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To cross or not to cross: modeling wildlife road crossings as a binary response variable with contextual predictors

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Abstract. Roads are significant barriers to landscape-scale movements of individuals or populations of many wildlife taxa. The decision by an animal near a road to either cross or not cross may be influenced by characteristics of the road, environmental conditions, traits of the individual animal, and other aspects of the context within which the decision is made. We considered such factors in a mixed-effects logistic regression model describing the nightly road crossing probabilities of invasive nocturnal Brown Treesnakes (*Boiga irregularis*) through short-term radiotracking of 691 snakes within close proximity to 50 road segments across the island of Guam. All measures of road magnitude (traffic volume, gap width, surface type, etc.) were significantly negatively correlated with crossing probabilities. Snake body size was the only intrinsic factor associated with crossing rates, with larger snakes crossing roads more frequently. Humidity was the only environmental variable affecting crossing rate. The distance of the snake from the road at the start of nightly movement trials was the most significant predictor of crossings. The presence of snake traps with live mouse lures during a portion of the trials indicated that localized prey cues reduced the probability of a snake crossing the road away from the traps, suggesting that a snake's decision to cross roads is influenced by local foraging opportunities. Per capita road crossing rates of Brown Treesnakes were very low, and comparisons to historical records suggest that crossing rates have declined in the 60+ yr since introduction to Guam. We report a simplified model that will allow managers to predict road crossing rates based on snake, road, and contextual characteristics. Road crossing simulations based on actual snake size distributions demonstrate that populations with size distributions skewed toward larger snakes will result in a higher number of road crossings. Our method of modeling per capita road crossing probabilities as a binary response variable, influenced by contextual factors, may be useful for describing or predicting road crossings by individuals of other taxa provided that appropriate spatial and temporal resolution can be achieved and that potentially influential covariate data can be obtained.

Key words: animal behavior; *Boiga irregularis*; Guam; invasive species; mixed effects logistic regression; movement ecology; radiotelemetry; road crossing avoidance; road ecology.

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Introduction

Roads are pervasive landscape features with the potential to have severe impacts on a diversity of wildlife taxa. Road effects include mortality from road construction, mortality from vehicle collision, alteration of the physical and chemical environment, spread of exotic species, increased human activity, and modification of animal behavior including a barrier effect to landscape-level movements (Trombulak and Frissell 2000). The effects of roads on wildlife have intrinsic components, pertaining to the abilities and behaviors inherent to the individual or species, and extrinsic components, modulating animal behavior in response to characteristics of the road and the ecological context (Forman et al. 2003, Andrews and Gibbons 2005). Effects of these components can vary among and within taxa (Benitez-Lopez et al. 2010), with some individuals or species more vulnerable to the detrimental effects of roads (Hels and Buchwald 2001, Fahrig and Rytwinski 2009). Similarly, variability in road characteristics and ecological context can lead to spatial or temporal "hotspots" of road mortality or "cold spots" of movement where the transportation infrastructure is impermeable to wildlife movement (Lewis et al. 2011, Beasley et al. 2013, Beyer et al. 2013, Crawford et al. 2014). Within the flourishing subdiscipline of road ecology, however, rarely are both intrinsic and extrinsic factors explicitly and quantitatively assessed within the same system.

The barrier effect of roads on animal movements can range from on-road mortality (Hels and Buchwald 2001) to lack of access to required resources (Law and Dickman 1998), slowing of migratory movements (Bouchard et al. 2009), loss of gene flow (Balkenhol and Waits 2009), and other effects of fragmentation (Saunders et al. 1991). Snakes can be particularly vulnerable to these effects (Bernardino and Dalrymple 1992, Row et al. 2007, Shepard et al. 2008*a*), which may vary by species and be influenced by interactions among demographic, ecological, and temporal factors (Jochimsen et al. 2014). Conversely, while roads may be detrimental for wildlife populations, any effects of roads on slowing movements of invasive species may be seen as advantageous from a management perspective.

The Brown Treesnake (*Boiga irregularis*) is native to the Australopapuan region. This rear-fanged, mildly venomous colubrid snake is nocturnal, primarily arboreal, and a generalist predator on small vertebrates. After its accidental introduction to the U.S. territory of Guam, circa 1945, it spread rapidly across the island, and by the mid-1980s all terrestrial habitats had been successfully invaded (Rodda et al. 1999*b*, Rodda and Savidge 2007). This irruption coincided with the rapid decline of Guam's native terrestrial vertebrate fauna (Rodda et al. 1997), including the extirpation or extinction of nearly all forest birds (Savidge 1987, Wiles et al. 2003). These losses have dramatically restructured Guam's food web (Fritts and Rodda 1998) and have had cascading ecological effects (Mortensen et al. 2008, Rogers 2011, Rogers et al. 2012). Prospects for the containment and suppression of this mobile species will be affected by its movement behavior, and roads are the most pervasive landscape feature that may pose partial barriers to movement. Our previous work demonstrated Brown Treesnakes on Guam do not cross roads at the same rates as would be expected if roads were neutral landscape features; in other words, Brown Treesnakes exhibit an apparent road crossing avoidance (Siers et al. 2014). However, we did not assess the effects of intrinsic and extrinsic characteristics on road crossing avoidance or quantify road crossing rates. In this study, we describe the relative influence of a suite of intraspecific, contextual, environmental and road characteristics on per capita road crossing probabilities of this costly invasive predator, and provide a model for predicting actual crossing rates given estimated levels of predictive factors.

Intrinsic factors

Variability in road crossing rates by Brown Treesnakes is likely to be influenced by characteristics of individual snakes, including:

Body size.—Among snakes, large-bodied species are more likely to cross roads than small-bodied species (Andrews and Gibbons 2005). Within some snake species, larger individuals have larger home ranges and make longer and more frequent movements (Pizzatto et al. 2009, Hyslop et al. 2014). Increased movement activity increases the potential for contact with roads and road mortality associated with vehicle-snake collisions, and more vagile species and life stages may be particularly vulnerable (Jochimsen et al. 2014). In many species, larger snakes suffer higher road mortality (Brito and Álvares 2004, Andrews and Gibbons 2005). However, previous radiotelemetry work on Brown Treesnakes did not show significant differences in movement rates (Santana-Bendix 1994, Tobin et al. 1999) or road crossings (Tobin et al. 1999) by size class. Because larger Brown Treesnakes are more prone to terrestrial locomotion and foraging (Rodda and Reed 2007), apparently due to foraging for larger terrestrial lizards (Siers 2015) or potentially due to reduced vulnerability of larger snakes to predation (e.g., Mushinsky and Miller 1993, Bittner 2003), if there is a correlation with body size, we predict that larger snakes will cross roads more frequently.

Sex.—Males of many species of snake have significantly larger home ranges and move further and more frequently than females (Pearson et al. 2005, Richardson et al. 2006, Glaudas et al. 2008, Hyslop et al. 2014), and natal dispersal is often male-biased (Keogh et al. 2007, Dubey et al. 2008). Greater use of roads by males may lead to them being found dead on roads at higher rates than females (Andrews and Gibbons 2008, Shepard et al. 2008*a*, DeGregorio et al. 2010). Capture-mark-recapture studies of a geographically closed population of Brown Treesnakes on Guam indicate higher detection probabilities for males (Christy et al. 2010), which could be a result of greater movement activity. However, previous work on Brown Treesnakes showed minimal or nonsignificant sex differences in measures of movement (Santana-Bendix 1994, Tobin et al. 1999), road crossing (Tobin et al. 1999), foraging ecology (Savidge 1988), and effectiveness of control tools (Tyrrell et al. 2009, Lardner et al. 2013). Therefore, we do not expect to observe sex differences in road crossing rates, but if they exist, we would predict them to be male-biased based on the general trend of higher movement rates and road use by males of other snake species.

Reproductive class.—Reproductive activities strongly influence snake movements (Gregory et al. 1987). Differences in movement among male and female snakes are often the result of the reproductive status of the individual. Reproductive males may have larger home ranges (Shine 1987, Marshall et al. 2006) and make longer, more frequent, and more bold movements while seeking mates, particularly during breeding seasons (Secor 1995, Rouse et al. 2011). This may lead to more frequent interactions with roads and subsequent mortality (Shepard et al. 2008*a*). Reproductive female snakes are often known to move less or cease movement completely while gravid (Seigel et al. 1987, Charland and Gregory 1995, DeGregorio et al. 2011) or tending a clutch (Pearson et al. 2005), but may make particularly long movements before (Brown et al. 2005) or after (DeGregorio et al. 2011) oviposition. Brown Treesnakes are typically grouped into reproductive categories based on size class as determined by Savidge et al. (2007); however, aside from obviously gravid females, actual reproductive status (oogenesis and parturition history, spermatogenesis) is impossible to fully determine without necropsy and microscopy. Given the general trends in other snakes and our inability to accurately assess true reproductive status, we suggest that if there is an effect, juvenile snakes (<910 for females and 940 mm for males) and snakes of intermediate maturation (910–1025 and 940–1030 mm) will cross roads more than mature females (>1025 mm) and less than mature males (>1030 mm).

Body condition.—Body length to mass ratios are considered to be good indicators of nutritional status and metabolic reserves in snakes (Bonnet and Naulleau 1996). Animals in poor body condition may forage more and be less vigilant (Bachman 1993), and therefore more prone to risking cross-road movements. However, longer movements may require more metabolic stores, so snakes in low body condition may opt for a sit-and-wait foraging mode rather than actively foraging, resulting in lower crossing rates for snakes in poor condition. Upon experimental suppression of rodent prey on Guam, Brown Treesnakes in poor body condition exhibited greater site fidelity (Gragg et al. 2007) and individuals in better body condition moved more irrespective of plot treatment (M. T. Christy, personal communication). On the basis of these results, we would predict greater road crossing rates by snakes in better body condition.

Extrinsic factors

In addition to characteristics of the snake, factors external to the snake can play a role in influencing a snake's decision to cross a road:

Road characteristics.—Physical or behavioral road barrier effects and on-road mortality are likely to be influenced by factors such as gap width between habitat edges (Tremblay and St. Clair 2009, van der Ree et al. 2010) and road surface type (e.g., paved or unpaved; Fortney et al. 2012, Robson and

Blouin-Demers 2013, Hyslop et al. 2014). Road noise and traffic levels also have a strong deterrent effect on cross-road movements of snakes and other wildlife (Alexander et al. 2005, Andrews and Gibbons 2005, McCown et al. 2009, Shannon et al. 2014) and increase the risk of on-road mortality (Sutherland et al. 2010). We predicted that all measures of road magnitude (e.g., gap width, surface type, traffic volume) would have negative effects on the crossing rates of Brown Treesnakes.

Contextual factors.—Some circumstances affecting road crossing decisions vary on a daily basis. In addition to average traffic volumes characteristic of a given road, traffic levels may vary on a daily and nightly basis. Road crossing avoidance (Reijnen et al. 1995, Andrews and Gibbons 2005, Zurcher et al. 2010) and on-road mortality (Mazerolle 2004) may therefore vary on a daily basis, and we hypothesized that road crossings by Brown Treesnakes would be negatively associated with higher than average nightly traffic volumes. We hypothesized a "distance effect," assuming that a snake close to a road at the beginning of its nightly movements would be more likely to cross that road than a snake beginning further away. As part of our snake collection methods (see below), snake traps baited with live mice were present along road edges for a variable number of nights until an adequate sample was achieved. We hypothesized that the local attractiveness of prey odors associated with baited traps would result in reduced road crossing rates by snakes on nights when traps were present.

Environmental factors.—Many snake species exhibit dramatic seasonal variation in activity areas and movement rates (Shine and Lambeck 1985, Blouin-Demers and Weatherhead 2001, Brito 2003, McDonald 2012). Increased seasonal movement may lead to increased road crossing and road mortality rates (Bernardino and Dalrymple 1992, DeGregorio et al. 2010, Rahman et al. 2013). Guam's tropical climate is characterized by a warm, humid wet season and a cooler dry season, and metrics of Brown Treesnake activity (power outages caused by snakes in electrical infrastructure, envenomation reports, and sighting rates) have historically been higher in the wet season (Rodda et al. 1999*b*). Because McCoid and

Table 1. Codes and summary statistics for fixed effects considered for model inclusion.

Factor	Code	Summary
Site-level effects (n = 50 sites)		
Width between forest edges (m)	*gap*	mean = 11.5, SD = 5.6, range = 3.5–27.7
Minimum width of gap (m)	*min*	mean = 9.6, SD = 5.5, range = 2.6–26.4
Width of paved surface (m)	*srf*	mean = 6.5, SD = 1.7, range = 0–11.6
Road surface (paved/unpaved)	*pav*	n = 30 paved/20 unpaved
Average traffic (vehicles/night)	*atr*	mean = 259, SD = 786, range = 0–3972
Season (wet/dry)	*sea*	n = 26 wet/24 dry
Snake-level effects (n = 691 snakes)		
Snout-vent length (mm)	*svl*	mean = 943, SD = 149, range = 381–1525
Sex (female/male)	*sex*	n = 367 females/315 males
Reproductive class (juv./interm./ad. female/ad. male)	*rpr*	n = 249/269/78/95
Body condition index	*ci*	Standard normal (mean = 0, SD = 1)
Trail-level contextual effects (n = 2785 trials)		
Snake's distance from edge (m)	*dst*	mean = 19, SD = 20, range = 0–165
Mouse-baited traps (y/n)	*trp*	n = 632 yes/2153 no
Nightly traffic count (veh/night)	*ntr*	mean = 235, SD = 740, range = 0–4237
Trial-level environmental effects (n = 2785 trials)		
Moonlight index	*mn*	mean = 2.7, SD = 2.1, range = 0–6.5
Cloud-adjusted moon index	*cmn*	mean = 2.1, SD = 1,8, range = 0–5.9
Precipitation (NWS) (mm/h)	*pr*	mean = 0.24, SD = 0.63, range = 0–7
Precipitation (plastic gauge) (mm/d)	*prg*	mean = 3.7, SD = 13.9, range = 0–88
Humidity (0.00–1.00)	*hum*	mean = 0.84, SD = 0.06, range = 0.67–0.96
Temperature (°C)	*tmp*	mean = 26.9, SD = 1.1, range = 23.8–28.8
Wind speed (m/s)	*wnd*	mean = 3.15, SD = 1.7, range = 0.1–8.9
Wind gust (m/s)	*gst*	mean = 0.73, SD = 1.68, range = 0–11.96

Hensley (2000) reported higher rates of Brown Treesnake road mortality in Guam during the wet seasons of 1989 and 1990, we hypothesized a similar increase in road crossing rates during the wet season. In addition to seasonal variability, environmental factors may vary on a daily basis. On the basis of patterns suggested by literature on activity and movement of Brown Treesnakes and other snakes, we hypothesized a positive effect of temperature (Sperry et al. 2013), humidity (Daltry et al. 1998), and precipitation (McDonald 2012) and a negative influence of wind (Christy et al. 2010) on road crossing rates. For nocturnal animals relying on darkness for predator avoidance and cryptic foraging, moonlight can have a negative effect on activity levels (Yamagishi 1974, Lima and Dill 1990, Griffin et al. 2005). Because small Brown Treesnakes have been documented to move less on nights directly following a full moon (Lardner et al. 2014), captive snakes used open areas in enclosures less under high simulated moonlight (Campbell et al. 2008), and high moonlight decreased Brown Treesnake detection rates during visual surveys (Christy et al. 2010), we predicted a reduced probability of road crossing on nights with brighter moonlight.

By short-term radiotracking of snakes in close proximity to roads, we sought to measure actual per capita road crossing rates and to assess the influence of nightly conditions and snake and road characteristics on crossing probabilities. Potentially influential factors and *a priori* hypotheses for their effects are summarized in Tables 1 and 2.

Table 2. List of fixed effects considered for model inclusion at each level (a–d) of model selection.

Code	Effect	P_{sole}	ΔAICc	P_{final}
(a) Site-level effects (base model = [*site*])				
gap	−/−	0.011	−4.9	0.015
min	−/−	0.014	−4.5	–
srf	−/−	0.003	−6.4	–
pav	p−/p−	0.012	−3.9	–
atr	−/−	<0.001	−14.3	0.007
sea	w+/w+ (NS)	0.828	+1.9	–
(b) Snake-level effects (base model = *gap* + *atr* + [*site*])				
sex†	m+/m− (NS)	0.174	–	–
svl	+/+	0.015	−4.0	0.021
rpr	?/?	0.012–0.270	−1.2	–
ci	+/+ (NS)	0.548	+1.6	–
(c) Trial-level contextual effects (base model = *svl* + *gap* + *atr* + [*site*])				
dst	−/−	0.003	−9.7	<0.001
trp	−/−	0.036	−3.0	0.004
ntr	−/− (NS)	0.496	+1.6	–
(d) Trial-level environmental effects (base model = *dst* + *trp* + *svl* + *gap* + *atr* + [*site*])				
mn	−/− (NS)	0.546	+1.6	–
cmn	−/− (NS)	0.378	+1.2	–
pr	+/+ (NS)	0.501	+1.6	–
prg	+/+ (NS)	0.324	+1.0	–
hum	+/+	0.003	−6.4	0.003
tmp	+/+ (NS)	0.959	+2.0	–
wnd	−/+ (NS)	0.772	+1.9	–
gst	−/+ (NS)	0.713	+1.9	–

Notes: "Effect" is the hypothesized/observed influence of the factor (i.e., sign of the regression coefficient; "NS" = not significant). $\mathrm{P}_{\mathrm{sole}}$ is the P-value for the regression coefficient when it was added alone to the level-respective base model, followed by the ΔAICc value (differences less than -2 AICc units are considered to have adequate support for inclusion in models). $\mathrm{P}_{\mathrm{final}}$ is the P-value for the term in the final model.

† The effect of sex was assessed in a separate model eschewing observations of snakes too small to determine the sex, and was therefore not included in the same AIC model selection process as the other snake-level effects.

METHODS

Site selection

We selected 50 road, path, or utility corridor segments passing through forest habitats across the geographic expanse of Guam. Each of the selected segments was characterized by at least 200 m of relatively straight road or corridor with at least 100 m of forest depth on both sides. Occasional minor tree pruning at very narrow sites ensured that snakes could not cross gaps arboreally. We selected sites to be geographically dispersed (Fig. 1) and to be representative of the full range of road or path types and traffic conditions occurring on the island (Fig. 2). As an exception, we did not conduct trials along Guam's busiest roads out of safety considerations and due to the extremely low probability of observing crossings at such sites. Safety also necessitated that high-traffic roads have substantial shoulders from which to conduct operations.

Snake capture and processing

At each site to be surveyed, snakes were captured by funnel traps baited with live mice (Rodda et al. 1999*c*) and by hand during nighttime visual surveys. We placed traps along both road edges and at depths of up to approximately 15 m from forest edge.

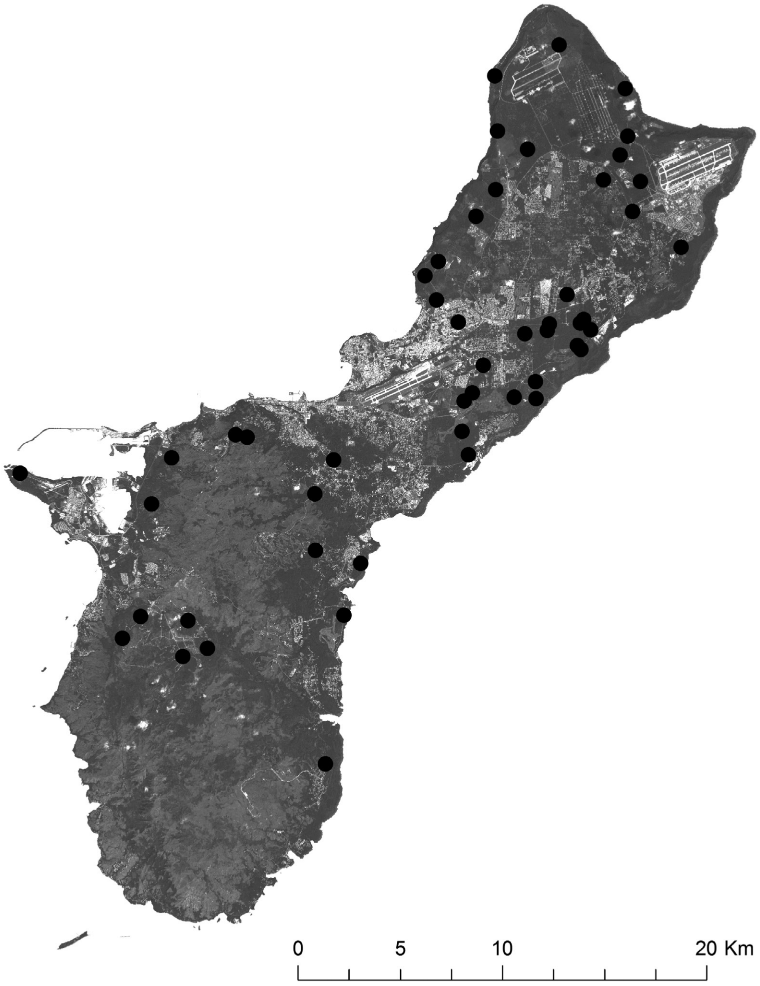

Fig. 1. Map of the U.S. territory of Guam depicting geographic distribution of the locations of 50 road, path or utility corridor segments (black dots) monitored for crossings by radiotelemetered Brown Treesnakes.

Trapping continued for one to four nights until an adequate sample size of snakes was obtained. We conducted hand captures only on the first night at each site to avoid observers interfering with movements of snakes previously implanted with transmitters. Upon capture, we collected morphometric data including snout-vent length, weight, and sex. A lubricated VHF transmitter (Holohil Systems Ltd., Carp, Ontario, Canada) was then gently massaged down the esophagus and into the stomach (Fig. 3). Generally, depending on transmitter availability, snakes under 650 mm snout-vent length received either a 0.51-g model BD-2N or 1.8-g BD-2, those from 650 to 950 mm received a 1.8-g BD-2, and those over 950 mm received a 3.8-g PD-2. We then released snakes at the location of capture.

Telemetry methods

After release, we relocated snakes on a daily basis via triangulation with a null peak antenna array (Precision Direction Finding Antenna RA-4-NS, Telonics, Inc., Mesa, Arizona, USA) consisting of two three-element Yagi antennae mounted in parallel on a 1.8-m cross-mast atop a portable 5.2-m aluminum center mast. Each site had 21 georeferenced triangulation stations along the 200-m road segment. We recorded bearings at all triangulation stations from which

Fig. 2. Photographs depicting the variability in characteristics of roads, paths and utility corridors on Guam monitored for crossings by Brown Treesnakes.

Fig. 3. Gastric implantation by massaging a lubricated VHF radiotransmitter down the esophagus and into the stomach of the snake, immediately followed by release at the location of capture.

adequate signals could be received (at least three bearings); if a sufficient number of bearings could not be obtained from these stations, *ad hoc* triangulation stations were added and their GPS locations recorded. Maximum-likelihood estimates of the signal location and error ellipses were obtained using the program LOAS™ 4.0 (Ecological Software Solutions LLC, Hegymagas, Hungary). If any bearings obtained with the null peak antenna could not unambiguously determine which side of the road the signal was coming from, we used a handheld antenna to dispel this uncertainty. We recorded locations during the daytime when the nocturnal snakes were in refugia. We considered the distance between two successive daily locations the nightly relocation distance. We determined that the single daily location of snakes in refugia was the desired sampling rate given logistical difficulties of taking multiple nighttime locations of moving snakes and the potential for observer interference in snake movements. We tracked each snake for up to 9 d, during which time we recovered the majority of transmitters from the ground or vegetation after being evacuated by the snakes. Trials during which we observed no movement and the transmitter was recovered after being located in the same location as prior locations were dropped from the analysis under the assumption that the transmitter had been regurgitated or defecated (i.e., only trials where the transmitter was known to be in a snake were included in the analyses).

Site-level effects

We considered several descriptors of road magnitude as predictors of road crossing rates. We calculated gap width (*gap*) as the average of 12–16 field measurements of the width between forest edges on opposite sides of the road at increments of equal length along the entire segment. If forest edges were not discrete, we began measurements where vegetation exceeded 150 mm. We also measured the minimum gap (*min*), the point along the road segment where the gap between forest edges was narrowest. Surface width (*srf*) was the width of the road surface at paved sites, with unpaved roads assigned a value of zero. We classified roads with a binary categorical variable (*pav*) to indicate whether the road was paved or unpaved. We obtained average traffic levels at each site (*atr*) by taking the mean of all nightly traffic counts from sunset to sunrise during the survey period as recorded with pneumatically activated traffic counters (5600 Series Roadside Unit, Metrocount, Fremantle, Western Australia, Australia). To improve normality and equality of variance, we log-transformed all traffic counts. Because each road segment was tested in only one season (wet or dry), we considered season (*sea*) as a potential factor at the site level despite it not actually being a characteristic of the road; to avoid introducing a seasonal bias to the other road characteristics, we made an effort to balance those characteristics seasonally, for example, an equal number of high vs. low traffic, wide vs. narrow, paved vs. unpaved roads, between seasons. Additionally, to account for latent influence of unmeasured characteristics of individual sites, we included a random effect of site ([*site*]) in all models. Many sites had zero observed crossings by snakes, which led to a high variance among sites on the logit scale, resulting in an increased influence of the random effect and diminished influence of fixed effects. We elected to retain the site-level random effect and present conservative estimates of the significance of the fixed effects.

Snake-level effects

We measured snake body size, or snout-vent length (*svl*), by gently stretching snakes along a flexible tape. Preliminary exploratory modeling indicated no quadratic effect of snout-vent length, which would suggest higher or lower crossing rates by mid-sized snakes, so a quadratic term (svl^2) was not considered in the model selection process. Sex (*sex*) was determined by probing (Reed and Tucker 2012); a small number of snakes too small to be reliably sexed as male or female were classified into a third "unknown" category. We assigned each snake to a reproductive class (*cls*) of either juvenile, intermediate, adult female, or adult male based upon snout-vent length classifications reported by Savidge et al. (2007), as previously described in the introduction. Condition index (*ci*) represents the standardized residuals from a fourth-order polynomial fit of a log (mass) to log (snout-vent length) regression of all individuals within the data set. We considered including a random effect of snake ID to account for multiple repeated measures of individuals; however, due to a small number of observations per snake ($\overline{X}$ = 4, SD = 2.2) and a large number of snakes with "all-zero" observations (no crossings; 89.7% of snakes), we determined that individual variability beyond that described by the preceding fixed effects could not be known given the data.

Trial-level contextual effects

We obtained the "distance effect" covariate (*dst*), or the snake's distance from the road at the beginning of the trial, from coordinates recorded by GPS at release or estimated by triangulation. We estimated distance errors for triangulated locations as the distance between the estimated transmitter location and the edge of the estimated error ellipse (as plotted by LOAS™ 4.0) perpendicular to the forest edge. To assess whether the presence of snake traps reduces a snake's probability of crossing a road, we recorded a binary covariate (*trp*) to indicate whether or not traps were present at the survey location on the trial night. To test the effect of nightly traffic rate variation beyond the average recorded at the site level, we also considered the nightly log-transformed traffic count (*ntr*) as a trial-level covariate.

Trial-level environmental effects

We calculated humidity (*hum*), temperature (*tmp*), precipitation (*pr*), wind speed (*wnd*), and wind gust speed (*gst*) as the means of all hourly values between sunset and sunrise on the night of the trial as reported by the National Weather Service weather station at the Guam International Airport (http://www.nws.noaa.gov). We considered 24-h precipitation values from temporary plastic rain gauges at the survey sites as an alternative measure of precipitation (*prg*). We obtained information on moon elevation and apparent magnitude from the NASA Jet Propulsion Laboratory HORIZONS system (http://ssd.jpl.nasa.gov). In the absence of any citable standard methods for indexing relative moonlight values, we calculated an *ad hoc* moonlight index value (*mn*) as *sine* (*elevation/max. elevation* × 0.5 × π) × *apparent magnitude* × −1, with the sine function attenuating moonlight as it moved lower on the horizon and multiplication by −1 converting negative apparent magnitude values to positive values representing brighter moonlight. We also considered a cloud-adjusted moonlight score (*cmn*), "penalizing" moonlight values as *mn*− (0.66 × *mn* × *cloud cover*), where cloud cover was the mean hourly nighttime proportion of cloud cover from the National Weather Service data.

Statistical analysis

We considered each nightly relocation as a Bernoulli trial, with a response variable of 1 or 0 indicating whether the snake did or did not cross the road. We employed mixed-effects logistic regression using the "glmer" function from the R package "lme4" to assess the effects of covariates. We based model selection on Akaike's Information Criteria corrected for small sample size (AICc). We included the site-level random effect ([*site*]) in all models, with model selection conducted on possible combinations of level-specific fixed effects.

We approached model selection in a stepwise fashion, first considering all candidate site-level effects. Each term was first assessed for its individual fit in addition to the base model (random site effect only for the site-level selection process) before all possible combinations of candidate terms were considered in an AIC model selection process. We added the most influential effects to the base model and carried them over for selection of additional fixed effects at the next level. We repeated this process through the snake-level, trial-level contextual, and trial-level environmental subsets, finally arriving at a top model describing the most influential factors affecting road crossing probabilities. *P*-values for each term included in this top model are also reported in Table 2.

We visualized effect sizes by plotting predicted logistic response curves and 95% confidence intervals (±1.96 × SE) for the most significant results. Standard procedures do not exist for estimating standard errors for model predictions with random effects, so these effect sizes and standard errors are from models containing the fixed effects only. We acknowledge that unmeasured site-level effects may introduce more uncertainty about the estimates. Because the absence of traps represents the natural condition, all representations of predicted effect sizes hold the predictions constant at the trapless state.

Model simplification and simulation of absolute road crossings

We also derived a simplified model based on easily measured significant predictor covariates that a managing agency might use to predict the probabilities of road crossings based on road and Brown Treesnake population characteristics. In addition to reporting the model formulation, coefficients and their standard errors, and *P*-values, we used this model to simulate differences in absolute road crossing rates based on actual size distributions and random movement within 100 m of a hypothetical road edge. We used actual size distributions from samples of 100 snakes collected at each of two sites surveyed during another project (Siers 2015), a limestone forest site on the Naval Magazine, Naval Base Guam, and an urban residential area in the village of Dededo. These sites varied in mean snout-vent length, with the Naval Magazine sample averaging 740 mm and the Dededo site averaging 914 mm. For these simulations, each sample of 100 snakes was assumed to be a hypothetical population of 20 snakes per hectare, randomly distributed as far as 100 m from the road edge along a 500-m segment of road. We predicted the per-capita per-night crossing probability for each snake—using the simplified fixed-effects model—based on a randomized distance from the road for each individual snake (0–100 m), a gap width of 10 m, a humidity of 85%, with no traps present, and using actual snake lengths from the two samples. We made a random draw from a binomial distribution with the predicted nightly crossing probability to simulate whether the snake crossed the road. We ran the nightly estimation procedure—re-randomizing the distance from the road—30 times (representing 1 month) for each iteration, and summed up the numbers of predicted nightly crossings. We ran this monthly simulation for 1000 iterations, producing a distribution of simulated monthly road crossings for each site to demonstrate differences in numbers of road crossings based on variation in size distributions among sites.

Results

We conducted trials at two pilot sites from 14 June 2011 to 1 August 2011, with trials at the remaining 48 sites occurring between 11 June 2012 and 29 May 2013. We implanted transmitters in a total of 728 snakes, of which 691 yielded successful trials. We tracked those snakes for one to nine trials each (where trials equal consecutive days an individual was successfully located), with a mean of four trials per snake (SD = 2.2 trials), for a total of 2785 trials. Throughout the trials, we recorded a total of 95 road crossings.

Snakes ranged from 381 to 1525 mm snout-vent length. Very small and very large snakes were under-represented, as both were difficult to obtain and track; small transmitters emitted weak signals and were often lost, and very large snakes were rarely collected and often left the sites shortly after implantation. Approximately 80% of our trial observations were of snakes between 760 and 1096 mm, with a mean of 943 mm (SD = 149 mm) snout-vent length. The mean transmitter-to-snake mass ratio was 3.78% (SD = 1.48%).

Distance errors for GPS locations (release and transmitter recovery locations) were from ±2 to ±6 m, depending on canopy interference. Distance errors were correlated with estimated distance from the edge ($R^2 = 0.36$, $P \ll 0.001$), with an estimated distance of 5 m having an estimated error of ±1.0 m, out to an estimated error of ±31.2 m for a location estimated at 100 m from the road edge. These errors only add noise to the distance covariate (*dst*) and would not affect estimates of road crossing rates as all locations were unambiguously assigned to the correct side of the road.

Crossings per site ranged from zero to eight, with no observed crossings at 20 (40%) of the sites. The variance associated with the random effect in the base model ([*site*]) was 0.769 (SD = 0.577); inclusion of the selected model terms reduced this variance to 0.333 (SD = 0.577).

Among the site-level effects (Table 2a), all measures of road magnitude were significantly negatively correlated with road crossing rates as predicted. When each factor was taken as a sole covariate in a fixed-effects model, all P-values were $\ll 0.001$. When the site-level random effect was included, all P-values were ≤ 0.014 ("P_{sole}" column in Table 2) and all ΔAICc values were less than or equal to −3.9 Because most of these measures were autocorrelated, we selected only the most significant predictor (average nightly traffic volume, *atr*) and the most readily measurable metric of the physical magnitude of the road (gap width, *gap*) to add to the base model for successive model comparisons. These two variables were only moderately correlated ($r = 0.464$); because the correlation is positive the effect on predictions would be to diminish the effect size of each, so inclusion of both could be considered to give conservative estimates of effect size. The coefficient for an effect of wet season was positive as predicted, but the effect was nonsignificant ($P_{\text{sea}} = 0.828$). Effect sizes of traffic volume and road gap are depicted in Fig. 4a.

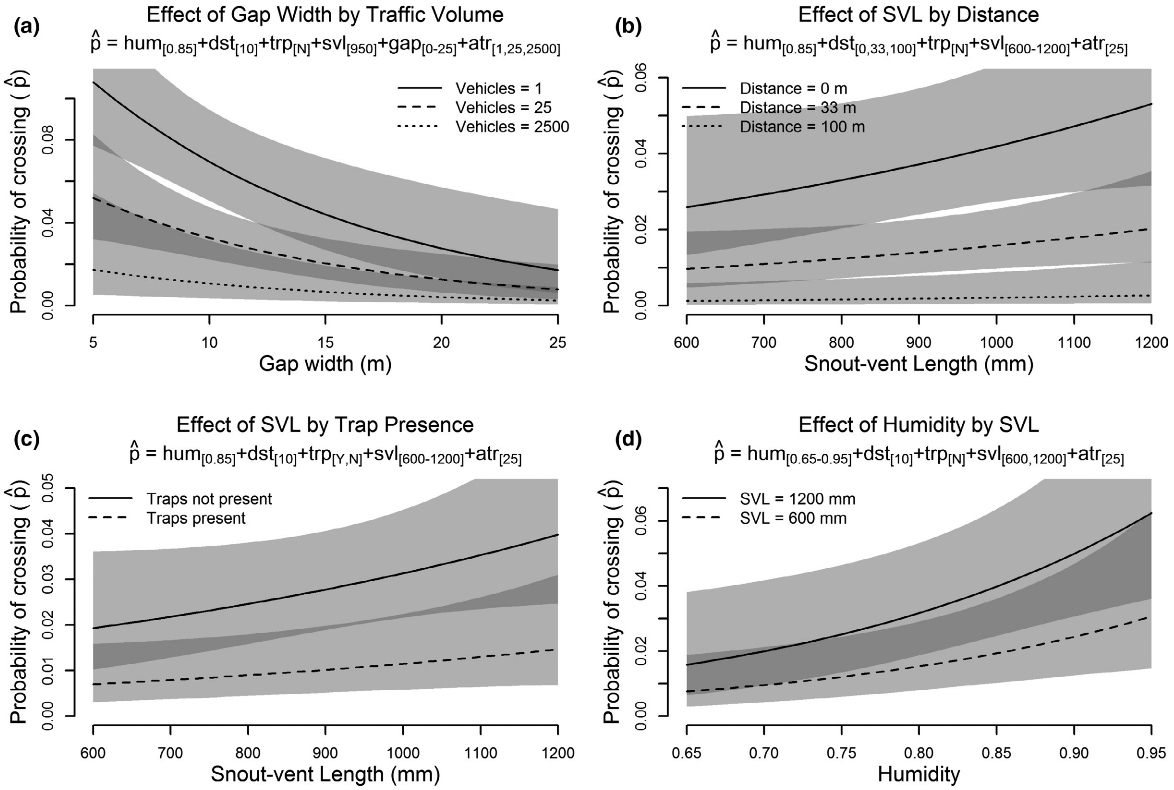

Fig. 4. Effect sizes of road, individual, contextual, and environmental factors influencing road crossing rates of radiotelemetered Brown Treesnakes on Guam. Values associated with model terms ("[value]") are the values at which response curves were predicted. Gray polygons represent the 95% confidence intervals for the estimates (±1.96 × SE). Figure parts reflect the influences on probability of crossing by the predictor variables: gap width and traffic volume (a); snake snout-vent length and distance from the road edge (b); snout-vent length and trap presence (c); and humidity and snout-vent length (d).

Carrying the average traffic and gap width fixed effects and the random site effect over as the base model for snake-level effects (*atr* + *gap* + [*site*], Table 2b), snout-vent length was the only significant intrinsic predictor of road crossing rates ($P_{\text{svl}} = 0.015$) with a positive effect (i.e., larger snakes being more likely to cross roads) as predicted. After censoring 26 movement records of nine snakes too small to be sexed, there was no significant difference between sexes in crossing rates ($P_{\text{sex}} = 0.174$) nor was there a significant interaction between sex and snout-vent length. In classifying snakes by reproductive class (*cls*) there was a significant difference in crossing rates among juvenile, intermediate and adult groups, but these differences were consistent with the effect of increased snout-vent length. In a *post hoc* model including movements of only adult snakes there was no difference between crossing rates of adult males and adult females. Therefore, snout-vent length more parsimoniously explains crossing rates and was selected as a base term for successive model comparisons. The coefficient for an effect of body condition was positive as predicted but the effect was not significant ($P_{\text{ci}} = 0.548$). The effect of snout-vent length on road crossing rates is represented in Fig. 4b,c.

Among contextual factors recorded at the trial level (Table 2c), distance and trap effects were highly significant. Snakes further from the forest edge at the start of the trial were much less likely to cross the road, as predicted ($P_{\text{dst}} = 0.003$; Fig. 4b). On nights when mouse-baited snake traps were present, snakes were less likely to cross the road ($P_{\text{trp}} = 0.036$; Fig. 4c). Nightly variation in traffic volume was negatively associated with crossing rates as predicted, but the effect was not significant (P_{ntr} = 0.496); variation among nights adds little beyond the highly significant effect of average traffic volume at a site. The terms *dst* and *trp* were carried over as part of the base model for assessing environmental effects.

Moonlight, as represented by our index, had a negative effect as predicted but was not significant (P_{mn} = 0.546). The cloud-adjusted index performed slightly better but was also nonsignificant (P_{cmn} = 0.378). Rainfall as measured by an on-site plastic gauge provided a slightly better fit than data from the NWS weather station, and effect estimates were positive as predicted, but both effects were nonsignificant ($P_{\mathrm{prg,pr}}$ = 0.324, 0.501). Humidity was the only environmental variable that was significant when included as the only additional term to the base model. When all possible combinations of terms were considered, combinations of humidity, temperature and wind speed were highly significant; however, these terms are highly negatively correlated and because humidity was the only significant term when included alone (P_{hum} = 0.003; Fig. 4d) it was the only environmental variable we chose to add to our final model:

$$\begin{aligned}\mathrm{logit}(p_{\mathrm{ijk}}) = {} & \beta int + \beta hum_{\mathrm{ijk}} + \beta dst_{\mathrm{ijk}} \\ & + \beta trp_{\mathrm{ijk}} + \beta svl_{\mathrm{jk}} + \beta gap_{\mathrm{k}} + \beta atr_{\mathrm{k}} \\ & + \gamma_{\mathrm{k}} \gamma_{\mathrm{k}} \sim N(0,\sigma^2)\end{aligned}$$

where the estimated probability of crossing (p) on trial *i* by snake *j* at site *k* is the intercept term (*int*, or the average crossing probability) plus the product of the covariate values and the coefficient estimates (βs), offset by the [*site*] random effect for site *k* (γk) which is assumed to be a normal random variable with a mean of zero and a variance estimate of σ^2.

As estimated by this model, all β effects were significant at α = 0.05, with negative effects of traffic volume (P_{atr} = 0.007) and gap width (P_{gap} = 0.015), positive effect of snake size (P_{svl} = 0.021), negative distance and trap contextual effects ($P_{\mathrm{dst,trp}}$ < 0.001, 0.004), and a positive humidity effect (P_{hum} = 0.003). The variance estimate for the [*site*] random effect (σ^2) was 0.333. This model constituted an improvement of fit of 41.36 AICc units over the base model of random site effect only. By this model, a relatively large snake (1200 mm) under very high crossing-probability conditions—directly on the forest edge at the beginning of the night on a road with no traffic, a 5-m gap between forest edges, and 90% humidity—would be 27% likely to cross that road, with that probability dropping rapidly to 0.51% for an average (950 mm) snake 25 m from the edge of a road with an average of 250 vehicles passing per night, a gap of 15 m, and a humidity of 80%. Under even lower probability conditions (600 mm snake, 50 m from road edge, 1000 vehicles per night, 25 m gap, 70% humidity) the probability of crossing would be vanishingly small (0.0167%).

We reported beta estimates from a simplified model using untransformed data in Table 3 in order to allow the reader to make estimations of crossing probabilities based on new data in the native scale. Mixed effects models would not converge when using untransformed data, so we report the coefficient and standard error values from a fixed effects model. Untransformed traffic values were not significant in the fixed effects model so we dropped the term from this simplified model and relied on gap width as an easily measured proxy for road magnitude. The presence of traps (*trp*) was a categorical variable, with the natural trapless state being the baseline ("0") condition, so the user can drop this term ($0 \times \beta_{\mathrm{trp}} = 0$) when traps are not present at road edges. The simplified model is as follows:

$$\begin{aligned}\mathrm{logit}(p_{\mathrm{ijk}}) = {} & \beta int + \beta hum_{\mathrm{ijk}} + \beta dst_{\mathrm{ijk}} + \beta trp_{\mathrm{ijk}} \\ & + \beta svl_{\mathrm{jk}} + \beta gap_{\mathrm{k}}\end{aligned}$$

and the equation for estimation of the probability of road crossing (p), then, is

$$p = 1/(1 + e^{-(-10.01 + (7.94 \times hum) + (-0.0323 \times dst) + (-0.958 \times [0,1]) + (0.00203 \times svl) + (-0.126 \times gap))})$$

Using this simplified model, holding road, contextual and environmental conditions constant (*gap*, *tr*, *hum*), randomizing distance from the road (*dst*), and using actual snake sizes (*svl*) from sites differing in size distributions (Fig. 5a), simulations demonstrated the potential for considerable differences among sites in absolute numbers of road crossings events resulting from differences in snake size distributions among sites (Fig. 5b).

Table 3. Fixed-effects betas (coefficient estimates) from the simplified model based on untransformed (native scale) predictor variables (new data for predictions should not exceed the range of values on which the model was based).

β	Factor	Range	Estimate	Std. error	P-value
βint	Model intercept (average)	NA	−10.01005	1.779558	≪0.0001
βhum	Humidity	0.67–0.96	+7.94182	1.993966	<0.0001
βdst	Distance from edge (m)	0–165	−0.03225	0.008618	0.0002
βtr	Traps present (0 = no, 1 = yes)	0,1	−0.95761	0.331804	0.0039
βsvl	Snake snout-vent length (mm)	381–1525	+0.00203	0.000733	0.0055
βgap	Gap width (m)	3.5–27	−0.12591	0.027693	≪0.0001

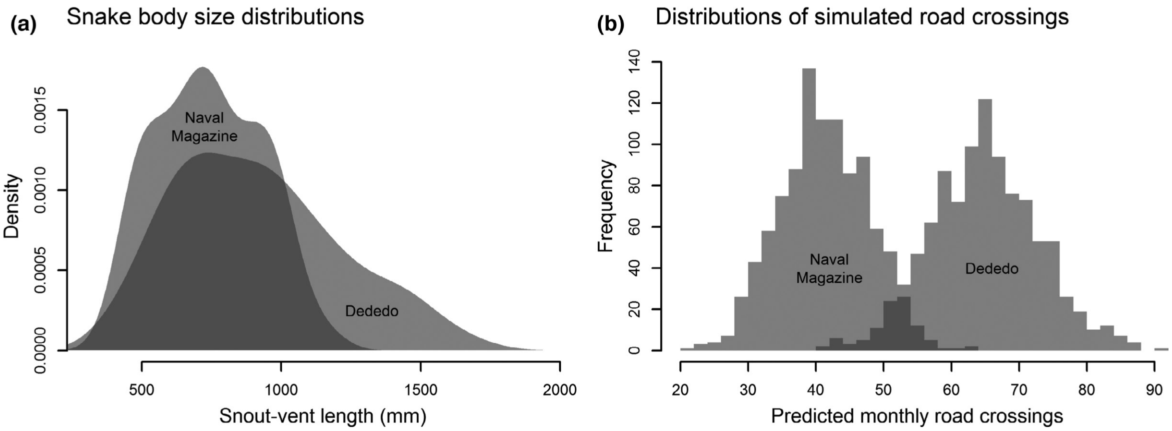

Fig. 5. Size distributions of samples of 100 snakes each from two sites on Guam (a), and simulated differences in predicted road crossing events per month (b) resulting from differences in snake size distributions based on the simplified road crossing prediction model. Simulations were run over 1000 iterations, with randomized distances from the road (0–100 m), standardized humidity (85%) and gap width (10 m), and absence of mouse-baited snake traps.

DISCUSSION

Our results indicate strong influence of a multitude of extrinsic factors on the nightly probability that a Brown Treesnake on Guam will cross a road. All metrics of increasing road magnitude served to reduce crossing probabilities. Disentangling which specific factors add which components of variation is nontrivial. While disentanglement may be desirable from a behavioral standpoint, the point may be relatively meaningless in practice when predicting which roads are likely to be crossed more often, as roads tend to be wider and more likely to be paved as traffic volume increases. Traffic levels are readily measurable with pneumatic roadside units, but gap width may be a more easily measured predictor of crossing rates. That gap width remains significant when accounting for traffic levels and random site effects suggests a behavioral aversion to terrestrial movement and/or exposure upon leaving forest cover. For an individual snake on a given night, extrinsic factors such as the location of the snake with respect to the road and the presence of local prey cues had strong effects on probability of crossing a road. While we had a case for predicting a strong effect of moonlight, precipitation, and season on road crossing rates, the only environmental effect with which we were able to demonstrate a significant relationship was humidity, with fewer crossings on less humid nights.

The presence of snake traps containing live mouse lures was initially considered a regrettable nuisance effect of observer interference with the system being studied, but in retrospect offers potentially valuable insight into the behavioral decisions made by snakes. It appears that the presence of strong prey cues—as resulting from the presence of bait mice in traps—had an effect of reducing or localizing the movement of snakes, at least with respect to probability of road crossings. Forest habitats on Guam are depauperate of the bird and mammal prey preferred by larger Brown Treesnakes (Savidge 1988; Siers 2015), and we presumed that both sides of a surveyed road segment were at equilibrium with respect to prey densities. While these data cannot demonstrate an increased rate of road crossing by snakes following stronger prey cues from the opposite side of the road, they do demonstrate a reduced rate of road crossing when local prey cues are artificially high. We encourage future research on the effect of prey density differentials on road crossing rates of Brown Treesnakes and other snake species.

Snake size was the only intrinsic factor appearing to influence road crossing probabilities. This positive effect of snout-vent length was consistent with observations of increased terrestrial locomotion by larger Brown Treesnakes (Rodda and Reed 2007) and greater movement rates and road use by larger snakes of other species (Brito and Álvares 2004, Andrews and Gibbons 2008, Hyslop et al. 2014). If road crossing avoidance results from a reluctance of snakes to depart forest cover as a form of antipredator behavior, as suggested by the gap width effect, it may be logical that such avoidance is greater in smaller snakes that may be more vulnerable to a wider variety of predators (Mushinsky and Miller 1993, Bittner 2003). This antipredator behavior may decline with growth of the snake (e.g., Roth and Johnson 2004). Alternatively and nonexclusively, smaller Brown Treesnakes prey almost exclusively on small lizards (Savidge 1988, Lardner et al. 2009, Siers 2015), which are ubiquitous and hyperabundant (Campbell et al. 2012), whereas larger snakes tend to take bird and mammal prey which are rare and heterogeneously distributed in Guam (Savidge 1988, Siers 2015). This may potentially lead to a greater drive for inter-habitat movements by larger snakes seeking size-appropriate prey. During our observation of 2945 nightly movements of 728 snakes within close proximity to a road, we observed only one snake mortality, a 1271 mm male found dead near the forest edge on the shoulder of a high-traffic road. This snake was at the 97th percentile of snake sizes monitored during this study. We were unable to determine if the snake had been killed by vehicle collision or by other causes. If so, this might support the trend of larger snakes more frequently crossing and being killed on roads (Andrews and Gibbons 2008, Shepard et al. 2008*a*).

Very large snakes that are more likely to exhibit reproductive behavior were under-represented in this study. While we were unable to demonstrate differences in road crossing rates by snakes considered to be fully mature based on size classes, true reproductive status cannot be verified without necropsy and no obviously gravid snakes were encountered during our sampling. While the potential exists for road crossing behavior to vary among actively reproductive snakes, we were not able to demonstrate such differences. Large reproductive snakes are relatively rare on Guam, so crossings by this small proportion of individuals are not likely to have a large impact on the overall number of road crossings; however, such movements by reproductive snakes may have disproportionate consequences for management outcomes.

Our method of monitoring the nightly relocation distances of snakes makes re-crossings of a road within a single night undetectable. However, the rarity of crossing events and the very low rates of visual detection of snakes on roads or within road gaps suggest that such “double-crossing” events must be rare. Over the course of more than 2300 h of recent Brown Treesnake surveys along habitat edges at 18 sites during optimal snake activity hours (Siers 2015), we made no observations of snakes on roads. As such, we are confident that our results accurately characterize the factors affecting the majority of road crossings by snakes on Guam.

Per capita, road crossings as modeled here are relatively rare events, consistent with published assessments of road crossing avoidance by Brown Treesnakes (Siers et al. 2014) and other snakes (e.g., Shine et al. 2004, Andrews and Gibbons 2005, Shepard et al. 2008*b*, Miller et al. 2012, Robson and Blouin-Demers 2013). Actual numbers of snakes crossing a road during a given timeframe will depend on additional factors such as snake density and spatial distribution with respect to the road. Our results demonstrate that snakes closer to road edges are more likely to cross the road; however, these data cannot demonstrate what proportion of snakes utilizing the landscape were within close proximity to the road. Affinity for edge habitat has been documented in multiple snake species (e.g., Blouin-Demers and Weatherhead 2001) and Brown Treesnakes appear to have no aversion to forest habitat at road edges, as this is where the majority of visual observations of foraging snakes occur (P. Klug *personal communication*). If snake density is greater in edge habitat, this will increase actual crossings compared to a uniform distribution of snake densities across the landscape. Given the positive effect of snake size on road crossing probabilities, variation in the size distributions of snakes at a given site may modulate the actual numbers of road crossing events that occur within a given time period (Fig. 5).

Brown Treesnakes can be effectively eradicated from discrete habitat units if immigration can be controlled (Rodda et al. 1999*a*, 2002), but high snake mobility makes this difficult to achieve (Savarie et al. 2001). Future plans to suppress Brown Treesnake populations involve aerial broadcast of toxicant-laden baits at the landscape scale (Savarie et al. 2001, Clark and Savarie 2012). Out of logistic necessity, not all areas can be treated at the same time, and it is likely that roads will form *de facto* boundaries for management units. Information on predictable "leak-back" rates from untreated areas will be important for modeling the prospects for success of such efforts, and this understanding of road, context, and snake characteristics on the partial barrier effects of roads may make such estimates feasible. An understanding of the effect of roads on landscape-scale movements of invasive snakes may also be useful in predicting the rates of spread of novel invasions. Variation in crossing probabilities by snake size introduces a "filter effect," where cross-road migrants will not be a random subset of snakes but rather a size-biased sample of larger snakes. This will have demographic consequences when considering novel invasions or re-invasions across barrier roads, particularly since cross-road migrants are more likely to be larger individuals and hence more likely to be reproductive.

Movement and road crossing rates of Brown Treesnakes on Guam appear to have declined in the ~60 yr since invasion. Qualitative descriptions by Santana-Bendix (1994) and Tobin et al. (1999) differ in that Santana-Bendix described the movements of snakes tracked between 1988 and 1990 to be without defined activity areas, whereas Tobin described snakes tracked in 1996 as having greater site fidelity. McCoid and Hensley (2000) recorded 184 roadkilled Brown Treesnakes during 20.4 km of daily driving over 2 yr, a rate that appears extraordinarily high compared to our contemporary but unquantified observations of roadkilled snakes (S. R. Siers, R. N. Reed, J. A. Savidge, *personal observations*). Rodda et al. (2008) hypothesized that ecological conditions on Guam prior to the irruption of Brown Treesnakes favored "high-moving" snakes that dispersed into prey-rich unoccupied habitats, with a reversal in selection for low movement and energy conservation subsequent to the collapse of populations of larger prey species. Fahrig (2007) suggests that wildlife populations that have inhabited landscapes with high habitat cover have evolved low boundary responses and high movement probabilities, making them highly susceptible to increased movement mortality resulting from habitat loss and reduced matrix quality.

By focusing our efforts on a large number of individuals at a large number of sites for the relatively short periods during which they were in close proximity to roads, we were able to elucidate a hierarchy of factors affecting road crossing rates by invasive Brown Treesnakes on Guam. These data are the first to provide managers with a reasonable baseline assessment of the barrier effect of roads on landscape-level movements of these costly invasive predators, and one of a very small number of studies that simultaneously assesses intrinsic and extrinsic factors affecting individual probabilities of road crossing by wildlife. Similar methodologies may be useful for those studying the movement of other organisms with respect to roads or other landscape features. With the global proliferation of roads due to development and resource exploitation, it will become increasingly important that we move from qualitative assessments of the effects of roads to a greater understanding of the multivariate, quantitative, and cumulative effects of roads on wildlife and how those effects vary among and within species.

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