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Population Monitoring

By William Hayes and Ronald Carter

A first step in developing conservation plans to protect or restore remaining iguana populations is to assess the status of populations in the wild. Once a conservation plan has been implemented, continued population monitoring is essential to evaluate the effectiveness of the program. Despite the recent attention given to several taxa, information as basic as population size is still lacking for many West Indian iguanas (Blair 1991a, 1994). For some taxa, the only data available are subjective impressions based on only a few hours of observation (Blair 1991b, 1992a,b; Ostrander 1982). Some estimates of abundance are decades old, whereas others urgently need to be reassessed due to recent threats to the population. Although rough estimates are important when nothing else is available, they are of limited value for establishing priorities and developing long-term survival plans.

Population estimates based on rigorous sampling are sorely needed, not only to update the endangered status of many taxa but also to monitor the success of conservation efforts. While numbers at or near carrying capacity suggest a healthy population, declining numbers or the absence or scarcity of certain size classes may be indicative of deteriorating habitat, disease, or the presence of introduced flora or fauna. Population viability can be better understood by repeated surveys that yield information on growth rates, sex ratios, reproduction, age of sexual maturation, and survivorship. Likewise, injury frequencies, habitat requirements and preferences, and movement patterns can be ascertained. Accurate surveys are particularly important for setting conservation priorities and allocating limited resources appropriately.

Standardization of all iguana population surveys, regardless of taxa, location, and purpose of study, is probably not possible because different habitats and study objectives require different techniques. Nevertheless, population estimates should be based on appropriate considerations, and uniformity of multiple sampling efforts is necessary for comparative or experimental studies. Because objectives of abundance estimation and hypothesis testing are different, as are their design requirements, investigators should determine whether the purpose of the study is to evaluate population density, population size, or rate of population change before embarking on any study of population numbers (Skalski and Robson 1992). Inferential studies are especially important to understand how population density changes across a gradient, varies over time, or differs among islands or treatment conditions. Constraints involving costs, manpower, and time must also be considered. Knowledge of methodological assumptions is critical in order that steps can be taken to ensure they are met in the field. Preliminary sampling can provide valuable insights on how to design an effective study, and prior familiarity with data treatment and adequate training of observers are essential.

A vast array of population estimation techniques are available, many of which are tailored to meet specific sampling conditions and requirements. Their specialized applications, assumptions, and calculations have been treated in detail by other investigators (Bibby et al. 1992; Skalski and Robson 1992; Buckland et al. 1993). Although less complex, single-sample techniques are not as accurate as many of the more complicated methods involving repeated sampling. The latter can be particularly sophisticated, and computer programs are now available to simplify computation.

While the terms census and survey are often used interchangeably, Buckland et al. (1993) emphasize that a census requires counting all subjects within a sample area (only rarely accomplished), whereas a survey samples only a portion of animals within an area. There are two basic approaches used for conducting population surveys. Distance sampling focuses on representative transects, estimates population density for those areas, and then extrapolates population size assuming a similar density for the entire area. Mark-

Table 7. Primary advantages and disadvantages to use of classical transect, distance sampling, and mark-recapture techniques for estimation of population density, population size, or rate of population change.

Methods	Advantages	Disadvantages
Classical Transect (counts within a prescribed area)	Ideal if all animals in sampled area can in fact be detected; useful for experimental studies to test hypotheses if carefully standardized; expedient and cost-effective.	Assumes that all animals in area sampled are detected, which is rarely realistic; nearly always underestimates population density and size; less precise than distance sampling.
Distance Sampling (measurements of distances)	Yields more reliable results for population estimation than classical transects; ideal for experimental studies; expedient and cost-effective.	Nearly always underestimates population density and size; yields minimal information on population demographics compared to mark-recapture methods.
Mark-Recapture	Can yield the most reliable population estimates; yields abundance of additional demographic information; ideal for experimental studies.	Costly and time-consuming to conduct; large sample sizes needed; high proportion of marked animals need to be recaptured or resighted in second and subsequent samples.

recapture studies involve the capture and marking of a subset of animals in the population which, based on the ratio of marked to unmarked animals determined from subsequent sampling, is used to estimate total population size. The advantages and disadvantages of each approach are outlined in Table 7. Two of the most important considerations regardless of the approach are the need for control populations when possible and the use of randomization and replication of treatments whenever possible to increase precision (repeatability) and accuracy (proximity to actual population density or size) of estimates and provide valid and appropriate inferences on population abundance (Skalski and Robson 1992).

Distance sampling methods

Many West Indian iguanas occupy relatively large islands where it is not practical to count animals over the entire island. In such cases, population estimates must be based on population subsampling, for which distance sampling is particularly useful. Classical transect studies are a subset of, but distinct from, distance sampling models (Buckland et al. 1993). In classical transects, several linear transects or circular plots are randomly situated in appropriate habitat. Observers then proceed along the transect line or remain stationary at the center of the circular plot, counting all animals detected within a predetermined distance from the transect line or central point. No distances between the animal and the transect line or central point are measured. These methods assume that all animals within the sample area are encountered, which in virtually all cases is a practical impossibility. Because of this, classical transects nearly always underestimate animal density. Consequently, despite the much greater effort and expense required, mark-recapture studies have often been employed when precision is important.

Distance models, refined over the last two decades (Buckland et al. 1993), require measuring the perpendicular distance between the transect line or central point to where an animal is first seen. Boundaries of the sample area need not be established, and use of a unique detectability function precludes the assumption that all animals in the sample area are detected. The detection function specifies probabilities of detecting an animal in relation to distance from the transect line or central point, allowing estimates of density to be made under mild assumptions with greater accuracy than is normally achieved with classical transect methods. Assumptions of classical and distance models are compared in Table 8. Use of the computer program DISTANCE greatly facilitates analysis of data generated by distance sampling (Laake et al. 1993).

For distance sampling, line transects are most often used, especially in relatively open habitat, but point sampling may be preferable in denser habitat or under other circumstances. Other applications of distance

Table 8. Key assumptions of classical transect and distance sampling techniques.

Assumption	Classical Transect	Distance Sampling
1. All animals in transect area are detected	X	
2. All animals exactly on transect line or point are detected	X	X
3. Entire size of sample area is known	X	
4. Animal distances from transect line or point are accurate		X
5. Animals do not move before detection	X	X
6. Individuals are counted only once	X	X
7. Individuals behave and therefore are detected independently	X	X
8. Bias (from observers, seasons, weather) is understood	X	X

sampling, such as trapping webs and indirect counts of scats, burrows (Iverson 1979), or other signs, can be regarded as modifications to the basic distance theory (Buckland et al. 1993). The lengths of line transects must be known, and care must be taken to establish transects that are straight, randomly placed within representative habitats, far enough apart to avoid double-counting of animals, and preferably parallel to one another and to any known density gradient. Established routes such as roads and ridgetop trails are subject to bias and should be avoided, and clustered populations warrant special consideration (Buckland et al. 1993). Preliminary surveys are particularly important for making decisions on transect design. Buckland et al. (1993) offer an excellent discussion on strategies for placement of lines or points across areas to be sampled.

The measurement of distances can be unwieldy, making distance methods more time-consuming than classical transects, particularly when departure from the transect line is necessary to mark or measure the point where each animal is initially seen. Such interruptions may also disturb nearby animals. New and relatively inexpensive technologies, however, can greatly expedite data collection. Rangefinders or binoculars with reticles can be used to estimate distance without the need to leave the transect line, and simultaneous estimation of the sighting angle relative to the transect line can be accomplished using a hand held angle board or an angle plate on a tripod (Buckland et al. 1993). By rapidly collecting and recording distance and angle measurements for each animal seen, perpendicular distances can be easily calculated later using a trigonometric function. Cruder methods such as pacing and visual distance estimation can be used if the sacrifice in accuracy is acceptable. However, accuracy of distance measurements is critical when close to the transect line due to the mathematical properties of distance models. When distance estimates are less accurate, rounding to convenient values and collapsing of data into distance categories is commonly practiced, as is truncation, the setting of a limit to the furthest distance animals are counted. Although outliers can be removed before analyses, caution must be taken not to introduce systematic bias.

The transect design should provide for adequate sample size. As a general rule, the minimum sample size of all transects combined should be 60-80 individuals, although 40 may still provide reasonable precision (Buckland et al. 1993). Somewhat larger samples are recommended for point sampling (25% more) and when sampling clustered populations. Of course, for studies of rare or endangered animals these numbers may be unachievable, and alternative methods of analysis may prove more informative. In contrast to mark-recapture studies, the absolute size of the sample is important for distance sampling, rather than the fraction of the population sampled.

Iverson (1978) employed distance sampling to estimate population size of the Turks and Caicos iguana on Pine Cay. He established permanent transect lines through representative habitats in six sectors of the island and conducted numerous surveys at various times of the day over a three-year period. The perpendicular distance between the trail and where each iguana was initially seen or heard (generally flushed from cover) was measured and iguana density calculated using a classical transect model and three distance formulas, two of which incorporated detectability functions. Agreement among the computation methods was reasonable, but the classical transect calculations resulted in lower density estimates than those incorporating detectability functions.

Additional distance sampling considerations

During any given survey, some lizards inevitably will be underground or hidden in vegetation, refusing to flush. Activity, and hence detectability, of iguanas varies with time of day, season, and size and sex of individuals (Iverson 1979; Wiewandt 1977). Juveniles often are very secretive, so estimates may need to be restricted to adults (Iverson 1978). Adult males may be more conspicuous during the mating season when they defend territories, while adult females may be disproportionately under-represented subsequent to mating and during egg-laying. Recent weather conditions may also influence iguana activity. Because an unknown proportion of animals cannot be detected, both classical transect models and distance techniques often underestimate true population size.

Population underestimation can be minimized by repeated sampling at optimal times and inclusion of data for only the highest counts obtained, as done by Iverson (1978). It is also possible to adjust estimates if information about the percentage of animals encountered during a given survey is available. For example, Hayes et al. (1995) discovered in surveys of two cays that only a third of marked San Salvador iguanas were detected. Thus, they multiplied by three the number of animals counted by classical transects on other cays where few or no animals were marked to obtain more accurate estimates. With the exception of one population where iguanas have since been extirpated, estimates by Hayes et al. (1995), and even absolute numbers of iguanas seen, far exceeded earlier estimates by Gicca (1980) based only on classical line transects. Although it is possible that numbers actually increased during the intervening years, differences between the two studies more likely reflected the timing of Gicca's visit during a season of lower activity (December, 1974 versus March-July, 1994) and violation of the assumption that all animals within the transect were encountered.

Variation in habitat may complicate estimation of total population size. On larger islands, iguanas typically occupy a range of habitats. To accurately estimate total population size, it may be necessary to conduct distance surveys in randomly selected sites within each habitat and calculate population density for each. If the island-wide distribution of each habitat is known, population estimates for all habitats can be summed to estimate total population size (Iverson 1979). For very small cays, it may even be possible to sample the entire island (Hayes et al. 1995). Critical habitat such as nesting areas should also be surveyed during the appropriate season to evaluate management needs (Haneke 1995).

Distance sampling models assume that animals do not move prior to detection and that individual iguanas are detected independently. This may become a problem at higher densities, when an observer may disturb an iguana, potentially resulting in double-counting and affecting the behavior of other nearby lizards. Obtaining distance and angle measurements may also make determining initial locations of animals difficult when a number of iguanas are in view at once, and bias may occur when selecting the next focal animal. Slow, deliberate movement can minimize disturbance, and the departing animals may offset those which remain cryptic. At low densities, it may be advantageous to occasionally leave the transect line in search of iguanas, carefully probing vegetation with a long rod to assist in detection of animals reluctant to flush (Hayes et al. 1995). More than one observer can also be of value, as long as effort is focused close to the transect line or central point and decreases smoothly with distance so as not to introduce bias. A useful approach is to have one person remain on the transect line, while additional workers systematically search for iguanas on each side of the line.

For comparative and experimental studies, standardization and repeatability of sampling method, effort, and conditions during replicate surveys becomes very important. All possible sources of bias, including sampling method, differences in habitat, iguana density, seasonal and climatic factors, and observer experience, reliability, and technique should be identified and minimized. Standardized surveys conducted on an annual basis are necessary to assess population responses to adverse effects. Population changes need to be documented when management changes are implemented, including release of headstarted juveniles and habitat restoration. Comparisons of iguana density on islands with and without introduced species are needed to confirm their negative impact. If feral animals are eradicated from infested cays, annual surveys of juvenile to adult ratios may indicate increased reproductive success and recruitment. Even indirect measures of iguana abundance, such as the density of feces or burrows or the ratio of active to inactive burrows can be valuable in monitoring conservation efforts (J. Iverson, personal communication).

Information on sex or body size of iguanas sampled is helpful in assessing population structure and effective population size. Even more useful information can obtained if animals are captured supplementary to surveys. Measurements of body size and confirmation of sexual identity and reproductive condition are valuable for learning more about population demography, including the sex ratio, individual growth rate, frequency of injuries, reproductive rate, and age of sexual maturity (Iverson 1979).

Mark-recapture methods

Mark-recapture studies involve the initial capture of a random and representative sample of animals, which are marked and then released back into the population. At a later time, another random sample is captured, or in some circumstances sighted, and the number of animals previously marked is recorded. If certain assumptions hold, the ratio of marked animals to total animals in the second sample, together with the known number of marked animals, can be used to estimate total population size using the Lincoln-Peterson equation: Nmarked / Ntotal = Nrecaptured / Nsampled. Multiple capture designs with varying assumptions can be incorporated, making the approach applicable to a diversity of sampling situations that yield more precise and accurate estimates than two-sample designs. As with distance sampling, experimental studies for hypothesis testing are served well by mark-recapture programs (Skalski and Robson 1992).

Mark-recapture studies have several advantages for conducting population surveys. First, they can provide a better estimate of population size than distance sampling techniques, which generally underestimate population size. Second, repeated sampling of marked individuals can generate additional demographic and ecological data. Finally, the proportion of marked animals sighted or recaptured can indicate the proportion of each sex and size class that is active during a given population survey, which in turn can be helpful in understanding biases that influence population estimation. Compared to distance sampling, the primary drawbacks to mark-recapture studies are their cost, time demands, and labor intensity. Large numbers of animals may need to be tagged, and a high proportion of marked animals must be resampled in order to meet statistically acceptable standards.

Although a variety of mark-recapture models exist, the two basic classes are closed and open population models. Closed population models assume that a population does not change composition during the course of the study (i.e. births, deaths, immigration, and emigration are negligible) and are probably best applied to data collected over the short term. Because iguanas are not highly vagile and many are restricted to small islands, this assumption is often met. Although violation of this assumption can become a problem when captures are taken over a long period, allowances can be made if these rates can be measured. For two-sample experiments, the Lincoln-Peterson estimator is widely employed. K-sample models, with many capture events, can also be used. The software program CAPTURE (Rexstad and Burnham 1991) has been widely utilized by ecologists in recent years for the analysis of multiple-sample closed population models.

Open population models are designed to accommodate animals entering and leaving the population during the course of the study. Populations may be modeled as completely open (both losses and gains) or partially open (losses and no gains, or vice versa). Two of the more common models employed are the Cormack and Jolly-Seber models, which can be handled most readily by a number of software programs (Nichols 1992). The programs SURVIV (White 1983) and SURGE (Cooch et al. 1996; manual currently available on the internet at: http://mendel.mbb.sfu.ca/wildberg/cmr/surge_guide.html), in particular, are extremely powerful and especially flexible for tailoring analyses to specific field situations (Nichols 1992). Assumptions of closed and open models are compared in Table 9.

In models based on multiple capture events, complete capture histories must be obtained for individual iguanas. In these cases, iguanas must be marked for individual recognition, a condition not required of two-sample studies. Capture histories generally consist of a series of 1s and 0s corresponding to the sequence of sampling events, the former denoting capture and the latter indicating no capture. A statistical model, the choice of which depends on assumptions about sources of variation associated with capture, can be used to evaluate probabilities of capture at each sampling event. Results can then be used to estimate population size and change over time. Because repeated sampling results in reduced sampling error, multiple-sample models can lead to greater accuracy and precision in population estimates. Although complex, multiple-sample techniques can be extremely powerful in evaluating population viability and making management decisions. Further treatment of multiple-sample models can be found in Bibby et al. (1992), Nichols (1992), and Skalski and Robson (1992).

Hayes et al. (1995) employed mark-recapture methods to estimate population size of San Salvador iguanas. Using color-coded beads, they marked numerous animals captured on several offshore and inshore cays during May, 1993 and May, 1994. Upon returning in July, 1994, they conducted Lincoln-Peterson estimates on two cays. Investigators systematically covered each island, recording with the aid of binoculars all iguanas seen as either unmarked, marked, or too poorly seen to ascertain the presence of beads. The

Table 9. Key assumptions of mark-recapture studies for closed or open population models. Parentheses indicate that relaxation of assumptions is permitted in certain models. After Bibby et al. (1992)

Assumption	Closed Models	Open Models
1. Closed population (unless immigration and emigration rates are known)	X	
2. Every animal in population has equal probability of capture in first sampling	X	
3. Marking does not affect catchability/detectability	X	
4. Second (subsequent) sample(s) are random	(X)	
5. Marks are permanent	(X)	X
6. Capture/sighting probability constant for all time periods	(X)	
7. Every animal in population has same probability of recapture/resighting in all sampling efforts		X
8. Every marked animal has equal probability of survival		X
9. Sampling time is brief		X
10. Losses from emigration and death are permanent		(X)
11. Population closed to recruitment only		(X)

Lincoln- Peterson equation was then used to estimate total population size based on well-seen animals, while the number of poorly-seen iguanas was multiplied by the ratio of total marked iguanas to the number of iguanas resighted to derive a second estimate. These two estimators were then summed to yield total population size. The proportion of iguanas in the population encountered during these surveys was used as a multiplier to derive population estimates for other islands visited under similar weather conditions. The availability of marked lizards and the small sizes of the cays (each treated as a single transect) made the integration of mark-recapture and classical transect data ideal given limited time on the cays.

Additional mark-recapture considerations

Because so many iguana populations are confined to islands, the assumption of a closed population is often valid, at least over the short term. Nevertheless, as long as sufficient time is provided for animals to mingle, it is good practice to minimize the interval between marking and resampling to reduce the likelihood that marks disappear or animals die between sampling events. Fortunately, adult iguanas are long-lived and generally have high survivorship (Iverson 1979). Although difficult to fulfill, an important assumption of closed population models is that every animal in the population has an equal probability of capture. Juveniles in particular can be hard to find, wary, and difficult to capture, making it preferable in some cases to restrict inferences to adults (Iverson 1978). Differences in seasonal activity between the sexes may also influence capture rates, even among adults. Recognition of such biases can help direct capture efforts, but it may still be necessary to derive population estimates for different classes of iguanas independently. Sampling efforts must also be distributed appropriately across different habitats.

Some models assume that marking does not affect catchability or detectability, and that subsequent samples are random. Yet, certain marking systems may influence activity or survival, or lead to bias in captures, especially when animals are collected by hand. Experience with San Salvador iguanas suggests that animals marked with colored beads are conspicuous and more easily targeted for capture by researchers (W. Hayes and R. Carter, personal observation). Less conspicuous marking systems such as toe-clipping can mitigate recapture bias (J. Iverson, personal communication). When it is assumed that capture probabilities are constant for all periods, care should be taken to conduct sampling under similar weather conditions, using equal sampling effort. Permanence of marks is especially important for repeated sampling and for open models. If, however, the loss rate of marks is known, adjustments to models may be possible. Duplicate marking systems (e.g., colored beads and PIT tags) can provide a backup when one system fails.

Conclusions

Before embarking on population studies, it is important to carefully consider objectives and constraints in order to select an appropriate technique and field design. Preliminary sampling using distance methods can provide rough information on population size and structure which can be useful in appropriately designing further population surveys. The primary advantages to this technique are the expediency and cost-effectiveness with which population estimates can be obtained. By comparison, mark-recapture studies often require specialized equipment and an extended time investment to capture and mark the animals, which then must be surveyed again at a later date. Whenever numerous populations must be surveyed in a limited amount of time, distance sampling is the clear method of choice. When attempting to survey Turks and Caicos iguanas on more than 100 cays within a period of several months, Gerber (1996) relied on distance techniques, but nevertheless captured and marked animals on many cays that can be re-surveyed in the future.

If time and resources are available to capture and obtain measurements from animals, it is of considerable value to mark animals for future studies. Mark-recapture studies can yield reliable estimates of population size, but also offer the opportunity to extract detailed demographic and ecological data. Recapture frequencies can indicate the proportion of male and female iguanas of different size classes that are active during any given sampling period. Multiple sampling designs yield by far the most information about population viability, potentially providing data on population changes, growth rates, frequency of injuries, reproductive rate, age of sexual maturation, mortality rates, survivorship, and longevity.

Both distance sampling and mark-recapture are excellent for comparative or experimental studies associated with hypothesis testing, such as assessing iguana density across gradients, in different habitats, over time, or following experimental manipulation. Multiple standardized surveys can be carried out under similar field conditions to yield strong inferential data. Clearly, both transect and mark-recapture techniques can be extremely useful for analysis of iguana populations. Although one may be more suitable than the other in answering a particular question, the combined use of both approaches should be attempted whenever possible to derive maximum information from remaining iguana populations.

While publicizing the status of highly endangered species can be essential to raising the funds and awareness important for assembling recovery programs, such publicity can arouse the murkier interests of poachers and others who may wish to exploit the situation. A further dilemma can arise when population surveys suggest that a species or population exists in greater numbers than previously believed. Integrity in reporting becomes an issue, especially when a downgrading from endangered status could jeopardize support for research and conservation programs. There are no easy answers to questions raised by these concerns, but they certainly need to be addressed by the conservation community.

Comments by senior author (10-23-05): Our description of distance transects (e.g., Table 7—disadvantages) requires a point of clarification. If one assumes that *all* iguanas on the transect line are detected (as normally assumed for this method), ***then distance transects do not underestimate population size and require no further adjustment***. However, in some habitats, iguanas on the transect line may be missed, which would result in underestimation. Iguanas may, for example, be underground or in dense shrubbery, or may move away from the transect line with the approach of the investigator. Investigators will need to use their best judgment to determine whether or not density estimates using this method require adjustment.

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This extra page has resulted from the incorporation of references, which in the original publication were compiled for all chapters at the end of the book.