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Sampling techniques for an arboreal snake, *Boiga irregularis*

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Abstract—We evaluated four techniques for estimating densities of the Brown Tree Snake, *Boiga irregularis*, which is nocturnal and difficult to detect in natural habitats: snake traps, time-constrained visual censuses, distance-constrained visual censuses, and mark-recapture programs. Snake traps are best suited to small areas (<5 ha) and can be maintained by individuals without special skills; but they are labor intensive and have an extremely high sampling coefficient of variability (65–200%). Furthermore, traps do not lend themselves to either relative or absolute density comparisons between sites. Both types of visual censuses provide estimates of relative abundance only, have a high coefficient of variability (40–90%), and are sensitive to differences in snake behavior among sites, uncontrolled variability in environmental conditions, observer skill, and habitat differences. A 95% confidence of detecting a 25% difference between the mean values of two sites requires about 100–200 visual censuses for each site. Mark-recapture provides absolute population estimates, but the method can only be applied to snake populations with a high density (>20/ha). Mark-recapture requires an intensive commitment to capturing many snakes in a short time and a high density trail network or other access to all parts of a study area.

Introduction

Ecologists are often faced with the problem of quantifying the abundance of a population whose members are cryptic, hidden, nocturnal, or at low density. In the case of snakes, the investigator is often faced with all four conditions simultaneously. The Brown Tree Snake, *Boiga irregularis*, which has been intro-

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duced to Guam, is cryptic, hidden by vegetation, nocturnal, and rare in some localities (Fritts 1988). In evaluating population estimates for this and similar species it is vital that scientists, decision-makers, and managers understand the limitations and advantages of each technique and appreciate the dissimilarities between these population estimates and those for more readily studied animals.

Sampling techniques for reptiles and amphibians have been reviewed in several recent publications (Turner 1977, Gibbons & Semlitsch 1981, Jones 1986, Fitch 1987, Parker & Plummer 1987), but most studies have been on species that are relatively easy to sample, such as diurnal lizards. Moreover, crucial information on the variability of results has not been published.

Most reviewers have concluded that snakes are rarely amenable to population estimation; for example, Fitch (1987) concluded, "attempts at censusing [snakes] have usually been unsatisfactory." The mark-recapture technique has attracted special criticism (e.g., Turner 1977) because of the difficulty of satisfying all of the assumptions of the simple Lincoln-Petersen index. However, modern computational methods have relaxed the need for satisfying all assumptions (White et al. 1982) and the crypticity of snakes makes it especially important to obtain some estimate of the fraction of the population hidden from view. Unfortunately, mark-recapture methods are difficult to apply to species that are difficult to capture, and the suggested standards for precise application of mark-recapture techniques are difficult to satisfy. For example, White et al. (1982) concluded that no mark-recapture measurement can provide precise and unbiased estimates of population size if the probability of recapturing an individual on any given occasion is less than 35% and the population being sampled is less than 100 individuals. For the Brown Tree Snake, our visual censuses indicate that the recapture probability for a single occasion rarely exceeds 10% and is more often around 5%. A population of 100 individuals of the arboreal Brown Tree Snake is usually spread over a huge volume of forest, and would require a search of unprecedented scale.

The advocated standards for consistency of results are difficult to reach. White et al. (1982) argued that the coefficient of variation (CV) of population estimates should be no more than 20% for reliable scientific studies, and the objective in all cases should be to obtain a CV of less than 10%. Our lowest coefficients of variability with the mark-recapture method have been around 35–40%. In our visual counts of the Brown Tree Snake, the lowest CV that we obtained was 43%, and our trap captures sometimes gave CVs approaching 200%. Thus conventional standards cannot be routinely satisfied by measurements of species like *Boiga irregularis*. But we cannot abandon efforts to monitor Brown Tree Snake populations merely because they are difficult to sample; the urgent conservation needs at present require population estimates of this highly destructive invader (Savidge 1987, Fritts 1988). Fortunately, accurate estimation of snake numbers is possible (e.g., Szaro et al. 1988) and we believe that existing techniques can be improved substantially.

In this paper we describe the four basic techniques that we have used for population sampling of *Boiga irregularis*, critique each in terms of its applicability and limitations, summarize the strong and weak points of each method, and identify the aspects of each method that are most amenable to significant improvement.

Descriptions of Sampling Techniques

The four techniques evaluated were: trapping, time-constrained visual searches, distance-constrained visual searches; and mark-recapture population estimation.

TRAPPING

Trapping techniques for *Boiga irregularis* are detailed in Savidge (1986, 1987), Fritts (1988), and Fritts et al. (1989). Briefly, cylindrical wire or plastic mesh traps with inverted funnel entrances were baited with a suitable prey item or prey odor and hung 1–2 m above the ground in trees in the forest. We checked traps daily to minimize escapes of snakes and maintain the bait animals. For an array of 60–80 traps, the daily trap check required about 2 person hours. We usually arrayed traps in a square or rectangular grid with 15–25 m between traps, and used mice, quail, geckos, or chicken litter for bait. We have trapped Brown Tree Snakes for more than 10,730 trap nights.

DISTANCE-CONSTRAINED VISUAL CENSUSES

This technique requires the searcher to walk at night along a measured transect while looking for snakes in the foliage. Usually, we walked for 2–3 km along a roadside in a rural area, scanning vegetation at a net walk rate of about 0.8 km/h (range 0.2–1.3 km/h). Distance-constrained searches are equivalent in concept to the transect or area searches that have been widely used for reptiles (Luckenbach 1982, Bayliss 1987, Szaro et al. 1988). We have conducted a total of more than 480 km of distance-constrained censuses.

One variant on distance-constrained sampling involves the visual searching for snakes on chain-link fences that are free of vegetation. Easy detection of snakes against the regular symmetry of the fences increases censusing speed. We have been able to inspect fence lines from a slow-moving automobile (mean 4.8 km/h).

TIME-CONSTRAINED VISUAL CENSUSES

This technique differs from distance-constrained searching because the search is variable in length but fixed in time and the searchers are encouraged to adjust their searching rate in response to the visual complexity of the vegetation and the yields obtained. In areas of few sightings the searchers were encouraged to walk more quickly in order to expend less time in unproductive areas; in areas of many sightings the searchers slowed down to concentrate their effort on the better places. In principle, this approach maximizes the number of captures per hour.

Our use of time-constrained sampling differs from most of the previous herpetological efforts (e.g., Bury & Raphael 1983, Campbell & Christman 1982, Raphael 1988) in that we walked along a linear transect for the duration of the timed period. For many of our time-constrained censuses we simultaneously monitored our distances; consequently the yield from a single census may be computed in both time-constrained (sightings per hour) and distance-constrained terms (sightings per km). We have conducted a total of more than 1080 person-hours of time-constrained searches.

MARK-RECAPTURE

Mark-recapture requires a capture method (any of the preceding techniques) and the marking of individuals. Because the probability of an animal moving in or out of a study area increases with time, we prefer to capture and recapture the animals within 7–10 days (Rodda et al. 1992). For such a short timespan, a variety of marking techniques can be used. We have successfully used ventral scale-clipping (the trailing free edge of a ventral scale being trimmed on one side) and paint marking (a number or letter painted on the snake's head). In our mark-recapture efforts we attempted to capture and mark all animals within a 1–2 ha area, using a network of trails spaced no more than 25 m apart. One could search for snakes in a bounded area without constructing trails. This approach entails a loss of valuable information on snake positions and movements, but also reduces the trail construction labor costs. The computational aspects of mark-recapture population estimation have been adequately analyzed elsewhere (Caughley 1977, Otis et al. 1978, White et al. 1982, Seber 1982). We have conducted five mark-recapture estimates of Brown Tree Snake populations.

Evaluation of Sampling Techniques

In this section we discuss each major factor that determines the applicability of a sampling method. We have grouped the factors into eight categories (Table 1): sampling objectives, yield, coefficient of variability, geographic applicability, sampling radius, applicable snake densities, effort required, and other potential problems. In each category we evaluate each sampling method. The key attributes of each method are summarized in the subsequent section.

SAMPLING OBJECTIVES

The appropriateness of a sampling technique depends on the objective of the project. For example, sampling to compare two sites has different constraints than sampling to contrast one site at different times. Another objective might be to ascertain whether a snake population has become established on a new island. This would entail demonstrating the presence of the snake, which all methods could do, although trapping would probably do it most efficiently. In other situations the objective might be to eliminate the snakes from a warehouse, in which case no information about population density is needed; rather, the goal might be to maximize snake capture rate per unit area. In this case a combination of methods might be preferred.

The special problems of site comparisons

A frequent objective is to determine whether or not snakes are more abundant in a particular place or habitat. For example, are snakes more common in areas of the ubiquitous tangantangan tree (*Leucaena leucocephala*) than in other vegetation? When comparing sites, sampling is much more problematic, for two reasons: 1) the visibility or catchability of snakes could differ between habitats due to the structure of the habitat, and 2) the visibility or catchability of snakes could differ between areas due to differing behavior of the snakes. For example, we suspect that snakes are less easily seen in dense vine tangles than they are in *L. leucocephala* (a tree that folds its leaves at night). This tree makes up over 90% of some transects, whereas vine tangles are prominent in others (problem 1). In addition, the snakes in certain areas are more likely to forage on the ground, where they are more readily seen and captured (problem 2).

To assess whether Brown Tree Snakes were more often seen in certain plant species, we compared snake sighting rates per unit search effort for major plant types. We quantified our search effort by keeping track of the amount of time we looked at each plant species or plant type (1611 spot samples) and compared this distribution to the distribution of 398 snake sightings from the same transects (Rodda 1991). The lack of concordance between these two distributions was highly significant ($G_{adj} = 31.3$, $P < 0.001$), and the vegetation categories 'mowed grasses' (more snakes seen than expected) and 'broadleaf trees with dense foliage' (fewer snakes seen than expected) were most responsible for the difference. Although this test cannot rigorously exclude the possibility that more snakes were present in mowed grass and absent from dense trees, comparisons between visual and mark-recapture population estimates suggest that snake visibility is an important factor that can bias visual census results.

Visual censuses have been widely used in herpetology for comparisons between habitats (Luckenbach 1982, Jones 1986, Raphael 1988), but the legitimacy of this extrapolation has rarely been considered. When visual counts have been tested for correlation with absolute population estimates (Bayliss 1987, Szaro et al. 1988), the visual counts were not reliable. Additional error may be introduced if a relative count of unknown precision is multiplied by a visibility correction factor of unknown precision (e.g. Luckenbach 1982).

Unlike visual censuses, trapping is not biased by differences in snake visibility. However, unbiased trap sampling of site differences requires that snakes be equally attracted to the bait in all sites. Equal attraction is not a certainty. For example, if snakes in one area are more attuned to rodent prey (e.g., the snakes are larger) and snakes in another area eat primarily lizards, a comparison of trap success with gecko bait might suggest that snakes were more abundant at the second site, whereas the use of mice for bait would have yielded the converse result. Compared to hand capture, traps are relatively ineffective for small snakes (Rodda et al. unpub. data). If the size of snakes differs between sites, relative trap success will be unequal and spurious capture rate differences between sites can occur. In addition, behavioral changes between sites can invalidate comparisons of trap success between sites. Snakes that are foraging on the ground may be less likely to enter traps set in the trees. If the relative frequency of ground foraging differs between sites, trapping will not provide valid comparisons between sites (Table 1).

Table 1. Summary of methodological considerations discussed in this paper.

		Visual Censuses		
Analysis Criterion	Trapping	Time-Constr.	Dist-Constr.	Mark-Recapture
Sampling objectives:				
Relative density (across space)	N	P	P	Y
(across time)	P	P	P	Y
Absolute population estimate	N	N	N	Y
Yield				
(units)	(per trap-night)	(per man-hour)	(per man-km)	(est./month)
range	0.001–0.25	0–15	0–25	0–4
approx. mean	0.10	1.3	1.6	2
Coefficient of variability (typical)				
per 64 traps per one night	75–100%	na	na	na
per trap over 20 nights	100%	na	na	na
per census	na	60%	70%	35–40%
approx. no. nights to detect a:				
25% diff. with 95% prob.	235	150	200	300
50% diff. with 50% prob.	19	12	16	30
50% diff. with 80% prob.	38	25	32	55
Geographic applicability				
Small areas (< about 5 ha)	Y	P	P	Y
Large areas (> about 5 ha)	P	Y	Y	N
Within forest	Y	Y	P	Y
Along roadsides	P	Y	Y	N
Urban	N	Y	P	P
Sampling radius (m)	200?	5	5	100
Applicable snake densities				
low (e.g. incipient colonization)	P	N	N	N
medium (e.g. 5–20/ha)	P	Y	Y	P
high (e.g. > 20/ha)	Y	Y	Y	Y
Necessary effort				
requires experienced workers	N	Y	Y	N
labor investment high	Y	P	P	Y
can spread effort over months	N	Y	Y	N
must concentrate effort in time	N	N	N	Y
Potential problems				
disturb./vandalism	Y	N	N	P
changes in snake habits	Y	Y	Y	N
environmental conditions	N	Y	Y	N

Y = method applicable, N = method inapplicable, P = method potentially applicable (see text), na = criterion not applicable. These assessments are based on the assumption that the techniques will be used for population sampling in typical Guam habitats using reasonable effort with present knowledge of biasing factors.

These limitations on the use of traps apply to visual censuses. However, during visual censuses one can assess snake population size structure, snake behavior, vegetation structure, and relative prey abundances, and snakes can be captured in all strata of the forest, not just the one where traps are located. If the habitats can be shown to be equal in terms of snake visibility, a properly matched set of visual censuses can be used to tentatively compare snake densities by comparing the snake sighting rates in two areas. However, it is unlikely that snake visibility will be precisely matched, and information does not yet exist to numerically correct for the various biases produced by habitat and behavior differences.

Distance-constrained visual searches are slightly better for site comparisons than are time-constrained visual searches if the time-constrained searchers are maximizing their sighting rates by adjusting their searching rate to gloss over areas of fewer snake sightings and if the walk rate adjustment has a significant influence on the number of snakes seen. If the walk rate adjustment is effective, the searcher would spend less time on the poorer habitat and the number of snake captures *per hour* might be the same between two areas that differed in snake density. However, whether searchers are able to adjust their walk rates enough to influence snake sighting rates is not known. Using data from two observers who repeatedly censused the same snake transect near Orote Point on Guam in Sept.–Oct. 1988, we attempted to correlate yields with the associated walk rate (Fig. 1). The expectation was that sighting rates would be reduced at walk rates above and below some optimum, thereby allowing the observer to maximize per hour yields by modest adjustments in walk rate. No influence of walk rates on yields is evident in Fig. 1. This lack of influence has also been documented in analyses of variance based on repeated searches of transects (all walk rate effects: $P > 0.18$). While these tests are insufficient for demonstrating that walk rate has no effect on capture rates, the lack of a strong functional response (Fig. 1), suggests that time-constrained sampling does not predictably maximize capture rates. If verified, this conclusion would suggest that time-constrained searching offers little advantage other than the convenience of not having to conduct censuses along a measured transect.

Measuring population changes over time

Compared to measuring differences in snake abundance between places, measuring snake abundance changes across time at a specific site is relatively straightforward. All techniques can be used in appropriate circumstances (Table 1). The time interval between trapping efforts must not be great enough for any substantial shift in the prey base or size or age structure of the snake population. Small Brown Tree Snakes eat primarily lizards, whereas larger individuals are more likely to eat endotherms (Greene 1989). If a trapping site were to have primarily small snakes in one year and large snakes at the time of a later trapping effort, no valid conclusion could be drawn from the difference in trap yields. Similarly, changes in prey base may invalidate trap comparisons at a single site

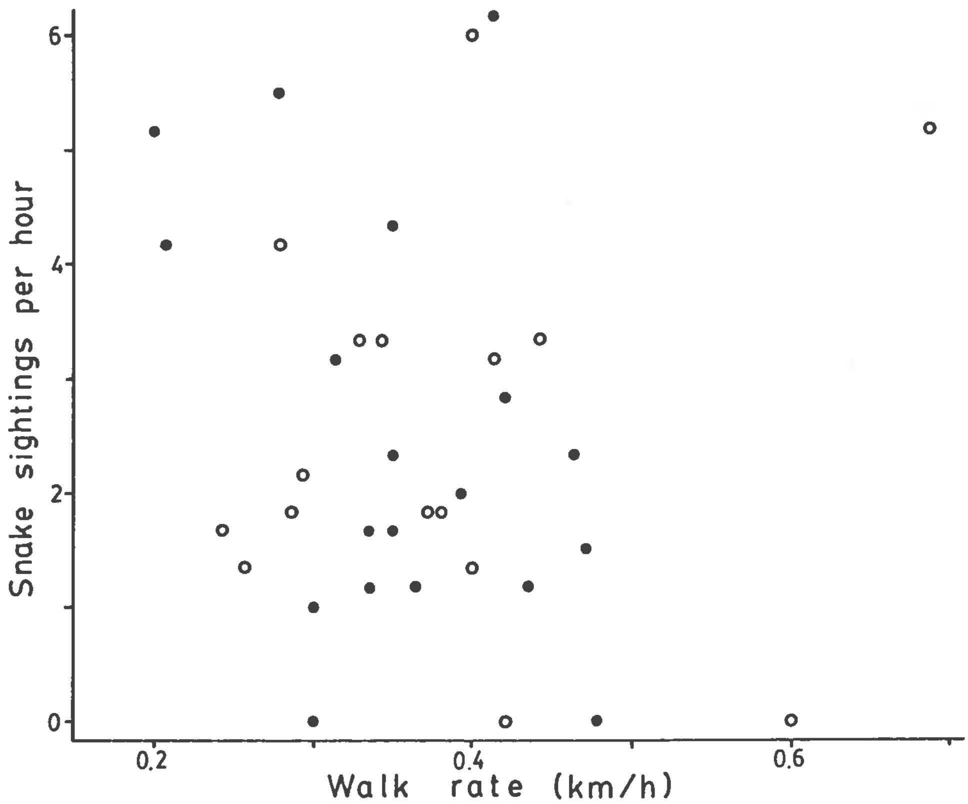

Figure 1. Relationship between net walk rate and sighting rate for two observers (solid symbol = obs. A; open symbol = obs. B) for repeated censuses of a snake transect near Orote Point, Guam, 1988. Time spent processing snakes was excluded from the computation of walk rate.

across time, unless the traps were baited with something that attracts all snakes equally. At the present, no such bait is known.

Either type of visual census is appropriate for detecting changes in snake density over time if the habitat and the habits of the snakes have not changed enough to significantly alter snake visibility. Mark-recapture is also appropriate and is not sensitive to differences in snake visibility.

Estimating absolute population density

Only mark-recapture can provide an estimate of absolute population density (Table 1). Fortunately, mark-recapture estimates are free of the complicating factors discussed above. In particular, differences in snake visibility between sites or times are not a problem in mark-recapture studies. Of course, it is still necessary for the mark-recapture assumptions to be satisfied. In our mark-recapture efforts with the Brown Tree Snake, program CAPTURE (White et al. 1982) has detected violations of every assumption with one data set or another. If the population under study has immigration or emigration, no simple mark-recapture estimate may be obtained. We have found there to be negligible population migration of Brown Tree Snakes if the mark-recapture interval is less than 10 days. If the assumption of equal capture probability per sampling occasion is satisfied, a population estimate may still be obtained while simultaneously violating the assumptions of: 1) no behavioral change due to marking, and 2) no differences between individuals in probability of capture (White et al. 1982). In our experience with Brown Tree Snakes, the assumption most likely to be violated is number 2 (esp. if traps alone are used for captures; traps fail to capture very small snakes). The problem with heterogeneity in capture probabilities among sampling occasions is minimized by intensifying capture efforts. The problem with heterogeneity in capture probabilities among animals is mitigated by using a variety of capture methods concurrently.

YIELDS

All other things being equal, the most informative sampling method is the one that maximizes the number of snakes captured. However, the yield of captures is highly variable both within and among methods. Yields of Brown Tree Snakes from trapping experiments have varied between 0.0014 and 0.25 captures per trap per night in areas of very high snake density (no medium or low density sites have been trapped). The highest captures rates per unit area for any method have been obtained using traps with mouse bait.

Yields from a single night of distance-constrained visual searches have varied from 0 to about 25 snakes per km, but averages for individual transects were in the range of 0.7 to 2.0 snakes/km. The average for all distance-constrained censuses on Guam from 1985 to 1989 was 1.6 snakes/km, but this value is inflated by the large number of censuses that were conducted at the most productive sites. For fences next to forested areas, the mean yields are about the same per km as from visual searches of foliage, but fewer hours are required for the fenceline search. Because snake searchers usually walk at a rate of slightly less than 1 km/h, average time-constrained snake sighting rates for forested areas are usually slightly lower numerically (average about 1.3/h) than yields per km (Table 1).

The yield from mark-recapture efforts is most easily expressed in population estimates per unit of time. To search for snakes throughout most forested areas, pathways must be cleared for nocturnal searches. For a 1 ha study area, clearing and censusing usually require about two weeks. We conduct mark-recapture efforts in conjunction with trapping experiments that require and use the same grid of forest trails. If a study area is already accessible, a reasonable (CV = 35%) estimate of population density can be obtained in 5–10 nights of trapping and visual searches. In our studies this amount of effort resulted in the marking of 30–40% of the snake population.

COEFFICIENT OF VARIATION

The coefficient of variation is a vital index for any sampling technique because it can be used to determine the number of sampling events that must be conducted to obtain an estimate of required accuracy (Sokal & Rohlf 1981). Because the modal success of individual traps on a specific night is usually zero, the numerical distribution of single night trap yields approaches that of a rare Poisson event. To obtain the desired normal distribution of scores, we pool trap yields across days for individual traps or across trap grids for individual days. Using 20 day totals for gecko baited traps (mean yield = 0.03/trap/night), we registered coefficients of variation of 140–190%. The best CV obtained for a 20 day trapping period was 65% (using mouse-baited traps).

The coefficients of variation can be used to estimate the number of nights that one would have to set 64 traps to detect an arbitrary difference in mean trap yields (Table 1). For example, to have a 95% assurance of detecting (with alpha = 0.05) a 25% difference between mean trap yields at two sites requires setting traps for about 235 nights for each sampled site (Table 1). If we relax the criteria for detecting differences between sites, for example, having only a 50% probability of detecting (with alpha = 0.05) a 50% difference in means between two sites, only about 19 trap nights are needed for each of 64 traps at each site. This is a minimum effort because no further reduction in trapping requirements can be gained by reducing the probability of detecting a real difference (as long as the alpha level is maintained). Intermediate between the stringent and relaxed criteria is the more reasonable goal of having a 80% probability of detecting a 50% difference in means. For all methods the intermediate criterion dictated a number of nightly searches that is about double the sample requirement of the most relaxed criterion (Table 1). Table 1 lists comparable values for all four sampling techniques, but it must be understood that all of these figures are extremely sensitive to the CVs of the sampling used, and that the values chosen for these computations are representative but may be widely in error for specific applications. The computation for the mark-recapture method assumes a CV of 35% for each six night series of intensive collecting.

GEOGRAPHIC APPLICABILITY

A major difference between techniques is the geographic scale over which they may be applied. Trapping is well suited to eradicating snakes or monitoring snake populations on a very small scale (a few hectares). Visual searches are not as well suited for small areas; distance-constrained searches are especially difficult to arrange, unless the area of interest has a fine-grained network of trails. Both types of visual censusing are well suited for sampling snakes over a large area with roadside access. But until more is known about how snake densities vary from place to place, it may be premature to draw any conclusions about snake populations over large areas (Parker & Plummer 1987).

Mark-recapture can only be conducted in small areas (although the problems of geographic closure (i.e., no population migration) are more acute in the smaller areas because smaller areas have a relatively larger edge). With a large source of labor and an extensive trail network, mark-recapture might be conducted in areas as large as tens of hectares, but capture intensity is likely to decrease with increasing size of study area. In our mark-recapture efforts covering 1–2 ha areas, mean capture probability per individual per night has typically been 6–8% (maximum 14%), which is far below the recommended value of 35% (White et al. 1982). Thus any increases in capture area must be accompanied by concomitant increases in capture efficacy.

Visual censuses of a small area usually require access via a trail network to provide enough forest edge to permit several hours of searching (shorter censuses provide insufficient information). One possible solution to the problem of conducting visual searches in small areas, without going to the effort of constructing a trail grid, is to search an area twice in the same night. Because the searched strip is only a few m wide (Table 1), previously undetected snakes may enter the transect area irrespective of the earlier presence or absence of snakes. To ensure that the same snakes are not counted twice, the snakes seen on the first pass can be removed or marked. In Sept.–Oct. 1988 we conducted 31 such double pass censuses. The observers worked opposite sides of a road for one hour, switched sides and searched the partner's terrain while walking back toward the starting point. We obtained significantly fewer sightings on the second pass ($F = 6.22$, $P = 0.016$ for snakes per hour; $F = 11.94$, $P = 0.001$ for snakes per km; both computed with the effects of site and searcher removed). In our case the second pass registered about 55% of the sightings rate per hour of the first pass and 35% of the sightings rate per km of the first pass; other ratios might apply to other situations. Accordingly, searching an area twice on the same night is a relatively undesirable method. One cannot directly compare a first pass census with a second pass or mixed census.

Visual censuses along a roadside are usually undertaken to estimate the relative density of snakes in the adjacent forest. Snakes may accumulate along road edges if the denser roadside vegetation provides more habitat or more food or if snake movements tend to follow a habitat edge when they encounter one (rather than crossing the road or reversing direction). If the vegetative structure of the roadside changes from site to site or time to time (perhaps due to periodic road maintenance or plant successional changes), roadside counts may not be appropriate for estimating the abundance of snakes in the adjacent forest.

All of our techniques can be used within forested tracts, although they would all benefit from the existence of a regular grid of trails. Mark-recapture cannot be conducted in a linear form, such as along a road edge, because the assumption of negligible snake migration could not be satisfied along a roadside. Traps are likely to be disturbed by people if traps are placed in a visible location along a roadside, and we consider trapping to be impractical in urban areas for this reason. Distance-constrained visual searching and mark-recapture efforts are physically possible in urban areas, but both are subject to access problems and difficulties in the interpretation of results if one wishes to relate the sighting rate to a recognizable volume of habitat.

SAMPLING RADIUS

Unless one can count the animals on an entire island or other natural geographic unit, one usually estimates animal populations by their density (e.g., sightings/ha). For accurate density estimation one must know the area from which the sampled animals originate. In the case of visual censuses, the sighted snakes are simply those that are within the visual range of the transect line (i.e., about 5 m). In the case of trap or mark-recapture studies that span a period of days or weeks, the capture radius depends on the home range size of snakes over the time interval utilized. Radiotelemetric studies of Brown Tree Snake movement may eventually provide precise estimates of this value. In the meantime we provide crude estimates based on movements of recaptured marked animals over the duration of a typical trap or recapture study (Table 1).

APPLICABLE SNAKE DENSITIES

At the present time, only trapping offers a reasonable probability of sampling a low density (e.g., incipient) population of snakes (Table 1). Our experiences with trapping and mark-recapture efforts suggest that these techniques are difficult to use on populations at medium density (5–20/ha). It is not known if visual searches at low density are likely to be successful, but with a capture probability for an individual snake on any one occasion of less than 8%, one should plan on repeating a visual census many times if one wishes to have a high probability of detecting all or most of the snakes in a low density population. All techniques are appropriate for sampling snake populations at high densities (Table 1).

SAMPLING EFFORT AND LABOR REQUIREMENTS

The four sampling methods differ in the amount of time they require, whether unspecialized workers can be used, and whether the sampling can be spread over long periods of time (Table 1).

Trapping and mark-recapture are the two methods that require a high density network of trails and are therefore the more laborious of the four sampling methods. In addition, traps must be monitored on a regular basis. We visit traps daily, but if an escape-proof trap is developed this interval could be lengthened, at a great savings in time investment. In areas where traps are not vandalized, traps may be closed between visits, allowing intermittent sampling.

Visual censuses can be conducted intermittently over a period of weeks or months. If one wished to obtain a yearly average that was independent of any suspected seasonal effects (none have yet been significant in our analyses of variance), one might wish to conduct visual censuses at monthly intervals. Such a schedule would not be possible for mark-recapture sampling.

Brown Tree Snakes are mildly venomous (Fritts 1988). Therefore trapping is the preferred method for workers who are reluctant to handle snakes or who are unavailable for nighttime searches.

Inter-observer differences imply special labor requirements for visual censuses

One salient attribute of visual censuses is that different observers may have different abilities to see Brown Tree Snakes, which are drab, vine-like in body form, and often immobile in the foliage at night. Considering all of our 1988–1989 sightings of snakes in the trees (there are no differences among observers in numbers of snakes seen on the ground, P = 0.9) at the four best studied sites (total person hours = 265, total snakes sighted = 321), the observer effect on per hour yields was significant (F = 2.49, P = 0.03), whereas that for per km yields was not (F = 1.45, P = 0.21). In this comparison there was a ten-fold range between the lowest and highest observer's mean yields per hour (0.10 v. 1.06), and a 2.7-fold range between the lowest and highest observer's mean yields per km (0.73 v. 1.95). The observer effect is one of the largest influences on sighting rates; in many of our comparisons it was the largest measured effect. In several comparisons both per hour and per km sighting rates have exhibited significant inter-observer differences. Therefore it is extremely important that the effect be controlled or minimized, either by using the same set of observers for all visual censuses, or by calibrating each observer with enough paired comparisons between the original observer and his or her replacement that sufficient statistical power remains for the comparison of interest. As a practical matter, this means that only trained, regularly-available observers can be used for visual censuses. To maximize the number of data obtained, it is also desirable to avoid the use of observers with relatively low mean sighting rates.

The problem of inter-observer variability in visual searches has not received much attention in the herpetological community. We found no publications that mentioned the necessity of making observer-paired comparisons; nor did we find any quantification of the difference in sighting rates between different observers. Because of their discovery that differences between observers may be the major source of variation in counts, ornithologists have devoted considerable effort to inter-observer standardization (Ralph & Scott 1981, Verner 1985, 1987). With reference to locating reptiles, Jones (1986) noted that " . . [generally] reptile data collection does not require the degree of expertise required for surveys of animals such as birds. ." Visual searches for *Boiga irregularis* may be an important exception to this generality.

OTHER CONSIDERATIONS IN CHOOSING A SAMPLING METHOD

Traps are subject to vandalism, even in many nominally protected areas such as military bases (Table 1). Mark-recapture estimation may not be practical in public areas, due to uncontrolled disappearances of marked animals.

Reptile activity is often limited by prevailing environmental conditions (Gibbons & Semlitsch 1981, Jones 1986, Block et al. 1988). For example, Brown Tree Snake activity may be influenced by time-of-night and moonlight. For trapping, these effects are relatively unimportant because traps are usually set for a period long enough to average out short term variation in yields. However, the effect of environmental influences on visual sighting rates can be severe, especially if only a few censuses are conducted to characterize the snake population at a specific time or place.

Although we do not yet have adequate information on the environmental factors that influence snake activity, we can estimate the combined influence of the various environmental effects by demonstrating that snake sighting rates tend to be similar for different observers on a specific night, indicating that some common environmental factor or factors are influencing the activity or visibility of snakes. For example, on 23 nights in 1988 we conducted a total of 61 censuses at the three best studied areas in Guam. For these 61 censuses, the largest source of sighting rate variation was sample day (for per km comparisons: $F = 6.41$, $P < 0.001$) and inter-observer differences produced the only other significant effect ($F = 2.71$, $P = 0.048$). This indicates that night-to-night variation in snake activity may obscure the year-to-year or site-to-site differences of interest. Any information that can be used to avoid this environmental variation or compensate for it will reduce the number of censuses needed to detect true differences in snake abundance.

We attempted to quantify the effects on snake activity of time-of-night, rainfall before censuses, rainfall during censuses, and moonlight. None of these have proved significant, although the reduced frequency of ground snake activity under bright moonlight (0.37 v. 1.03 snakes/km) was nearly significant ($F = 2.67$, $P = 0.077$). A moonlight effect was not detected for arboreal snake sightings. However, the highly significant overall effect of sample day suggests that considerable night-to-night variation in snake activity is yet to be explained.

Summary of Each Sampling Method's Key Attributes

TRAPPING

Traps are effective in small areas. When baited with mice, traps capture the highest percentage of the snake population of any sampling method. The setting of traps (which can be done during normal working hours) is often more acceptable to workers than capture by hand. Trapping may be appropriate for monitoring changes in snake density over time at a single site, but high labor and material costs reduce its appeal compared to other methods.

TIME-CONSTRAINED VISUAL CENSUSES

Time-constrained visual censusing may be the most appropriate technique for sampling low density populations. Time-constrained sampling is preferred in situations where the time investment of laying out measured transects or preparing a network of trails is not warranted. It requires calibrated observers who will be available for matched censuses throughout the anticipated sampling period. Interpretation of results will be difficult, especially for comparisons of snake densities in different areas. If habitat or snake behavior differ among sites or times, valid comparisons may not be possible.

DISTANCE-CONSTRAINED VISUAL CENSUSES

Distance-constrained visual censuses are limited by most of the problems that apply to time-constrained visual censuses, with the additional requirement of needing to lay out a measured transect. However, distance-constrained censuses may be slightly more powerful than time-constrained censuses for detecting differences in snake densities. In addition, inter-observer differences are likely to be less influential than with time-constrained sampling.

MARK-RECAPTURE

Mark-recapture may require a network of trails and cannot be used for snake populations at low density. However, mark-recapture provides absolute population estimates and it can be conducted with unspecialized observers. For many comparisons among sites, it is the only technique that can be used without resorting to assumptions about equality between sites in snake behavior and visibility. Mark-recapture can only be applied to small areas. Mark-recapture can be used to contrast snake densities in different habitat types, a comparison for which the other sampling techniques are unsuitable.

Improvements in Sampling Techniques

TRAPPING

The utility of trapping could be substantially increased by reducing trap escape rates (Rodda et al. unpub. data) and reducing the labor involved in trap maintenance. The labor in trap maintenance is largely due to the tending of bait animals. The discovery of a durable inanimate bait would be an enormous help.

A variety of laboratory studies (Chiszar 1989, Chiszar et al. 1988a, Chiszar et al. 1988b) have demonstrated that *Boiga irregularis* respond poorly to airborne odors, yet Fritts et al. (1989) trapped snakes with airborne and trap odors and Rodda et al. (unpub. data) were unable to increase trap yields by augmenting airborne odors with substrate-borne odors (in the absence of odors, no snakes were caught—Fritts et al. 1989). The information gained through unraveling these apparent paradoxes may allow significant improvements in trapping success.

VISUAL CENSUSES

The number of visual censuses required for a given degree of accuracy is much larger than it would have to be if the environmental factors influencing snake activity were better understood. Visual censuses would be more useful for comparing sites if differences in snake visibility were quantified in different habitats and if the relation between tree and ground foraging snakes was clarified.

MARK-RECAPTURE

In most mark-recapture efforts, traps or hand capture are used with the assumption that these gather snakes from the area bounded by the outermost trap ring and a buffer strip half the width of the spacing between trap lines (Seber 1982). This assumption, and that of geographic closure, are likely to be invalid in some Brown Tree Snake studies. Quantification of the area from which snakes are drawn would be an important step in improving the accuracy of mark-recapture population estimates.

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