Journal of Applied Ecology

Journal of Applied Ecology 2009, **46**, 128–135 doi: 10.1111/j.1365-2664.2008.01591.x

Evaluation of trap capture in a geographically closed population of brown treesnakes on Guam

Claudine L. Tyrrell[1], Michelle T. Christy[1], Gordon H. Rodda[2]*, Amy A. Yackel Adams[2], Aaron R. Ellingson[2], Julie A. Savidge[1], Kathy Dean-Bradley[2] and Richard Bischof[2]

[1]*Department of Fish, Wildlife, and Conservation Biology, Colorado State University, Fort Collins, CO 80523, USA; and* [2]*USGS Fort Collins Science Center, 2150 Centre Avenue, Bldg C, Fort Collins, CO 80526, USA*

Summary

1. Open population mark–recapture analysis of unbounded populations accommodates some types of closure violations (e.g. emigration, immigration). In contrast, closed population analysis of such populations readily allows estimation of capture heterogeneity and behavioural response, but requires crucial assumptions about closure (e.g. no permanent emigration) that are suspect and rarely tested empirically.

2. In 2003, we erected a double-sided barrier to prevent movement of snakes in or out of a 5-ha semi-forested study site in northern Guam. This geographically closed population of >100 snakes was monitored using a series of transects for visual searches and a 13 × 13 trapping array, with the aim of marking all snakes within the site. Forty-five marked snakes were also supplemented into the resident population to quantify the efficacy of our sampling methods. We used the program MARK to analyse trap captures (101 occasions), referenced to census data from visual surveys, and quantified heterogeneity, behavioural response, and size bias in trappability. Analytical inclusion of untrapped individuals greatly improved precision in the estimation of some covariate effects.

3. A novel discovery was that trap captures for individual snakes consisted of asynchronous bouts of high capture probability lasting about 7 days (ephemeral behavioural effect). There was modest behavioural response (trap happiness) and significant latent (unexplained) heterogeneity, with small influences on capture success of date, gender, residency status (translocated or not), and body condition.

4. Trapping was shown to be an effective tool for eradicating large brown treesnakes *Boiga irregularis* (>900 mm snout-vent length, SVL).

5. *Synthesis and applications.* Mark–recapture modelling is commonly used by ecological managers to estimate populations. However, existing models involve making assumptions about either closure violations or response to capture. Physical closure of our population on a landscape scale allowed us to determine the relative importance of covariates influencing capture probability (body size, trappability periods, and latent heterogeneity). This information was used to develop models in which different segments of the population could be assigned different probabilities of capture, and suggests that modelling of open populations should incorporate easily measured, but potentially overlooked, parameters such as body size or condition.

Key-words: behavioural response, *Boiga irregularis*, capture heterogeneity, ephemeral effect, Huggins closed capture model, invasive species, size selectivity

Introduction

Density estimation is one of the fundamental steps in modelling population dynamics in ecology, and for controlling invasive species, such as the brown treesnake *Boiga irregularis* (Bechstein 1802), an introduced predator on the Pacific island of Guam (Savidge 1987). Search effort indices, and open and closed models for density estimation each involve a variety of assumptions. Prompted by difficulties encountered in past attempts to obtain precise and accurate estimates of population size and composition for *B. irregularis*, we aimed to develop a system for assessing some of these assumptions.

Initial attempts to assess population densities in the 1980s using search effort indices (numbers of snakes sighted per hour), failed to reveal high absolute densities, with bias from variable detection rates and uncontrolled factors such as

*Correspondence author. E-mail: gordon_rodda@usgs.gov.

© 2008 The Authors. Journal compilation © 2008 British Ecological Society

observer, habitat, time, and environmental conditions (Rodda & Fritts 1992). Mark–recapture trapping studies were also problematic, with analyses dependent upon unreliable assumptions of equal catchability ('open' models), or population closure ('closed' models) in sites exhibiting high daily rates of emigration and immigration. This was illustrated when a study in 2000 at Munitions Storage Area, Andersen Air Force Base, Guam, showed a high incidence of bait removal in an area following 11 months of snake trapping, suggesting that *B. irregularis* were present in much higher densities than estimated from the low trap yields (National Wildlife Research Center 2003). Such results led to hypotheses of 'untrappable' snakes, and concern that trap capture heterogeneity was causing the trap-based control programme to miss a significant stratum of the snake population (Rodda *et al.* 2002).

To address the conflicting assumptions that underlay previous studies, we used a snake barrier to create a geographically closed population of *B. irregularis*, thereby eliminating immigration and emigration and allowing for use of closed population models capable of directly estimating behavioural response and capture heterogeneity. Predator and prey exclosures and augmentation have been used to manipulate density of focal species (Crawley 1992; Krebs, Boutin & Boonstra 2001), but confinement of focal species was not carried out in these studies, nor was population estimation the focus of the manipulation. To our knowledge, physical closure of a population has not been used for refining population estimation techniques for any species of reptile or amphibian, and only rarely for other taxa (Parmenter *et al.* 2003). However, the closure objective of the latter study was to fix total abundance for validation of various closed model analyses. Our closure objective was to eliminate population flux, allowing quantification of behaviours influencing capture [capture heterogeneity, enduring and ephemeral behavioural effects (see Yang & Chao 2005)] that are difficult to assess in an open population. In addition, 45 hand-caught snakes of varying size and sex were translocated from the surrounding area into the closed population to provide a known subpopulation for capture; thus, we could determine whether any strata of the population were untrappable. We present mark–recapture analyses from 101 days of trapping, based on 104 individuals known to have been present based on a subsequent census via visual surveys.

Materials and methods

STUDY SITE

In 2003, we created a geographically closed population by erecting a snake barrier to prevent movement of snakes in and out of a 5-ha study site on Andersen Air Force Base, northern Guam. The site, north of the runway complex known as Northwest Field, and described by Rodda *et al.* (2007), sits on a coralline limestone plateau about 170 m above sea level (Stone 1970). Representative of *B. irregularis* habitat on Guam, the area had been highly disturbed and much of the native vegetation affected by human activity. Vegetation was a partially forested mix of trees (*Leucaena leucocephala*, *Morinda citrifolia*, *Triphasia trifolia* and *Hibiscus tiliaceous*), small shrubs, invasive herbs (*Chromolaena odorata*, *Stachytarpheta jamaicensis* and *S. urticifolia*) and herbaceous vines, particularly *Mikania micrantha*. Higher-level predators were absent, but prey species were free to enter and leave the study site. Brown treesnakes were the only snakes found in the study site, except for tiny subterranean snakes (*Ramphotyphlops braminus*), which were not caught by the traps we used.

GEOGRAPHIC CLOSURE

We constructed a double-sided chain-link bulge barrier fence to prevent migration by snakes in or out of the study site (see Perry *et al.* 1998 for single-sided bulge barrier design; double-sided design illustrated in Rodda *et al.* 2007). The 1·5-m tall fence, consisting of support poles sandwiched between two layers of chain-link overlaid with hardware cloth (6-mm welded steel mesh), incorporated 100-mm radius overhangs of hardware cloth on the inner and outer faces at the top. A 0·6-m-wide concrete footer on either side inhibited vegetation, and anchored a skirt of hardware cloth that extended out from the base of the fence. Vegetation was cleared from transects and within 2 m of either side of the fence line, and re-cut as necessary to maintain these spaces. The inside corners of the fence were two 135° corners linked by a 3·5-m long diagonal panel (*B. irregularis* can climb 90° corners, Perry *et al.* 1998). The barrier was continuous, and portable ladders were used for entry and exit by staff. To allow population equilibration following fence construction, but prior to data collection, natural woody vegetation was placed against the fence at 10–20 m intervals for a period of 6–7 weeks, during which time any snakes displaced by fence construction could enter and exit. Barrier closure was assessed by monitoring traps outside the fence for potential escapees and marking potential invader snakes.

SUPPLEMENTATION OF SNAKES

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 snakes (SVL <900 mm; mass <50 g)] into the fenced site after full closure, prior to trapping. All were hand-captured during visual surveys adjacent to the study site, and none had previously experienced a snake trap. Prior to release at random locations within the site, all translocated snakes were measured, sexed, and marked following standard protocols (see below).

TRAPPING

Snake trapping commenced on 2 June 2004, and ran daily until 14 September 2004 (with brief interruptions for typhoons Chaba and Tingting). The trapping array had 13 × 13 traps equally spaced at 16-m intervals, uniformly covering the study site. Snake traps had the same entrance flaps used in operational trapping by Wildlife Services, but the trap bodies were slightly shorter (Rodda *et al.* 1999a). As with operational trapping, traps were suspended horizontally from rebar or natural vegetation on 9-gauge wire at around 1 m high. Within each trap, a chamber (200 × 100 × 45 mm) walled with 3-mm metal mesh housed and protected a live attractant mouse. Traps were checked each morning, and the grain mix and potatoes providing food and water for mice replenished as needed. Any dead bait mice were replaced immediately when possible, or within 2 days; dead mice have been shown to be roughly as effective as live mice for the first 2–3 days (Shivik & Clark 1997, 1999).

All trapped snakes were checked for identifying PIT tags and scale clips. Any unmarked snakes received both unique marks. Measurements of mass (using Pesola® spring scales), SVL and total length (by gentle stretching against a tape measure) were recorded on the first three capture occasions for each snake. We determined sex either by everting hemipenes, or using a suitable-sized snake probe on the left side of the cloaca only. When gender had been judged the same over at least three occasions, sexing was discontinued. Similarly, no more than three length and mass measurements were collected during any 30-day period. These stipulations were designed to minimize potential impacts to snakes of stretching and probing. All snakes were released at their point of capture following marking and measuring (within minutes of trap checking).

VISUAL SURVEYS

One hundred and nine visual surveys of the snake population were conducted after 101 trapping occasions. These visual surveys (reported elsewhere) revealed individual snakes that had been present but undetected throughout the trapping period. These individuals were added to the trap capture history matrix in the form of an appropriate string of zero captures, along with their individual covariates, to provide a more complete portrait of the individual traits associated with trap capture. To incorporate these untrapped individuals into the capture probability analysis, a dummy (102nd) occasion was added to the overall capture history matrix, but capture probabilities were not estimated for the dummy occasion (i.e. initial and recapture probabilities were fixed = 1 for this dummy occasion and did not affect overall capture probability estimates).

ANALYSIS OF CAPTURE HISTORIES TO ESTIMATE CAPTURE PROBABILITY

Our analysis focused on modelling sources of variation in trappability and estimating trappability; abundance estimation was excluded. All models were based on a conditional likelihood (Huggins 1989, 1991), but the usual inferential limitation of this approach (basing estimates strictly on captured individuals) was overcome by including untrapped individuals known from the visual surveys to have been present. In the program MARK, we used closed population mark–recapture models that allowed individual variation in trappability by measured covariates, latent (unexplained) heterogeneity through mixtures, or both. The global model included: effects for capture occasion (time), individual effects for body size, gender, residency status (translocated or resident), body condition, recent capture history, and latent individual heterogeneity.

Following the notation of Pledger (2000), the probability of capture of animal i on occasion j, p_{ij}, is assumed to be θ_{jha}, which is modelled with a linear logistic formulation:

$$\log\left(\frac{\theta_{jha}}{1-\theta_{jha}}\right) = \mu + \tau_j + \alpha_h + \eta_a + (\alpha\eta)_{ha} + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_k X_k$$

where μ is a constant parameter, τ_j (time) is a fixed main effect depending on the occasion j, α_h is a fixed behaviour main effect ($b = b_{ij} = 1$, if animal i was not caught before occasion j; otherwise $b = 2$), and η_a is a random main effect for latent heterogeneity where $a = 1, \ldots, A$ with probabilities $\pi_1, \ldots, \pi_A$, respectively. The term $(\alpha\eta)_{ha}$ is an interaction between behavioural response and the random effect for latent heterogeneity, allowing for heterogeneity in trap response. The remaining terms ($\beta_1 X_1, \ldots, \beta_k X_k$) represent individual covariates for each snake. Some covariates required multiple terms. For example, size was modelled as linear ($K = 1$) and quadratic ($K = 2$) functions, as well as, six size classes ($K = 5$). Significant parsimony was gained by modelling the time effect (τ_j) as a smooth function of the 101 occasion parameters ($j = 1, 2, \ldots, 101$):

$$\tau_j = \gamma_0 + \gamma_1 j^1 + \gamma_2 j^2 + \gamma_3 j^3$$

where the γs are the polynomial coefficients.

This is a version of the general M_{tbh} model of Otis *et al.* (1978). Although Pledger (2000) suggested that individual covariates and mixture models (models that partition animals into two or more groups with similar capture probabilities) may be combined in closed population mark–recapture models, this is the first instance we know of where field data have been fit to such hybridized models.

Models were fitted to data by maximum likelihood. Candidate models included subsets of parameters in the global model. 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). Models were considered competitive with the top-ranked model when $\Delta AIC_c \leq 2{\cdot}0$. Because of model selection uncertainty (models with $\Delta AIC_c < 7$ can be plausible; Burnham & Anderson 2002:70), we model-averaged effect sizes over all 14 models with a weighted average based on Akaike weights (Burnham & Anderson 2002:253, equation 5·8) to generate figures.

COVARIATES

As the size and body condition of snakes changed over the trapping period, multiple body size (SVL) measurements for each snake were regressed against time to estimate its average growth rate. Based on these linear regressions, the expected length for each snake on occasion 51 (midpoint of trapping session) was used in analyses. Size of snakes detected by visual survey following the trapping session (but never trapped), was extrapolated from linear regression of measurements taken during visual surveys, and the expected value at trapping occasion 51 used in analyses. Nineteen individuals whose size and growth rate indicated a possible hatching date after the start of trapping were excluded from this analysis.

Condition index was calculated as the ratio of individual body mass to expected mass given its length. Expected body masses for a given length were estimated by linear regression on logarithmic scales, based on over 5000 records of length and mass of *B. irregularis* sampled on Guam during 1980–2004.

In these models, we considered recent capture history as a covariate to determine whether snakes showed evidence of an ephemeral behavioural effect having a duration longer than one occasion (i.e. >24 h), unlike Yang & Chao (2005) who evaluated the ephemeral effect for only one occasion. Such autocorrelated time effects were modelled using the results of the immediately preceding 1–12 sample occasions for each snake, where the covariate equalled 1 for each prior occasion on which the snake was captured, and 0 otherwise. Our notation for a time lag of n days indicates the model incorporated inclusion of lagged time effects from days 1, 2, 3 ... n days (e.g. a model labelled 'LAG3' included three extra parameters: LAG1, LAG2, and LAG3).

Despite modelling several important covariates, our models also supported two mixtures, indicating unexplained (latent) capture heterogeneity. We explored the correlates of this latent heterogeneity in our top model, using Bayes' rule to assign snake posterior probabilities to our two heterogeneity classes: low and high capture

Table 1. Model selection results from the program MARK (using Huggins Full Heterogeneity Model) for a geographically closed population of brown treesnakes on Guam, 2004. Models with lowest AIC_c are considered best. ΔAIC_c is the difference in AIC_c between the current model and the top model (Burnham & Anderson 2002). K is the number of parameters in each model and w_i represents Akaike's model weight

Models[a]	K	AIC_c	ΔAIC_c	w_i
T^3 + b + h + SZ + SEX × CI + SUP + LAG7	23	6708·29	0·00	0·299
T^3 + b + h + SZ + SEX + SUP + LAG7	21	6708·35	0·06	0·289
T^3 + b + h + SZ + SEX + LAG7	20	6709·70	1·41	0·148
T^3 + b + h + SZ + SEX + SUP + CI + LAG7	22	6710·14	1·85	0·118
T^3 + b + h + SZ + LAG7	19	6711·27	2·98	0·067
T^3 + b × SZ + h + LAG7	24	6712·59	4·31	0·035
T^3 + b × h + SZ + LAG7	20	6713·14	4·85	0·026
T^3 + h + SZ + LAG7	18	6714·07	5·78	0·017
T^3 + b × h + SZ + SEX × CI + SUP + LAG7	24	6721·07	12·79	0·001
T^3 + h + SZ + SEX × CI + SUP + LAG7	22	6724·12	15·84	0·000
T^3 + b + h × SZ + LAG7	24	6780·13	71·85	0·000
T^3 + b × h + SZ + SEX × CI + SUP	17	6839·41	131·12	0·000
T^3 + b + h + SZ + SEX × CI + SUP	16	6856·16	147·87	0·000
T^3 + b + h + SZ	12	6863·83	155·55	0·000

[a]All models listed above used two finite mixtures to approximate individual heterogeneity (K = 1) and contain an intercept term. Capture probability is modelled as a function of: time in season as a cubic trend (T^3); behaviour (b); heterogeneity (h); size class of snake (SZ; K = 5); sex of snake (SEX); resident status (SUP); condition index (CI); recent capture history used to evaluate ephemeral behavioural effect (LAG7; K = 6); and the interactions of behaviour and heterogeneity (b × h), behaviour and size class (b × SZ), heterogeneity and size class (h × SZ), and sex and condition index (SEX × CI). Models containing high order polynomial effects contain the corresponding lower order terms and interactive models include the corresponding main effects.

probabilities (Pledger, Pollock & Norris 2003). The following five characteristics, related either to habitat use or body condition metrics, were compared with assigned posterior probabilities (>0·50, n = 81) to identify snake traits potentially discriminating between individuals of low and high recapture: (i) mean log of activity area, as defined by minimum convex polygon of captures; (ii) mean log distance moved per day; (iii) habitat associations of capture locations, in three strata: limestone forest (10·9% of site), degraded forest (44·1%), and non-forest (45%); (iv) growth index corrected for sex and size (observed growth divided by expected growth for an animal of that body length and sex); and, (v) trend of condition index (slope of regression of each individual's condition index against date).

Sample sizes differed for body condition trend (n = 72 snakes) and habitat (n = 61 snakes) analyses, as we only included snakes with at least 3 or 4 captures, respectively. Habitat associations were calculated as the number of captures in a given habitat divided by total captures for that individual. We used parametric t-tests and nonparametric tests so that critical assumptions could be met. Two-tailed tests were used except when testing the proportion of captures of *B. irregularis* in non-forest habitat (as low capture probabilities are typically associated with this habitat type, we predicted that the low capture class would have a higher proportion of captures relative to the high capture class). Since several snakes were near the boundary between heterogeneity classes (e.g. posterior probability of 0·51), we also performed these analyses on a subset of data that included only individuals with posterior probabilities >0·75 (n = 68 snakes).

Results

Recaptures of marked snakes on both sides of the snake barrier (>350 individuals marked outside; 122 marked inside; >3000 captures) revealed no emigration or immigration of snakes across the barrier. Of the 45 snakes translocated into the population, 44 were recaptured inside the barrier, either via trapping (1402 captures: 25 of 25 large and 6% of 20 small snakes), or visual survey (1010 captures: 22 of 25 large and 19 of 20 small snakes). The continued presence of the translocated snakes (none captured outside, despite presumed motivation to return to their original location) reflected the effectiveness of the barrier (Rodda *et al.* 2007). Closed population mark–recapture models were therefore used with assurance of geographic population closure.

There was overwhelming support for time and body size effects (Table 1), with a positive correlation between size and trappability (Fig. 1), and temporal variation in overall trappability (best approximated by a third-order polynomial that allowed smooth variation over trapping period; Fig. 2). All plausible models contained size as an effect; the best model without size resulted in a ΔAIC_c of 244·11, indicating a total lack of support relative to models with size. Our attempts to model size effects with continuous polynomial functions (simple, quadratic, or cubic) failed to improve AIC_c beyond fitting size as a function of six groups (n = 12–37, varying by group); thus, all subsequent models are based on six 100-mm wide classes to account for size selectivity of the traps.

The AIC_c values for models containing autocorrelated time effects (LAG7) indicated strong evidence for an ephemeral behavioural effect in individual snake trappability (Table 1). The best model without ephemeral trappability resulted in a ΔAIC_c of 131·12, indicating there was negligible support for such models in these data. Interestingly, if ephemeral trappability was excluded, models with heterogeneity in trap response interactions were favoured over those with additive trap responses (Fig. 3). It appears that individual temporal changes in trappability may be confused for traditional trap behavioural responses, that is, enduring trap-happy or trap-shy responses (Otis *et al.* 1978), if individual ephemeral effects are not modelled. While a modest behavioural response

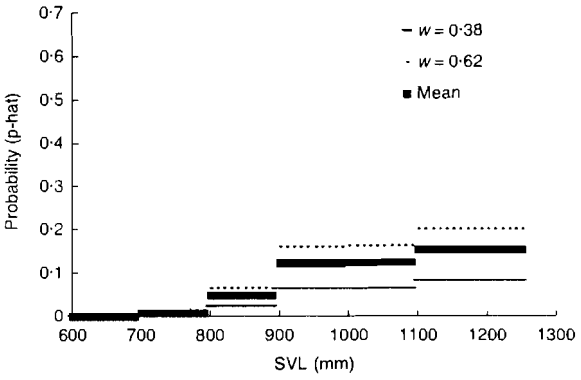

Fig. 1. Model-averaged probability of first capture for resident females of average condition index (CI = 0·914), showing the size function in trappability for the two distributions that form the overall mixture (thin lines) and overall mean (heavy solid line). The thin dashed line is the central tendency of a distribution constituting 62·3% of the population; the remaining distribution (thin solid line) therefore accounted for 37·7%. The spread between the individual distributions is a mixture-model representation of the latent individual heterogeneity not accounted for by the covariates in the model.

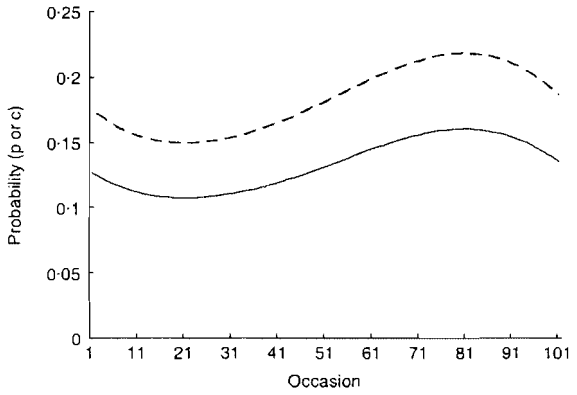

Fig. 2. Estimated capture (p, solid line) and recapture (c, dashed line) probabilities for large female resident brown treesnakes (900–999 SVL) of average condition index (CI = 0·914) over time, after applying a third-order polynomial to approximate temporal variation in overall trappability.

persisted (see below) in preferred models incorporating ephemeral trappability (Table 1), this did not include a strong enduring behavioural response or an enduring behaviour response × heterogeneity interaction.

As seen in Fig. 4, inclusion of a capture during each of LAG1–LAG4 dramatically and cumulatively increased expected capture probability, but inclusion of LAG5–LAG7 improved capture probability only relatively modestly. Inclusion of LAG8 captures (not shown in Table 1) marginally decreased capture probability relative to LAG7. Inclusion of LAG9–LAG12 in models did not improve AIC_c and all such additional covariates had beta values with confidence limits that broadly overlapped zero. Thus, it appears that most of the information provided by lags was in the days preceding a capture event, with negligible improvement in predictability after 7 days.

A model structure that used results of the prior seven trap occasions (LAG1–LAG7) as individual covariates was

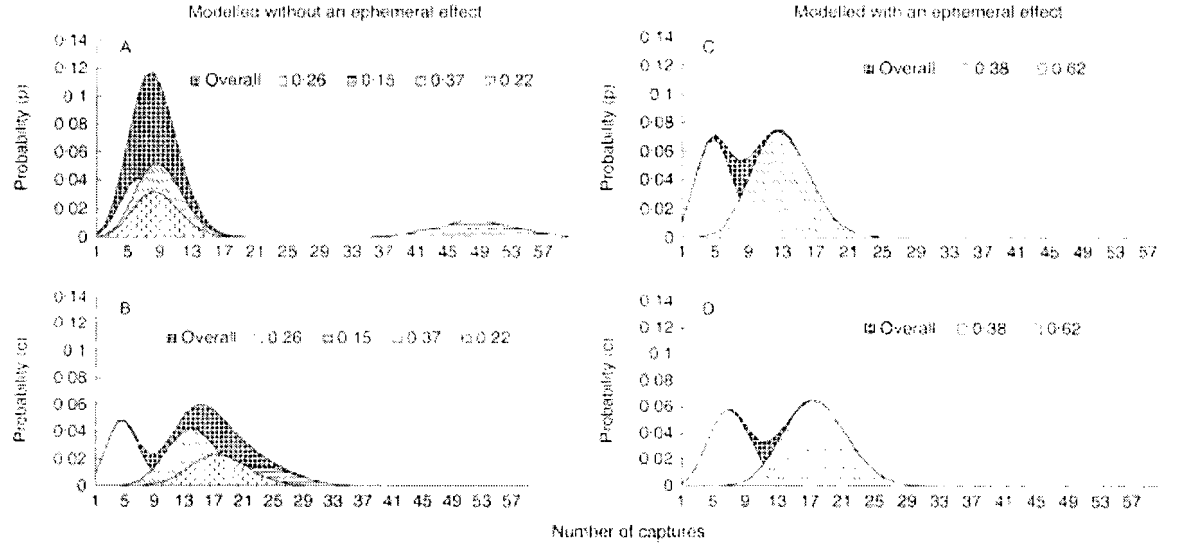

Fig. 3. In an analysis considering the effects of all covariates except an ephemeral behavioural effect, we found strong support for four-mixture models versus the same models with three or two mixtures. The presence of four mixtures in the top model (T^3 + b*h + SZ) does not necessarily imply four discrete classes of snakes, but rather a strong divergence in response to initial (p) and subsequent capture (c) as shown in 3A and 3B, respectively. The latent heterogeneity from this model was approximated by a mixture of four classes that comprised 26%, 15%, 37% and 22% of the population. Some of this latent heterogeneity in capture probability is explained when the previous-week capture history of an individual is considered (LAG7) and is demonstrated by a simplification of the distributions for p (Fig. 3C) and c (Fig. 3D) using the top model that supports two mixtures (T^3 + b + h + SZ + SEX*CI + SUP + LAG7). In contrast to the four-mixture model, the latent heterogeneity from this model is approximated by a mixture of two classes that comprise 38% and 62% of the population.

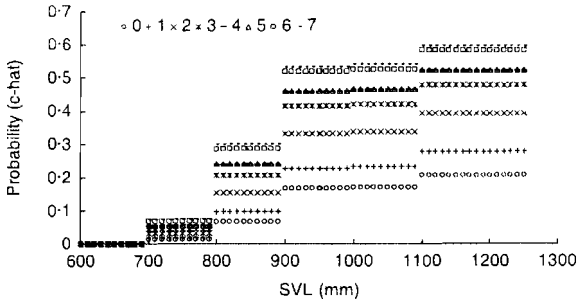

Fig. 4. Mean recapture probability for female resident of average condition index (CI = 0·914) that has been captured on prior occasions. 0 = not caught on previous occasion (o), 1 = caught on first prior occasion (+), 2 = caught on both first and second prior occasions (×), 3 = caught on first, second, and third prior occasions (*), and so on (4 = –, 5 = Δ, 6 = □) to 7 = caught on all seven prior occasions (–). The autocorrelation of captures indicates that individual snakes are going through periods of high capture probability. This effect is larger than any other covariate in the model.

overwhelmingly supported by these data, and the estimated effect sizes were much larger than those for any covariate other than size. For example, estimated mean capture probability for an average sized female resident increased by 0·11 if she had been caught the previous day. A snake that had been caught each of the prior seven occasions (an event that occurred several times) netted an estimated increase in mean capture probability of 0·41, an effect at least 10 times larger than those estimated for gender, resident status, enduring behavioural response, or condition index.

Relatively minor effect sizes were found for the individual covariates of gender and residency status. For an average sized snake (900–1000 mm SVL), estimated mean capture probability differed by only 0·02 between genders, with males 13% less trappable than females. The effect of being translocated (supplemented) was similar in magnitude. Estimated mean capture probability for translocated snakes was 0·03 less than similar resident snakes in the 900–1000 mm SVL range. Condition index effects on capture were relatively small in males, and virtually non-existent in females. The lower and upper fifth percentiles of condition index were less variable for males (0·80, 1·03) than for females (0·75, 1·05). Considering average sized females, the difference in capture probability for snakes of these condition index values was only 0·01. However, the same comparison for males resulted in low condition index (i.e. skinnier) snakes having estimated mean capture probabilities 0·04 greater than snakes of high condition index.

Even after accounting for associations between capture probability and individual covariates, consistent support for heterogeneity models indicated that a significant amount of latent individual heterogeneity remained. That is, individual snakes differed in capture probability in ways that were not explained by the included covariates. According to the top model, latent heterogeneity was approximated by a mixture of two latent classes of snakes that comprised 37·6% and 62·4% of the population, respectively. The smaller latent class had lower capture and recapture probabilities than the larger latent class; these differences constituted an effect size on par with those of body size and capture history, much larger than those measured for gender, residency, or condition index.

Of the five potential distinctions examined in *post hoc* analysis of low and high latent heterogeneity classes, only habitat association explained some of the latent heterogeneity in this population using posterior probabilities >0·50. A total of 1383 captures were associated with habitat (limestone forest, degraded forest, or non-forest). As predicted, in non-forest habitat, snakes assigned to the low capture class actually were more likely to be trapped than snakes assigned to the high capture class ($\bar{x}_{low} = 0{\cdot}51 \pm 0{\cdot}22$, $n = 27$, $\bar{x}_{high} = 0{\cdot}42 \pm 0{\cdot}20$, $n = 43$; $Z = 1{\cdot}86$, $P = 0{\cdot}03$); however, there was no difference between the two groups in either limestone forest ($\bar{x}_{low} = 0{\cdot}11 \pm 0{\cdot}19$, $n = 27$, $\bar{x}_{high} = 0{\cdot}12 \pm 0{\cdot}20$, $n = 43$; $Z = -0{\cdot}16$, $P = 0{\cdot}87$) or degraded forest ($\bar{x}_{low} = 0{\cdot}39 \pm 0{\cdot}17$, $n = 27$, $\bar{x}_{high} = 0{\cdot}45 \pm 0{\cdot}19$, $n = 43$; $Z = -1{\cdot}49$, $P = 0{\cdot}14$). When the smaller subset of snakes (with posterior probabilities >0·75) was used, none of the five characteristics explained latent heterogeneity at the $P < 0{\cdot}05$ level.

Discussion

The physical closure of a continuous population allowed us, on a landscape scale, to assess factors contributing to capture heterogeneity and thus improve mark–recapture models, without having to resort to the usual tactics of relying on habitat discontinuities or short time intervals to mitigate problems caused by lack of closure (Pollock & Otto 1983; Kendall, Pollock & Brownie 1995). Heterogeneity may induce very strong abundance estimation bias when detection probabilities are low (Pollock & Otto 1983; Pledger 2005), as in brown treesnakes and other cryptic, nocturnal species, but the amount of capture heterogeneity in open populations is almost never quantified (Pledger, Pollock & Norris 2003). As part of the move to incorporate mechanisms to compare the relative value of survey techniques for detecting species (Gompper *et al.* 2006), we are taking the next step of checking assumptions underlying the models. For example, the use of data from visual surveys allowed trappability to be estimated for the entire population of snakes present during the sampling period, not just those snakes that were actually captured.

Of the covariates we found to influence capture heterogeneity, body size was the most important. Capture probabilities for trapping were high for large snakes (>900 mm SVL), but negligible for small snakes (<800 mm SVL); with an abrupt and strong shift in trappability occurring in the 700–900 mm SVL size range. Attainment of full trappability coincided with the onset of reproductive maturity (Savidge, Qualls & Rodda 2007) and dietary shift toward endothermic prey (Savidge 1988). The effect of body size on trappability of brown treesnakes has been found in several studies (e.g. Rodda *et al.* 1999b, 2002, 2007); and, in combination with present confirmation using a relatively large sample size and known population, evidence for size selectivity in trapping of *B. irregularis* is nearly unequivocal. The capture probabilities we obtained for snakes <800 mm SVL (Figs 1 and 4) were so

low that precise population estimates for juvenile sizes would be difficult to obtain by trapping.

However, after size effects were accounted for, significant variation among individuals still remained, some of which could be explained by the snake's recent capture history, and some of which was modelled as latent heterogeneity. Comparatively, differences among gender, residency status, behavioural response, or body condition indices were small, but implied that capture probabilities were higher in skinnier snakes, once-captured snakes, females, and residents. The minor behavioural response exhibited was one of trap-happiness. Open models for abundance estimation, which do not easily accommodate behavioural response, and which relies on the assumption of equal catchability (all snakes caught with the probability exhibited by the more trappable snakes), will therefore underestimate abundance.

It was unexpected that snake condition index was only weakly correlated with capture probability (skinnier snakes more easily trapped), as capture probability of *B. irregularis* was previously found to be strongly correlated with body condition index at single sites (Gragg 2004; Boyarski 2005), and in a meta-analysis of multiple sites on Guam (G. H. Rodda, unpublished data).

The strong temporal autocorrelations were indicative of individual periods of trappability. That is, individual snakes appeared to go through periods of higher trappability, then periods of low trappability. These periods were asynchronous, and therefore did not manifest as a time effect, as they would have if snakes were responding to weather or any other concurrently experienced phenomenon. The lagged model structure used is essentially the same as autoregressive models in time-series analysis and the interpretation is the same. The proximate cause for individual ephemeral trappability is not known but is unlikely to be associated with traps because ephemeral effects are also supported when modelling visual survey data from this population (M. Christy, A. Yackel Adams, G. Rodda, J. Savidge, and C. Tyrrell, unpublished data). We have not called this effect a behavioural response (Yang & Chao 2005), because we are not convinced that the ephemeral behaviour is a response to the experience of capture. Instead, our ephemeral effects are hypothesized to be related to physiological cycles in the snake such as short-term satiety, moulting, or reproduction. Of these, short-term satiety is the most likely and plausible for the 7 days length detected, as a sated snake may be less motivated to enter a trap containing a prey-based attractant. Moulting also takes about 7 days in *B. irregularis*, but occurs only 2–4 times per year (Collins & Rodda 1994). Reproduction is likely to occur over an appreciably longer period (Whittier & Limpus 1996). As many snakes probably did not become sated in association with the 7-day period observed (attractant mice were protected in their own cages), it is possible that 7 days represent the optimal time investment before a snake changes foraging location. The snakes in our study infrequently re-entered the trap they had been caught in the previous night, but often visited traps nearby. Information about foraging behaviour should be investigated as a potential contributor to capture heterogeneity. Likewise, building an ephemeral behavioural effect into analytical mark–recapture models may greatly reduce a previously unsuspected source of capture heterogeneity. Although identification of ephemeral effect is more difficult to detect with reduced numbers of occasions, investigators should be alert to the potential for unmodelled ephemeral effects to create apparent capture heterogeneity and thereby bias abundance estimates (Fig. 3).

Our discovery that considerable latent heterogeneity persists after consideration of gender, behavioural response, size, body condition, residence status, and ephemeral effects suggests that future research on this species should be directed at identifying additional covariates that influence trappability. On a subset of individuals with adequate information, we screened several additional covariates (growth, trend of body condition, and habitat) in a *post hoc* analysis of the latent heterogeneity groups to identify favorable prospects for future research. Although only one habitat factor surpassed the conventional ($\alpha = 0{\cdot}05$) statistical threshold, vegetative structure is a plausible explicator of trappability and warrants further consideration. Our experimental design precluded direct incorporation of habitat factors in our primary analysis because habitats were extensively intermingled in our area and non-capture events (zeros in the capture history matrix) could therefore not be associated with a particular habitat.

In addition to complicating population estimation, if high capture heterogeneity is present and heritable, intensive trapping pressure in control programmes could result in selection favouring less-trappable individuals. If so, continued trapping would make control progressively less effective, and if trap yield is used as a population index, declining yields could be falsely interpreted as evidence of progressive population depletion.

In the short term, trap heterogeneity (whether heritable or not) poses a serious challenge for those control programmes directed at eradicating incipient or nearly extirpated populations, where trappability of the least trappable individual drives the level of effort needed for eradication success. Our latent class of less-trappable snakes, like that of the more-trappable latent class, exhibited size-based differences in trappability: snakes >900 mm SVL were much more easily caught than smaller individuals. However, in the less-trappable class, even large snakes exhibited low trappability (<0·1).

The major outcomes of this study relevant to wildlife management are that:

1. Using a physical, landscape scale, enclosure of a population of cryptic, nocturnal predators (brown treesnakes), we tested assumptions about capture heterogeneity that underlie mark–recapture analyses, and were able to quantify size bias as well as behavioural and temporal responses.

2. Our results suggest that population estimates and strategic planning for managing species would benefit from incorporating factors such as body size, heterogeneity, and ephemeral behavioural effects to detection or control methods such as trapping. For example, we were able to confirm that trapping is an effective tool for control of large brown treesnakes >900 mm SVL, but not for snakes <800 mm SVL. Although

eradication using traps is feasible for large snakes (all large snakes in the study site were trapped within 53 days), further research and development of effective control measures for small snakes is urgently required.

3. Given appropriate adjustment for behavioural effects and heterogeneity, previously collected survey data can be reanalysed using mark–recapture modelling to provide additional robust population estimates.

4. If the variation implied by latent heterogeneity has a heritable basis, trap aversion could evolve in invasive species subject to control programmes that rely heavily or exclusively on trapping. Development of other control tools is therefore important to avoid selecting for trap-avoidance.

Many survey and management efforts assume that all individuals of the target population are equally detectable or at equal risk of capture. Failure to recognize an undetectable or untrappable stratum could invalidate management efforts for a species, and failure to quantify capturability lags could suggest the existence of non-existent interactions of heterogeneity and behavioural responses. Thus, the challenges revealed by this novel application of artificial closure could be of crucial importance in abundance estimation, population characterization, and control programmes for a wide variety of applied ecological studies.

Acknowledgements

Colorado State University Animal Care and Use Committee provided approval (Protocol Approval no. 03-249A-01). The US Office of Insular Affairs provided support. Andersen Air Force Base (M. McElligott and D. T. Lujan) provided the site, which was selected with the assistance of C. F. Aguon, Guam Division of Aquatic and Wildlife Resources. US Fish and Wildlife Service provided laboratory facilities and advised on site selection. Project management was provided by T. M. Kman and E. M. VanGelder. G. White provided valuable suggestions on modelling covariates. R. N. Reed, B. M. Lardner, S. R. Siers, and T. R. Stanley suggested improvements to the manuscript. We appreciate field assistance provided by I. C. Chellman, J. L. Farley, K. L. Garrod, G. R. George, M. P. Greene, J. D. Hackman, D. S. Janeke, C. C. Kessler, P. A. Reynolds, M. Schallenberg, J. B. Vickers, A. S. Wiewel, P. S. Wenninger, J. A. Willey, and C. P. Winchester.

References

Bechstein, J.M. (1802) *Herrn De la Cepede's Naturgeschichte der Amphibien oder der eyerlegenden vierfüssigen Thiere und der Schlangen*. Vol. 4. Industrie-Comptoirs, Weimar, Germany.

Boyarski, V.L. (2005) *Trappability and activity of juvenile brown treesnakes* (Boiga irregularis) *on Guam*. M.S. Thesis, Colorado State University, Fort Collins, CO, USA.

Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. 2nd edn. Springer-Verlag, New York.

Collins, E.P. & Rodda, G.H. (1994) Bone layers associated with ecdysis in laboratory-reared *Boiga irregularis* (Colubridae). *Journal of Herpetology*, **28**, 378–381.

Crawley, M.J. (1992) *Natural Enemies: The Population Biology of Predators, Parasites and Diseases*. Blackwell Science, Oxford, UK.

Gompper, M.E., Kays, R.W., Ray, J.C., Lapoint, S.D., Bogan, D.A. & Cryan, J.R. (2006) A comparison of noninvasive techniques to survey carnivore communities in northeastern North America. *Wildlife Society Bulletin*, **34**, 1142–1151.

Gragg, J.E. (2004) *Rodent reduction for enhanced control of brown treesnakes* (Boiga irregularis). M.S. Thesis, Colorado State University, Fort Collins, CO, USA.

Huggins, R.M. (1989) On the statistical analysis of capture–recapture experiments. *Biometrika*, **76**, 133–140.

Huggins, R.M. (1991) Some practical aspects of a conditional likelihood approach to capture experiments. *Biometrics*, **47**, 725–732.

Kendall, W.L., Pollock, K.H. & Brownie, C. (1995) A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics*, **51**, 293–308.

Krebs, C.J., Boutin, S. & Boonstra, R. (2001) *Ecosystem Dynamics of the Boreal Forest: The Kluane Project*. Oxford Univ. Press, New York.

National Wildlife Research Center (2003) Innovative solutions to human-wildlife conflicts: National Wildlife Research Center accomplishments 2002. *United States Department of Agriculture Animal and Plant Health Inspection Service*, Miscellaneous Publication no. 1587. Fort Collins, CO, USA.

Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978) Statistical inference from capture data on closed animal populations. *Wildlife Monographs* **62**, 1–135.

Parmenter, R.R., Yates, T.L., Anderson, D.R., Burnham, K.P., Dunnum, J.L., Franklin, A.B., Friggens, M.T., Lubow, B.C., Miller, M., Olson, G.S., Parmenter, C.A., Pollard, J., Rexstad, E., SHenk, T.M., Stanley, T.R. & White, G.C. (2003) Small-mammal density estimation: a field comparison of grid-based vs. web-based density estimators. *Ecological Monographs*, **73**, 1–26.

Perry, G., Campbell, E.W. III, Rodda, G.H. & Fritts, T.H. (1998) Managing island biotas: brown treesnake control using barrier technology. *Proceedings, 18th Vertebrate Pest Conference* (eds R.O. Baker & A.C. Crabb), pp. 138–143. Davis, CA, USA.

Pledger, S. (2000) Unified maximum likelihood estimates for closed capture-recapture models using mixtures. *Biometrics*, **56**, 434–442.

Pledger, S. (2005) The performance of mixture models in heterogeneous closed population capture–recapture. *Biometrics*, **61**, 868–873.

Pledger, S., Pollock, K.H. & Norris, J.L. (2003) Open capture–recapture models with heterogeneity: I. Cormack–Jolly–Seber model. *Biometrics*, **59**, 786–794.

Pollock, K.H. & Otto, M.C. (1983) Robust estimation of population size in closed animal populations from capture–recapture experiments. *Biometrics*, **39**, 1035–1049.

Rodda, G.H. & Fritts, T.H. (1992) Sampling techniques for an arboreal snake, *Boiga irregularis*. *Micronesica*, **25**, 23–40.

Rodda, G.H., Fritts, T.H., Clark, C.S., Gotte, S.W. & Chiszar, D. (1999a) A state-of-the-art trap for the brown treesnake. *Problem Snake Management: The Habu and The Brown Treesnake* (eds G.H. Rodda, Y. Sawai, D. Chiszar & H. Tanaka), pp. 268–305. Cornell University Press, Ithaca, NY, USA.

Rodda, G.H., Fritts, T.H., McCoid, M.J. & Campbell, E.W. III. (1999b) An overview of the biology of the brown treesnake, *Boiga irregularis*, a costly introduced pest on Pacific Islands. *Problem Snake Management: The Habu and The Brown Treesnake* (eds G.H. Rodda, Y. Sawai, D. Chiszar & H. Tanaka), pp. 44–80. Cornell University Press, Ithaca, NY, USA.

Rodda, G.H., Fritts, T.H., Campbell, E.W. III, Dean-Bradley, K., Perry, G. & Qualls, C.P. (2002) Practical concerns in the eradication of island snakes. *Turning the Tide: The Eradication of Invasive Species* (eds C.R. Veitch & M.N. Clout), pp. 260–265. IUCN Invasive Species Specialist Group of the World Conservation Union (IUCN), Gland, Switzerland.

Rodda, G.H., Savidge, J.A., Tyrrell, C.L., Christy, M.T. & Ellingson, A.R. (2007) Size bias in visual searches and trapping of brown treesnakes on Guam. *Journal of Wildlife Management*, **71**, 656–661.

Savidge, J.A. (1987) Extinction of an island forest avifauna by an introduced snake. *Ecology*, **68**, 660–668.

Savidge, J.A. (1988) Food habits of *Boiga irregularis*, an introduced predator on Guam. *Journal of Herpetology*, **22**, 275–282.

Savidge, J.A., Qualls, F.J. & Rodda, G.H. (2007) Reproductive biology of brown treesnakes, *Boiga irregularis*, during their colonization of Guam and in comparison to its native range. *Pacific Science*, **61**, 191–199.

Shivik, J.A. & Clark, L. (1997) Carrion-seeking in brown tree snakes: importance of olfactory and visual cues. *Journal of Experimental Zoology*, **270**, 549–553.

Shivik, J.A. & Clark, L. (1999) Ontogenetic shifts in carrion attractiveness to brown tree snakes (*Boiga irregularis*). *Journal of Herpetology*, **33**, 334–336.

Stone, B.C. (1970) The flora of Guam. *Micronesica*, **6**, 1–659.

Whittier, J.M. & Limpus, D. (1996) Reproductive patterns of a biologically invasive species: the brown tree snake (*Boiga irregularis*) in eastern Australia. *Journal of Zoology (London)*, **238**, 591–597.

Yang, H. & Chao, A. (2005) Modeling animals' behavioral response by Markov chain models for capture–recapture experiments. *Biometrics*, **61**, 1010–1017.

Received 18 March 2008; accepted 28 October 2008
Handling Editor: Andy Royle