that BTS may increase their use of underground refugia during the dry season. During extremely dry weather in March and April, Wiles (1987b) tracked two BTS for 25 and 21 d, respectively. During daytime and nighttime tracking occasions, both snakes used underground refugia for a large proportion of time: 30% for one and 90%
for the other. Visual surveys conducted during the wet season may therefore be more likely to detect surface-active snakes. Seasonal effects on spatial distribution and detection probabilities of the target species (e.g., Kery 2002, Bailey et al. 2004a, Cubaynes et al. 2010, Ehnes et al. 2018) can thus be especially important to consider when the goal is habitat characterization of at-risk species, early detection of a new invader, or during attempts at eradication.

Among other factors that can influence detection, spatial variation in density/abundance should be positively correlated with detectability (McCarthy et al. 2013). Through KDE, we found that visual surveys and telemetry were not concordant in predicting areas of high use by BTS and visual surveys failed to detect the heaviest used area in the HMU. Although this hot spot was bisected by an established transect, visual surveys failed to detect these telemetered snakes. One potential reason for this is that the telemetered animals represented a unique subset of the population and telemetered and non-telemetered snakes would not be anticipated to be found in the same locations. However, BTS have not been documented to be territorial (Rodda et al. 1999b), have high site fidelity (Santana-Bendix 1994, Clark 1998, Tobin et al. 1999), or any other qualities that would preclude us from assuming telemetered BTS were reflective of population-level behavior.

The need for methods to account for habitat-specific detection can be further highlighted by the difference in captures of snakes on edge vs. interior forest transects. From a 2-dimensional perspective, the KDEs based on visual survey captures indicated that the perimeter of the HMU was the only heavily used area. Visual surveyors captured more snakes in less time on edge transects compared with interior transects, and this was consistent across time (before, during, and after toxicant application). Indeed, this finding is also consistent with previous work demonstrating that relative to interior forest, BTS had higher detection rates in forest edges along roadsides (Rodda and Fritts 1992). In contrast, radiotelemetry-based estimates indicated a single interior location was used more than any edge locations. We see at least two possible hypotheses to explain high rates of capture along edge transects (i.e., an edge effect, Murcia 1995) during visual surveys. First, snakes may use forest edge more frequently than interior forest, perhaps because when they encounter edges, they are reluctant to enter treeless space bordering the edge and move along it instead—a drift fence-like effect for forest edges. Alternatively, snakes may be attracted to forest edge more than interior forest due to greater availability of prey that may be responding to increased plant growth/productivity in these microhabitats (Williams-Linera 1990, Chen et al. 1992). Evidence from other vertebrate predators, including snakes, supports the existence of an edge effect (Bider 1968, Durner and Gates 1993, Gehring andSwihart 2003, Salek et al. 2010). However, our telemetered snakes did not appear to make foraging movements toward the barrier edge, if they did not have activity areas that occurred along edge habitats (S. M. Boback et al., unpublished manuscript). Second, BTS may be captured at higher rates on edge transects because they have higher detection probabilities on edges. A recent study investigating BTS movements near roadways found the majority of snake movements were parallel to road edges (Siers et al. 2014). Snakes on the edge of the HMU that moved parallel to and concurrent with visual surveyors would have a greater probability of detection; edge snakes may be within surveyors’ detection buffers for greater amounts of time relative to snakes on interior transects that move randomly with respect to the transect. Additional field tests would be necessary to distinguish between these competing hypotheses to explain the higher CPUE for snakes encountered on edge transects. Importantly, edge surveys are frequently used to inventory herpetofauna, especially in densely vegetated habitats (Foster 2012). Habitat suitability estimates that incorporate such surveys may be extremely biased if edge detections are not parameterized differently from interior habitat detections.

CONCLUSIONS

Overall, our results suggest that applying visual surveys for cryptic species can be effective but requires knowledge of how to minimize perception (e.g., Christy et al. 2010) and availability bias. Identifying microhabitats that pose the greatest potential for availability bias such as
specific habitat types (densely foliated plants such as Pandanus, epiphytic, and terrestrial ferns) and locations (edge vs. interior forest) can identify resources to manipulate or target for management purposes. Moreover, integration of visual surveys with radiotelemetry holds promise for improving our overall understanding of availability bias in such surveys and how environmental features influence our ability to estimate fundamental ecological parameters including abundance, density, and resource use (Franco et al. 2004, Linden et al. 2018).

Acknowledgments

The following individuals were instrumental in collecting data in the field: P. Barnhart, J. Capano, M. Cook, K. Donmoyer, F. Erickson, A. Gavel, G. Haddock, T. Hinkle, M. Hogan, E. Holldorf, J. Kaseman, A. Knox, B. Lardner, R. Lechalk, A. Narzynski, M. Palmer, A. Ritter, C. Robinson, M. Rubinstein, E. Schultz, S. Siers, G. St Aubin, M. Spencer, T. Tadевoysan, A. Veselka, M. Viernes, and E. Wostl. This research was supported by the Department of the Navy, Joint Region Marianas (Agreement number N6112814MP002GS), the DOI Office of Insular Affairs, and the USGS Invasive Species Program and a Cooperative Agreement award (G17AC00283) to Dickinson College from the U.S. Geological Survey, Fort Collins Science Center. L.L. Bailey reviewed an earlier version of this work. Her comments were instrumental in formulating the manuscript in its current form. Additionally, the manuscript was improved by comments from B.J. Halstead and one anonymous reviewer. Research involving animal subjects was approved by the USGS-FORT Institutional Animal Care and Use Committee (FORT IACUC 2015-08). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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**DATA AVAILABILITY**

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3000/full