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Modelling detection probabilities to evaluate management and control tools for an invasive species

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Summary

1. For most ecologists, detection probability (p) is a nuisance variable that must be modelled to estimate the state variable of interest (i.e. survival, abundance, or occupancy). However, in the realm of invasive species control, the rate of detection and removal is the rate-limiting step for management of this pervasive environmental problem.

2. For strategic planning of an *eradication* (removal of every individual), one must identify the *least* likely individual to be removed, and determine the probability of removing it.

3. To evaluate visual searching as a control tool for populations of the invasive brown treesnake *Boiga irregularis*, we designed a mark–recapture study to evaluate detection probability as a function of time, gender, size, body condition, recent detection history, residency status, searcher team and environmental covariates.

4. We evaluated these factors using 654 captures resulting from visual detections of 117 snakes residing in a 5-ha semi-forested enclosure on Guam, fenced to prevent immigration and emigration of snakes but not their prey. Visual detection probability was low overall ($\bar{p}$ = 0·07 per occasion) but reached 0·18 under optimal circumstances.

5. Our results supported sex-specific differences in detectability that were a quadratic function of size, with both small and large females having lower detection probabilities than males of those sizes. There was strong evidence for individual periodic changes in detectability of a few days duration, roughly doubling detection probability (comparing peak to non-elevated detections). Snakes in poor body condition had estimated mean detection probabilities greater than snakes with high body condition. Search teams with high average detection rates exhibited detection probabilities about twice that of search teams with low average detection rates. Surveys conducted with bright moonlight and strong wind gusts exhibited moderately decreased probabilities of detecting snakes.

6. *Synthesis and applications*. By emphasizing and modelling detection probabilities, we now know: (i) that eradication of this species by searching is possible, (ii) how much searching effort would be required, (iii) under what environmental conditions searching would be most efficient, and (iv) several factors that are likely to modulate this quantification when searching is applied to new areas. The same approach can be use for evaluation of any control technology or population monitoring programme.

Key-words: *Boiga irregularis*, detection probability, eradication, heterogeneity, invasive species management, mark–recapture, visual searching

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Introduction

For most population biologists, detection or capture probability (p) is a nuisance variable that must be estimated to obtain survival, abundance or occupancy estimates. In contrast,

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estimating and modelling individual detection probability (p) is a key component for strategic planning of control or eradication programmes for invasive species. Focus on central tendency vs. distribution of p depends on whether one is aspiring to control the population or eliminate it. For control, mean removal rate ($\bar{p}$) is the value to be maximized. If *eradication* is the goal, however, one must maximize the detection probability of the least detectable individual (minimum individual p), as the effort needed to remove that last individual will determine the effort needed for a successful eradication. In mark–recapture analysis, individual variation in detection probability can either be associated with a recognizable class of individuals (through individual covariates) or be unidentified (latent individual heterogeneity).

Quantification of detectability for the purpose of evaluating control tools has rarely been conducted; the few examples are mostly from brown treesnakes *Boiga irregularis*. Savarie *et al.* (2001) evaluated a brown treesnake toxicant application, but quantified only mean removal rate ($\bar{p}$), which highlights expeditious population reduction. Tyrrell *et al.* (2009) used mark–recapture to estimate individual detection probabilities of invasive brown treesnakes subjected to trapping, and found that smaller snakes were completely refractory to trap capture (minimum $p = 0$) and therefore trapping could not be used for eradication. Kéry (2002) attempted to estimate the effort needed to detect a single average individual of several species of European snakes using occupancy modelling. However, occupancy modelling is limited to estimating a *population's* detection probability, not differences in detectability among specific individuals, which was our goal.

Eradication of invasive brown treesnake populations is a top conservation priority because of the ecological damage wrought on Guam and the prospect that similar damage is likely upon the snake's arrival on other islands (Savidge 1987; Fritts & Rodda 1998). Brown treesnakes have been detected in cargo or arriving as stowaways on many Pacific islands (Fritts, McCoid & Gomez 1999; Stanford & Rodda 2007). Eradication is a goal on Guam, and is planned for any incipient population elsewhere. Unfortunately, eradication efforts to date have been hampered by the absence of control tools that capture every individual (e.g. the toxicant and trap studies cited above; see also Rodda *et al.* 2007).

One potential control tool for incipient populations of this species is visual searches. In a preliminary examination of visual surveying, Rodda *et al.* (2007) demonstrated that visual searching was capable of putting all individuals of *B. irregularis* at risk of capture, but they did not quantify detectability or individual variation in detectability. If an adequate detection probability for all individuals could be demonstrated, visual searching might constitute a viable management tool, at least for eradication. However, we do not fully understand the various factors affecting our ability to visually detect this cryptic species. To that end, we geographically enclosed, censused, and individually marked a population of *B. irregularis* to identify factors affecting visual detection of the species.

Materials and methods

STUDY SITE

Our geographically closed population study site (5 ha) was on Andersen Air Force Base (AAFB) in northern Guam. We constructed a double-sided chain-link bulge barrier fence to prevent migration by snakes in or out of the area (Perry *et al.* 1998; Rodda *et al.* 2007). A 0·5-m wide concrete footer on either side of the fence inhibited adjacent vegetative growth, and anchored a skirt of hardware cloth that extended out 0·2 m from each side of the base of the fence. Vegetation was cleared from transects and within 2 m of either side of the fence line, and maintained during the study.

VISUAL SURVEYS

Twenty-six parallel transects were cut across the study area at 8-m intervals. The entire area was surveyed at 16-m intervals for each search occasion (one night), with the other set of 13 transects searched the following occasion. The entire perimeter of the snake barrier was searched each night. A nightly search was conducted by four searchers working in teams of two; each team searched 220-m long transects (one searcher per side) in 30 min per transect (0·5 km h^{-1}). Search order of transects was randomized and visual searching typically took place five nights a week. We conducted 109 visual searches between 27 September 2004 and 7 April 2005. All snakes were checked for identification (PIT tags and scale clips), and unmarked snakes received both unique marks. Measurements of mass (by Pesola® spring scales) and snout-vent length (SVL) were recorded on multiple occasions for each snake to account for change in size and body condition. The gender of each snake was determined on at least three separate occasions by everting the hemipenes or by using a sexing probe (Jordan & Rodda 1994).

To mimic typical visual survey conditions (searching along transects), we constructed our capture history matrices using only snake detections from transects (i.e. not perimeter searches). However, perimeter detections (along the barrier) during the visual surveys revealed the presence of four snakes that were never detected on transects; these undetected individuals were added to the visual capture history matrix, along with their covariates, to provide a more complete portrait of the characteristic traits associated with detection during visual surveys. To incorporate these 'undetected' snakes into the analysis, we added a dummy first occasion to the overall capture history matrix followed by 109 zeros to indicate their presence but lack of detection during standard surveys. Therefore, all 101 snakes known to be present from the previous trapping bout in this enclosed study area (2 June 2004–14 September 2004) received a value of one on the dummy occasion. Additionally, 16 hatchlings calculated to have been born during the visual survey period received a value of zero on the dummy occasion because these individuals were unavailable for detection during this occasion (the detection value for this dummy occasion was fixed = 1). We estimated hatch dates for small snakes by back-extrapolating from their first detection size to their latest probable hatch date, assuming a growth rate of 1·24 mm day^{-1} (upper 95% CL of initial growth of 11 small snakes caught during this study and recaptured at SVL < 500 mm) and a hatch SVL of 375 mm.

ESTIMATING DETECTION PROBABILITIES

We estimated apparent survival, detection probability (p), and recruitment using the Pradel survival and recruitment model (Pradel

1996) in program MARK (White & Burnham 1999). We evaluated two structural limitations of using the Pradel model for these data: (i) capture probabilities are estimated as a single parameter (p) rather than initial and recapture separately and (ii) latent heterogeneity of capture probability cannot be modelled. We assessed these limitations by using a closed model (Huggins 1989, 1991) in program MARK (n = 109 occasions). Closed models were used with assurance of geographic population closure because recaptures of marked snakes on both sides of the barrier (> 350 individuals marked outside; 122 marked inside; > 3000 captures) revealed no emigration or immigration. To meet the assumptions of demographic closure, we excluded snakes thought to have died (n = 12 snakes not subsequently detected) and those known to have been born (n = 16). Estimating capture probabilities as a single parameter appeared to be a reasonable constraint for these data because the closed model showed no evidence of a behaviour effect on recapture ($\hat{\beta}$ = −0·044, 95% CL = −0·401, 0·312). Additionally, we found negligible latent heterogeneity with these data; the closed model approximated a mixture of two latent classes of snakes, but almost all snakes (95%) were represented in the first mixture class. Based on these findings, we use the Pradel model to accommodate the 12 deaths and 16 births.

Our modelling emphasis was on detection probability because that was the parameter of interest to us from a management perspective. In modelling detection probability with the Pradel model, we modelled survival as a function of the additive effects of sex, body condition index (CI) (definition provided below), and SVL, while recruitment was modelled as a linear function of time. A number of factors are suspected to influence detection probability of *B. irregularis*; our covariate definitions and *a priori* hypotheses addressing these potential sources of variation were:

1. Sex: Based on slightly higher female trap capture rate than males in *B. irregularis* (Tyrrell *et al.* 2009), we anticipated a similar effect of gender on visual detection probability.

2. Snout-vent length: Based on the wide range of sizes detected visually (Rodda *et al.* 2007), we anticipated a negligible or weak effect of SVL on visual detection probability. We estimated average growth for each snake by fitting a line to individual regressions of SVL on capture dates across all captures for that individual. We used the resulting expected SVL for each snake at the midpoint of the visual surveys (elapsed day 97) in the analysis. A linear size function would not reflect a possible bimodal pattern of detection which might result if there were differences in detectability due to small snake sizes. To evaluate this possibility, we fit a quadratic size model.

3. Body CI: We explored the effect of three body condition metrics: CI, CI trend and growth index. CI was calculated for each individual as the ratio of mass to its expected mass given its length. Expected mass for a given size was estimated by linear regression on logarithmic scales, based on over 10 000 records of *B. irregularis* length and mass sampled from Guam from 1980 to 2004. We defined CI trend as the slope of the regression of each individual's CI against date. Growth index was calculated as the observed growth rate minus expected growth rate, with the latter estimated by linear regression of sex-specific growth rates on SVL. We anticipated skinnier and faster growing snakes with negative CI trend values to be more detectable because of increased foraging rates.

4. Supplemented snakes (SUP): To have a known number and size distribution of previously marked snakes in the study population, we translocated 45 snakes [25 medium/large (SVL > 900 mm; mass > 100 g), and 20 small (SVL < 900 mm; mass < 50 g)] into the fenced area 4 months prior to the commencement of visual surveys. Tyrrell *et al.* (2009) found that these supplemented snakes had a slightly lower trap capture probability. We did not anticipate that residency status would affect visual detectability because snake translocation occurred 118 days prior to this study.

5. Recent detection history (LAG): We anticipated a strong increase in detection probability for snakes that had been recently detected, based on periodicity of this species' trap vulnerability [bouts of elevated capture probability lasted about seven consecutive days; Tyrrell *et al.* (2009)]. Considerations of such auto-correlated time effects were modelled using the results of the immediately preceding 1–4 sample occasions for each snake, where the covariate equalled 1 for each prior occasion on which the snake was detected, and 0 otherwise. Our notation for a time lag of n occasions indicates the model incorporated inclusion of lagged time effects from prior occasions 1, 2, 3... n (e.g. a model labelled 'LAG2' included the parameters: LAG1 and LAG2). Occasions in this study were not always consecutive days, the mean occasion length = 1·77 days ± 1·30 SD with the mode = 1 day.

6. Time (T, T^2 and T^3): Due to the long duration of the study, we considered temporal variation in detection probability by modelling linear (T), quadratic (T^2) and third-order polynomial (T^3) time trends.

7. Searcher team (TEAM): Because searchers were grouped in teams, detected snakes on a given occasion could not be associated with a unique searcher. Therefore, we modelled only the aggregate effect of each search team. We first calculated a mean detection rate per observer (based on the entire data set) and then summed the values for the four search team members to assign to each occasion a TEAM effectiveness covariate. We anticipated that searchers with high sighting rates (working as a team of four drawn from a pool of 10) would increase detection probabilities compared to teams with low sighting rates.

8. We explored the effect of five environmental covariates on the top model. We predicted that rainfall in the previous 6 h would be likely to elevate movements of *B. irregularis* due to reduced desiccation stress or increased prey availability (Daltry *et al.* 1998). However, this effect might be negated by the rain impeding visibility and the searcher's ability to work effectively (the glimmer of shiny ventral scales is harder to spot among foliage glistening with rain drops). Searches were not conducted during heavy rains. In open areas on Guam, *B. irregularis* have shown a reduction of activity during nights of bright moonlight (Rodda & Fritts 1992; see also Campbell, Mackessy & Clarke 2008); therefore, we anticipated a reduction of detectability under these conditions. Relative brightness of the moon (MOON) was classified into three distinct categories [0 = none, 1 = some (bright moon low on horizon or moon frequently obscured by clouds); 2 = nearly full moon usually in a mostly clear sky and well above the horizon]. We anticipated surveys with sustained wind (WIND) and strong gusts (GUSTS; maximum value) to reduce snake detectability because: (i) increased visual noise from swaying tree limbs would reduce the ability of observers to easily detect *B. irregularis*, (ii) increased movement of tree limbs would potentially reduce *B. irregularis* activity after snakes sought shelter and became less visually detectable. Wind speed was approximated by the average condition recorded for each occasion using the Beaufort scale.

We considered only two potential interaction terms (SEX × CI) and (SEX × SVL, SEX × SVL^2). Model selection was based on Akaike's Information Criterion corrected for small sample size (AIC_c) because AIC_c approximates AIC as sample size increases (Burnham & Anderson 2002:66). We model-averaged slope estimates over all models with a weighted average based on Akaike weights (Burnham & Anderson 2002:253). We used the 95% confidence limit for each slope estimate (β) to judge effect size importance.

Results

We obtained 654 visual detections of 117 individual *B. irregularis*, for a detected snake density of about 23 individuals per ha. Overall, visual detection probabilities were low for this population ($\hat{p}$ = 0·07 per occasion) but more than doubled given optimal circumstances outlined below ($\hat{p} \leq 0{\cdot}18$). Detection probabilities were best explained by models that incorporated effects of time, sex by SVL^2 interaction, recent detection history (LAG), CI, searcher team, moon phase/brightness and wind gusts (Table 1).

Time was best approximated by a quadratic function that revealed a decline in detections during the midpoint of the survey ($\hat{\beta}_{T^2}$ = 0·022 ± 0·006, 95% CL = 0·011, 0·033; Fig. 1). We found sex-specific differences in detectability that were a quadratic function of SVL^2, with both small and large females having *c.* 39% lower detection probabilities than males of the same size ($\hat{\beta}_{SEX \times SVL^2}$ = 2·106 ± 0·856, 95% CL = 0·428, 3·784; Fig. 2a). Our attempts to model size effects with discrete size classes failed to improve AIC_c values.

Observed body CI values ranged widely (0·543–1·684), with lower and upper 5th percentiles for this population of 0·74 and 1·25 respectively. Body CI indicated a slight tendency for low condition (skinnier) male and female snakes of all sizes (under typical environmental conditions) to be 42% more detectable (0·02; predicted range = 0·01–0·03) than snakes with high body condition ($\hat{\beta}_{CI}$ = −0·730 ± 0·398, 95% CL = −1·510, 0·050; Fig. 2b). Condition index trend and growth rate covariates were not supported.

There was strong support for incorporating the recent detection history of a snake (previous two occasions which is roughly equal to 3·5 days) into the model structure ($\hat{\beta}_{LAG1}$ = 0·293 ± 0·153, 95% CL = −0·006, 0·593; $\hat{\beta}_{LAG2}$ = 0·468 ± 0·145, 95% CL = 0·184, 0·752). On average, adding LAG2 roughly doubled detection probability (Fig. 3a). Models incorporating LAG3 and LAG4 received no support: the confidence intervals for these effects were centered on zero.

On any given occasion, a team of four searchers with the highest *B. irregularis* detection rates increased detection probabilities almost twofold over search teams with the lowest detection rates ($\hat{\beta}_{TEAM}$ = 0·238 ± 0·076, 95% CL = 0·090, 0·387; Fig. 3b).

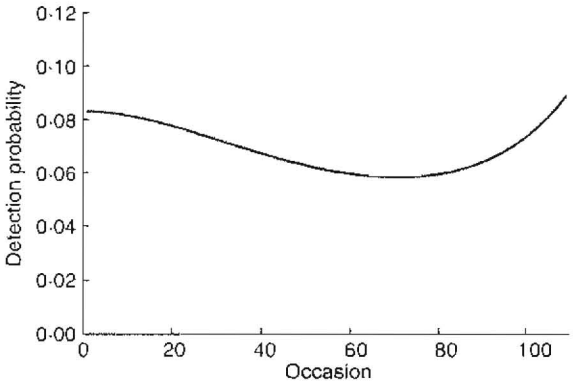

Fig. 1. Estimated detection probability for *Boiga irregularis* over time (27 September 2004–7 April 2005) in northern Guam using average covariate values for SVL (898 mm), body condition (0·99), and searcher team, along with typical environmental conditions of no moonlight and wind gusts between 20–28 km h^{-1}.

When added to the top model, residency status (SUP) had a very weak negative effect on detection probability ($\hat{\beta}_{SUP}$ = −0·128 ± 0·089, 95% CL = −0·302, 0·046). Estimated mean detection probability for translocated snakes was only 0·01 less than a similar resident snake. Adding the two environmental covariates of moonlight and wind gusts to the top model improved model fit; this new model had three times more weight than the same model without these covariates (Table 1). Of the two environmental covariates, moonlight ($\hat{\beta}_{MOON}$ = −0·118 ± 0·057, 95% CL = −0·229, −0·007; Fig. 4a) had a stronger effect than did wind gusts ($\hat{\beta}_{GUST}$ = −0·059 ± 0·033, 95% CL = −0·123, 0·006; Fig. 4b). Surveys on calm nights with no moonlight increase the probability of detecting female and male snakes of average size by 0·03 (42%) over nights with a full moon and strong wind gusts. Moonlight was present during 40% of occasions. Wind gusts > 20 km h^{-1} occurred during 54% of our night surveys. The other environ-

Table 1. Model selection results (95% confidence set) for detection probability (p) from program MARK (Pradel model) for *Boiga irregularis* on Guam, 2004–2005. All models shown below retain the probability of survival as a function of sex, body condition (CI), and snout-vent length (SVL), and recruitment as a linear function of time (T). Models are ranked by ascending ΔAIC_c; w_i is the model weight and K is the number of parameters. Sixty models were evaluated

p Models*	K	AIC_c	ΔAIC_c	w_i
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + MOON + GUST	20	5103·37	0·00	0·282
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + MOON	19	5104·41	1·04	0·168
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM	18	5105·57	2·20	0·094
T^2 + CI + LAG2 + SEX×SVL^2 + SUP + TEAM	19	5105·58	2·21	0·093
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + GUST	19	5105·69	2·32	0·089
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + WIND	19	5106·37	3·00	0·063
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + RAINp	19	5107·24	3·87	0·041
T^2 + CI + LAG2 + SEX×CI + SEX×SVL^2 + TEAM	19	5107·28	3·91	0·040
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + RAINn	19	5107·68	4·31	0·033
T^2 + CI + LAG2 + SEX×SVL^2 + TEAM + WIND + GUST	20	5107·73	4·37	0·032
T^3 + CI + LAG2 + SEX×CI + SEX×SVL^2 + TEAM	20	5108·92	5·55	0·018

*See methods for covariate definitions. Models containing high order polynomial effects include the corresponding lower order terms.

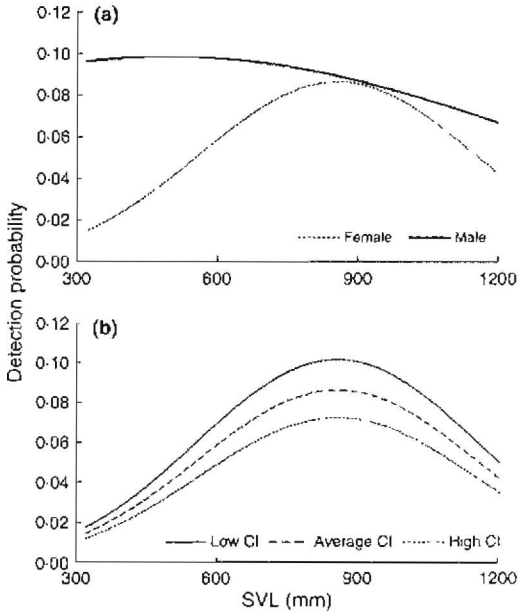

Fig. 2. Estimated detection probability of (a) male and female *Boiga irregularis* with an average condition index (CI = 0·99) at the beginning of the study, encountering no moonlight and wind gusts between 20 and 28 km h^{-1} (these conditions will be used in subsequent figures unless noted otherwise). Estimated detection probability for females (b) of low (0·74), average (0·99) and high (1·25) body condition with an average searcher team, no moonlight, and wind gusts between 20 and 28 km h^{-1}. A similar additive effect was seen in males but is not illustrated in this panel or subsequent figures.

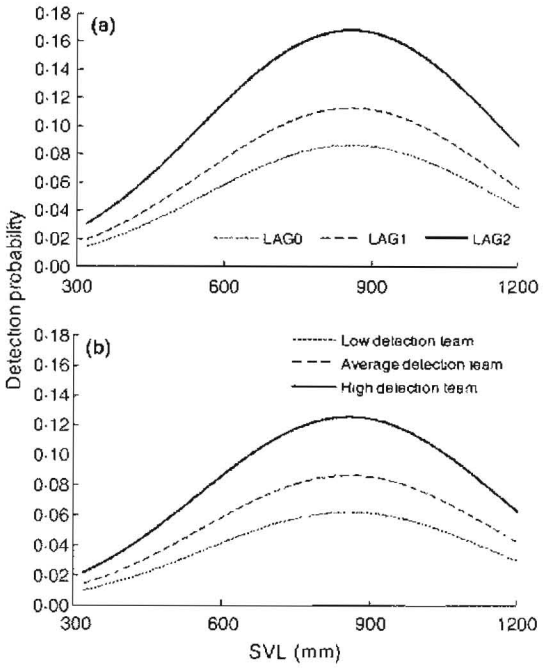

Fig. 3. Estimated detection probability for female *Boiga irregularis* of average body condition (CI = 0·99) with reference to detection history of previous two occasions (a): LAG0 = not seen on previous occasion, LAG1 = seen only on most recent occasion, LAG2 = seen on both prior occasions. The autocorrelation of detections indicates that individual snakes go through brief periods of high detection probability. Estimated detection probability for females of average body condition under varying search teams (b). Scale was adjusted in this panel to accommodate the effect of these covariates.

mental covariates had no support; the confidence limits on the beta estimates broadly overlap zero.

Discussion

Prior to Rodda *et al.* (2007), there was no known method for eradicating brown treesnakes (Rodda *et al.* 2002). Rodda *et al.* (2007) showed that visual searching was capable of removing all individuals, but did not quantify detection probabilities. The quantification of the detection probabilities that we provide here not only provides values that can be used for strategic planning of eradication efforts, it gives greater confidence in the practicality of eradication through visual searching. Mean daily detection probability through visual searching (0·07) was half of that achieved for vulnerable individuals through trapping (0·14), as reported in Tyrrell *et al.* (2009). Thus, visual searching will remove susceptible individuals at only about half the rate of traps, but because there are no individuals refractory to visual detection, visual searching can be used to remove all individuals (eradication), whereas trapping inevitably fails to capture the small snakes.

Our average visual searching removal rate (0·07) was not particularly high in comparison to other control tools (e.g. Tyrrell *et al.* 2009), but it indicates that eradication would be practical given adequate effort. Specifically, visual searches on 42 occasions would be necessary to ensure a 95% probability of removing the last individual in an area under average conditions similar to those in our enclosure and assuming no heterogeneity. However, our quantification of relevant environmental conditions and sources of individual variation in detectability allows us to now customize our searches more strategically, which should allow a population to be eradicated with less effort. For example, we found that search teams differed in efficacy, with about a twofold difference between quartets of searchers. If searching was to be used operationally for eradication, it might be prudent to employ searchers on the basis of above-average detection success rates. We found moonlight to be an important modulator of capture success, with capture success on moonless nights about 20% higher than with a full moon. A similar improvement was seen on windless nights. Thus, search efficacy could be improved by limiting searches to optimal search conditions (i.e. a high-detection search team conducting searches on nights with no wind or moonlight; $\hat{p}$ = 0·12). Under these optimal conditions, only 23 search occasions would be necessary to ensure a 95% chance of detecting any given individual. Thus, our quantitative results suggest that labour costs for an eradication could be reduced by about 45% through the strategic selection of search conditions.

Several of our evaluated covariates such as moonlight (Collier *et al.* 2007), time in season (Bailey, Simons & Pollock 2004) and searcher ability (Ralph & Scott 1981; Diefenbach,

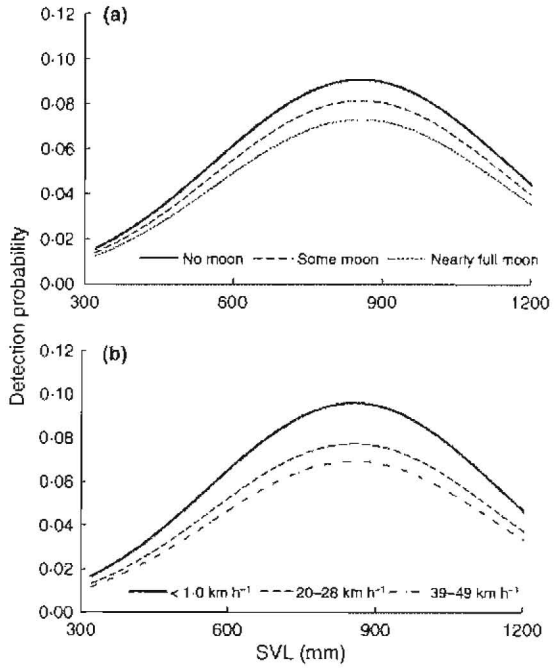

Fig. 4. Estimated detection probability for female *Boiga irregularis* of average body condition under varying amounts of moonlight (a) and under minimum, mode and maximum wind gust conditions (b).

Brauning & Mattice 2003) are known to affect visual detection in other species, as well as in *B. irregularis* (moon: Rodda & Fritts 1992; time in season: Tyrrell *et al.* 2009; searcher ability: Rodda & Fritts 1992; Lardner, Savidge & Rodda 2007). Choice of search season could potentially be optimized for a cost-effective eradication, but more information is needed to anticipate which seasons produce high efficacy.

The individually asynchronous episodes of higher detectability which we observed suggest another method by which visual searching can be made more effective: as temporarily less detectable snakes appear to cycle on a 4- to 7-day periodicity (with the biggest change registered over a period of about 4 days), an optimal search strategy would return searchers to a given locality roughly biweekly. In this way, searchers would be more likely to encounter a snake when it was at peak detectability. If the target search area is larger than that which can be searched on a single night, and it is desirable for searchers to work every night, it would be prudent to rotate effort from one geographic locality to the next on sequential nights, so that search effort is not wasted looking for snake individuals that remain in a condition of low detectability. As the magnitude of the detectability modulation is about twofold (Fig. 3), this phenomenon offers a substantial opportunity for detection rate enhancement.

A remarkable aspect of these individually asynchronous episodes of higher detectability is that an extremely similar phenomenon was observed in our quantification of trapping (Tyrrell *et al.* 2009). Although the periods of high trappability lasted 7 days, the largest enhancement was concentrated in the first 4 days. This finding is consistent with the visual survey results from this study, for which periods of elevated detectability lasted for two occasions, about 4 days. The existence of a comparable asynchronous episode of heightened detectability for both visual and trap detections provides a vital clue to the causation of the phenomenon, as it is therefore unlikely to be associated with a factor unique to either form of detection. For example, it is unlikely to reflect a behavioural response (such as trap happiness) unique to trap capture. The commonality in our trapping and visual search procedures is that all snakes were captured and handled, a seemingly aversive procedure. However, we observed the opposite of the expected trend for an aversive procedure. One would not expect that capture or handling *per se* would induce snakes to *increase* the probability of being detected on subsequent nights. Rather, it seems likely that the snakes exhibited intrinsic 4- to 7-day episodes of higher activity that resulted in increased detection by both methods. Intrinsic activity patterns may influence detectability in a wide range of species: Kerr, Bottema & Bull (2008) documented similar non-synchronized 6- and 2-day cycles in activity independent of weather conditions in a wild population of Australian sleepy lizards *Tiliqua rugosa* and proposed differing optimal thermoregulatory requirements for foraging and digestion as an explanation for the individual cycles. The lack of synchronicity in the brown treesnakes rules out causal explanations that invoke regional environmental conditions, and the length and regularity of the period would appear to rule out ecdysis or reproduction, but the cause remains to be identified.

One weakness of our study is that it involved only one study site. It is possible that the inferences we drew might be only partially generalizable to other areas. For example, to improve data density our study was conducted on an established medium-density population (23 snakes ha^{-1}). Thus, while we were able to precisely quantify detection probability under a variety of conditions, our estimates are strictly applicable only to a medium-density population. In a low density population, rarity of the targets would be likely to diminish searcher efficacy due to a lower positive reinforcement rate (Henke 1998), although experienced searchers may be able to maintain search effectiveness in the absence of frequent rewards. MacKenzie *et al.* (2005) advocated that information on detectability be 'borrowed' or inferred from other times, locations or even species. We think it reasonable to assume that our covariate effects are qualitatively density independent and would apply to visual searches in other areas.

Two of our covariates suggest features that would impair extrapolation from our study site to other areas: residency status (SUP) and CI. In both cases, the conditions ordinarily prevailing on Guam (resident snakes that are relatively skinny) would be more favourable for detection by visual searchers than would snakes in an incipient population on another island, where they might be newly displaced and well fed from the relatively greater abundance of prey (Rodda *et al.* 2008; Wiewel, Yackel Adams & Rodda 2009). Although both of these phenomena (SUP and CI) have been documented in other studies on Guam (CI: Boyarski 2005; CI: Gragg *et al.* 2007; SUP and CI: Tyrrell *et al.* 2009), we still lack sufficient

information to precisely predict how these effects would be manifest on a new island where brown treesnakes might get established. However, we can safely assume that conditions in a new population will be less favourable for detection than those we documented. These are the conditions under which minimum detectability is likely to occur, and which will determine the control effort needed for eradication.

If a new population were to develop a size distribution that was appreciably different from that in our study area, overall detectability could change. However, as detectability of males was relatively unaffected by body size and detectability of females was optimal for females of intermediate size, it would take a relatively large shift in size distribution to greatly alter overall detection probability. Detectability of large females has been tied to reproductive condition in other species of snakes (e.g. Luiselli 2006), but we regularly palped the females in our study population for developing follicles and did not detect evidence of reproduction at the time of our study. As *B. irregularis* on Guam are capable of breeding year-round (Savidge, Qualls & Rodda 2007), undetected gravidity should affect only a small proportion of females at any one time of year, and would have no bearing on the low detectability observed among juvenile females.

Some individual covariates modulated detectability by a factor of two or more (Figs 2 and 3), indicating considerable identified heterogeneity. Nonetheless in our system (our population and our search protocol), detection of the last individual required only slightly more than the 42 searches projected by simple extrapolation (no heterogeneity) of our mean detectability (0·07: see second paragraph of Discussion). In actuality, we needed only 47 searches to detect the last individual in our population (Rodda *et al.* 2007).

Latent heterogeneity was relatively minor in our searches, in contrast to our trap captures (Tyrrell *et al.* 2009). Unlike the nearly co-equal heterogeneity classes observed in trap capture, 95% of the individuals in our study were in the dominant heterogeneity class and the small number of remaining individuals were only slightly less detectable. Because latent heterogeneity was minor, extrapolation from the least detectable class will be a reasonable approximation of the needed eradication effort. To the extent that our results are generalizable, we can estimate eradication effort under any arbitrary distribution of snake covariates and environmental conditions

This study, in combination with Tyrrell *et al.* (2009) and other supporting evidence, led to the radical restructuring of brown treesnake management efforts for incipient populations (where eradication is the immediate focus). Prior to this work, it was assumed that visual searches were insufficient to warrant their use. Furthermore, it was not fully appreciated that visual searching exhibited much lower individual capture heterogeneity than did trapping. Thus, the management response to sightings of *B. irregularis* on previously snake-free islands was formerly addressed by the setting of traps at the site where the snake was sighted (Stanford & Rodda 2007). Although trapping had not been demonstrated to be effective, it was adopted on the basis that no better tool was available. Tyrrell *et al.* (2009) confirmed that traps were ineffective for small snakes. The present work demonstrates that although the detectability of *B. irregularis* by visual searching is low, the detectability of small snakes by vision is greater than by trapping. Vice & Vice (2004) demonstrated that most of the snakes appearing in cargo leaving Guam were too small to be trapped. The discovery that visual searching was not only practical for *B. irregularis* detection but optimal (among extant techniques) for detection of small snakes therefore revolutionized snake management on recipient islands and induced the formation of a mobile interagency team of highly trained visual searchers that is deployed to address sightings of snakes on previously snake-free islands (Stanford & Rodda 2007). Although our modelling was specific to one high-profile invasive species, many of the numerous factors we identified, several of them novel, should apply to other species as well. Improved understanding of detectability can play a large role in improving not only invasive species management, but any activity sensitive to detectability, including the estimation of survival, occupancy and abundance.

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