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Tools and Technology Note

Mark–Recapture Accurately Estimates Census for Tuatara, a Burrowing Reptile

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ABSTRACT Estimates of population size are necessary for effective management of threatened and endangered species, but accurate estimation is often difficult when species are cryptic. We evaluated effectiveness of mark–recapture techniques using the Lincoln–Peterson estimator for predicting true census size of a population of tuatara (*Sphenodon punctatus*), a burrowing reptile that is a conservation priority in New Zealand. We found that Lincoln–Peterson estimates ($N\hat{N} = 85$) were accurate for predicting the census size ($N = 87$) after only a 3-day mark–recapture survey. We recommend this method as a cost-effective way to accurately estimate population size for isolated, inaccessible tuatara populations, because it requires limited personnel, expertise, and time, and has low environmental impact on fragile sites.

KEY WORDS conservation management, cryptic species, Lincoln–Peterson estimator, mark–recapture, New Zealand, *Sphenodon punctatus*, Stephens Island, tuatara.

Population size estimates are often the first and most basic quantitative measure needed for monitoring status and justifying funding for management, thus making these estimates critical for effective management of threatened and endangered species (Shaffer 1981). Accurate and appropriate population size estimators can allow managers to predict effects of management activities, or lack thereof, on threatened populations and enable managers to monitor the recovery or decline of a population over time (Seber 1982, Beissinger and Westfall 1998).

Accurate estimates of population size and age and sex structure are notoriously difficult for species that are inaccessible or cryptic (e.g., camouflaged, fossorial, or subterranean). Many reptiles and amphibians are cryptic and have low detectability, which often requires long-term study or complex analyses to obtain accurate estimates. For example, it took decades of monitoring to reveal widespread amphibian declines (Wheeler et al. 2003, Bell et al. 2004). In spite of this, quantitative data are still almost completely lacking for some amphibian taxa whose life-history strategies make detection difficult (e.g., subterranean caecilians, Order Gymnophiona; Measey et al. 2003).

From a management perspective, achieving accurate estimates of population size needs to be economically and logistically feasible. Many populations are in remote locations, populations are small, and personnel and time are limited. Common approaches include change-in-ratio methods, catch-per-unit-effort, removal and depletion methods, line-transect distance sampling, and mark–recapture methods, which can be further categorized as closed-population, open-population, and robust design models (for reviews, see Seber 1982). Simple estimates that rely on counts, and do not require complex statistical analyses or specialist personnel, are preferable for their ease of use. However, these estimates have been shown to be inaccurate in the past, particularly when used to extrapolate across varying habitat types (Slade and Blair 2000).

Tuatara (*Sphenodon punctatus*) are the sole extant representative of the reptilian order Rhynchocephalia. Although historically distributed throughout the main islands of New Zealand, due primarily to the introduction of mammalian predators, natural populations are now restricted to approximately 30 small islands, which are difficult to access and are ecologically fragile because of extensive seabird burrowing (Newman 1982, Mulder and Keall 2001). Tuatara are medium sized (approx. 0.2-m snout–vent length), long-lived (80–100+ yr), have slow growth and reproductive rates, and spend much of their time in burrows, making detection difficult (Newman 1987, Cree et al. 1992). Adult tuatara are sexually dimorphic and sedentary, and males maintain stable territories and guard females during mating season (austral summer; Moore et al. 2009).

Tuatara are now a conservation priority in New Zealand (Gaze 2001, Nelson et al. 2002). Intensive management, including pest eradication and translocation, has been necessary for recovery of tuatara populations. Population estimates are needed before and after translocations to determine the status of translocated animals and assess the impact that removing founders may have on source populations (Towns et al. 2007). Historically, population estimates for tuatara have been imprecise, and often relied on simple count-based indices like catch-per-unit-effort (Crook 1973). The Tuatara Recovery Plan estimates many population sizes as "few tens," "low hundreds," or "few thousands" (Gaze 2001, appendix 1). The Tuatara Recovery Group has recently recognized a need for new surveys to

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Table 1. Population estimates and 95% confidence intervals using mark–recapture and the Lincoln–Peterson estimator for tuatara in a 1,290-m^2 area on Stephens Island, New Zealand, April 2003, including capture day, minimum number alive (MNA, total marked individuals), catch per unit effort (CPUE, tuatara/person-hr), and percent error compared to the census size of 87 individuals. We did not record recaptures on nights 4–6.

Capture day	No. of new captures	No. of recaptures	MNA	CPUE	Lincoln–Peterson estimate	95% CI	% error
1	11	0	11	14.7			
2	21	5	32	14.4	57.2	35, 140	−34.25
3	20	12	52	9.8	85.3	62, 133	−1.92
4	12		64				
5	5		69				
6	7		76				
7	3	35	79	18.5	82.5	77, 88	−5.16
8	6	50	85	24.9	88.5	83, 93	+1.70
9	2	44	87	25.6	88.9	85, 92	+2.14

reassess the status of each population, because the last major surveys were conducted in the late 1980s to early 1990s. Thus, a simple, effective method for estimating tuatara population size with minimal effort and cost is needed (Gaze 2001). We conducted a case study using mark–recapture and the Lincoln–Peterson estimator to predict actual census size for a population of tuatara.

STUDY AREA

Our study site, Stephens Island, New Zealand (Marlborough Sounds, 40°40′S, 174°00′E), holds the largest (approx. 30–50,000 individuals; Newman 1987) and densest population of tuatara. Stephens Island is a 150-ha island once covered with coastal forest until pastures were cleared for livestock grazing in the early 1900s (Brown 2000). All livestock were removed, and the island is undergoing an extensive reforestation program, although our study area was, historically and at the time of our study, one of the least disturbed areas on the island. Stephens Island was an important source for tuatara translocations and was also home to the only natural population of the endangered Hamilton's frog (*Leiopelma hamiltoni*).

Tuatara were identified as a predator of Hamilton's frogs (Newman 1977, Brown 2000), so in 1991 2 areas around the main frog habitat were enclosed by predator-proof fencing and tuatara inside the fence were removed. In September 2002, the 2 main areas were connected by predator-proof fencing to increase available habitat for the frogs. All tuatara were then removed from the 1,290-m^2 fenced connecting area in 2003 and translocated to establish a new population on neighboring Wakaterepapanui Island.

METHODS

From 7 April to 15 April 2003, we used mark–recapture to estimate the number of tuatara inside the predator-proof fence, prior to translocation. For 9 consecutive nights, 3 people with different levels of expertise walked 3 transects that ran the length of the 1,290-m^2 fenced area, captured all tuatara by hand, recorded their sex (based on sexually dimorphic characters), and marked them by applying a small dot of white correction fluid on the snout. Marks were easily visible throughout the remainder of the study. We surveyed the area once nightly, and search effort varied from 0.75 person-hours to 3.0 person-hours per night (Table 1). We searched the surveyed area 1–3 times (i.e., 1–3 sweeps), until we captured no new animals that night. Tuatara spend large amounts of time inactive, so we captured those that were above ground and few others typically emerged during that time. We recorded all recaptures and new captures for the first, second, third, seventh, eighth, and ninth nights. We recorded only new captures for the fourth through sixth nights. Temperature, wind, and humidity varied during the mark–recapture survey (varying 10–14° C/night, light to moderate wind from varying directions, and 82–95% relative humidity). The moon entered the first-quarter phase on 9 April, waxing to full on 16 April. Tuatara are ectotherms and are primarily nocturnal so their activity levels can vary depending on temperature, humidity, and moonlight. We considered these weather conditions to reflect a moderate level of activity.

We used the Lincoln–Peterson estimator (Peterson 1896, Lincoln 1930) to estimate population size. The Lincoln–Peterson estimator is the simplest method of estimating population size based on mark–recapture and is based on the notion that the proportion of marked to unmarked individuals in the population remains constant (Begon 1979). That is:

$$\hat{N} = \frac{rn}{m},$$

where ($\hat{N}$) is estimated population size, r is number of captured animals (marked and unmarked) in that session, n is the total number of individuals marked, and m is number of previously marked, recaptured individuals in that session. To assess the minimum number of survey nights necessary to achieve an accurate estimate, we calculated Lincoln–Peterson estimates for each night where we recorded recaptures, using number of individuals marked up until that night as n. We evaluated accuracy by comparing the census size (N) to the Lincoln–Peterson estimates ($\hat{N}$) using a percent error (PE) equation (e.g., Mccullough and Hirth 1988), where:

$$PE = \left(\frac{\hat{N} - N}{N}\right) \times 100$$

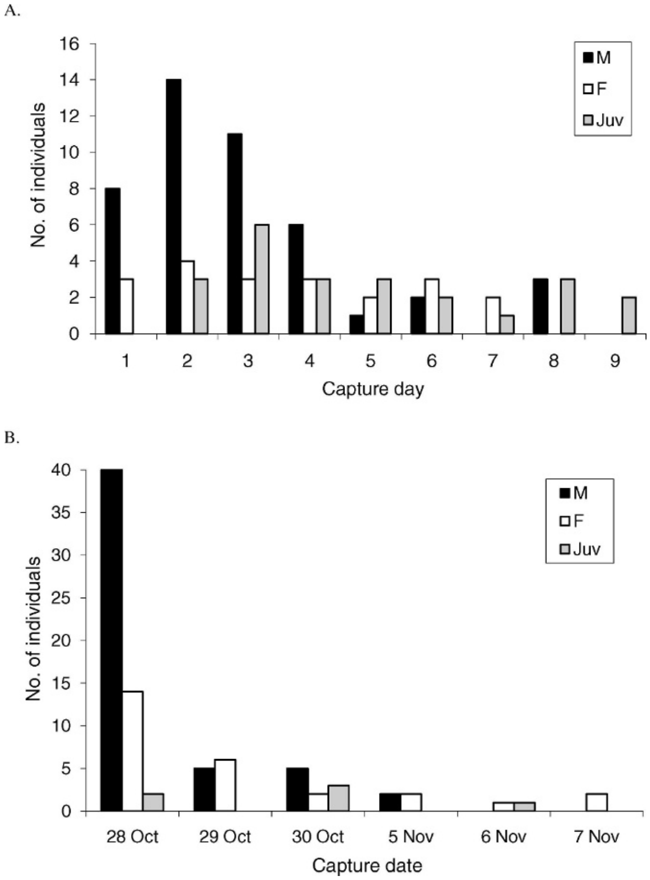

Figure 1. Capture data from tuatara surveyed using mark–recapture (A) and later, the same animals we captured and removed for translocation (B) from Stephens Island, New Zealand, April, October, and November 2003. We captured adult males first and captured adult females and juveniles throughout the sampling periods.

Due to the limited number of captures and recaptures we obtained, and that individuals did not have unique marks, we were unable to use more complex modeling methods (e.g., those that account for behavior).

From 28 October to 30 October and 5 November to 7 November 2003, we captured by hand all tuatara within the fence and removed them for translocation. Four to 5 people searched the fenced area during the day and night to ensure that we removed all tuatara. Upon capture, we recorded snout–vent length, tail length, mass, and sex (because these data can be used for monitoring following translocation). We periodically scanned the fenced area for 2 weeks after the initial removal to ensure that we captured all tuatara inside the fence, and we made no captures after the initial removal. Census size was, therefore, all tuatara that we removed from the fenced area.

RESULTS

From the 9-day mark–recapture study, we marked 87 tuatara (20 F, 45 M, and 22 juv that we could not sex) inside the 1,290-m^2 fenced area. After the third day of sampling, and with only 52 animals marked, the Lincoln–Peterson estimator gave a population estimate of 85.3 (95% CI = 62,133) individuals, with an error (compared to the census size) of -1.92% (Table 1). Population estimates increased in precision with more survey days. With up to 6 days of mark–recapture surveying (over a 9-day survey), population estimates remained constant, in the range of 83–89 individuals (Table 1).

We removed 87 tuatara (27 F, 54 M, and 6 juv that we could not sex) from the fenced area for translocation to Wakaterepapanui Island. In both the mark–recapture and the census–removal surveys, we captured, marked, and removed adult males earliest, whereas we captured, marked, and removed females and juveniles throughout the survey period (Fig. 1). Based on this census, the population density inside the fence was 674.4 tuatara/ha.

DISCUSSION

We found our Lincoln–Peterson estimate was accurate, which was after a 3-day mark–recapture survey only 2 individuals fewer than the true census size of this population. Our study provides preliminary support for mark–recapture and the Lincoln–Peterson estimator, and with further testing, this method may find great utility for accurate assessment and management of isolated tuatara populations.

The Lincoln–Peterson estimator has been criticized because of the inaccurate, often low estimates it provides (although conservative estimates may be appropriate in a conservation context). Assumptions of the Lincoln–Peterson estimator are briefly as follows: 1) the population is closed (i.e., no births, deaths, immigration, or emigration), 2) individuals have an equal probability of capture, and 3) marks are not lost or overlooked. These assumptions limit utility of this simple estimator for many circumstances. In the short term, at least assumptions 1 and 3 would hold true for most tuatara populations. Cassey and Ussher (1999) argue that because tuatara are burrowing animals, only a portion of the population is ever available for capture and that marking alters their behavior (making them trap-shy), which violates the assumption of equal probability of capture. Bailey et al. (2004) showed that Lincoln–Peterson methods can be just as effective as more robust methods for estimating the size of a superpopulation (i.e., individuals above ground and those that are below ground and unavailable for capture) of salamanders. Further, our data indicate that male tuatara may have a higher capture probability than females, which could result in negatively biased estimates if this heterogeneity is not accounted for (Pollock et al. 1990). Bailey et al. (2004) showed that variation in behavioral response (trap-happy or shyness) had a greater effect on population estimates of salamanders than unequal capture probabilities due to sex or species differences. Our results indicate that Lincoln–Peterson estimates are still accurate in spite of small differences in capture probabilities between sexes. Menkens and Anderson (1988) and Bailey et al. (2004) demonstrated that Lincoln–Peterson estimates are accurate in spite of small differences in capture probabilities, and only in cases with extreme heterogeneity in capture probabilities or extreme trap-happy or shyness does the Lincoln–Peterson estimator perform poorly.

Our sparse recapture data and lack of unique individual marks prevented us from testing additional modeling methods. However, in the future it would prove useful to compare different population estimation techniques for tuatara to better determine effects of observer bias and unequal capture probability (e.g., Bailey et al. 2004). A large, detailed data set and a longer sampling period are needed to more effectively address these issues. Likewise, validity of the Lincoln–Peterson estimator should be tested on other tuatara populations and future translocations may provide opportunities to do so.

Current population estimates for tuatara either do not exist or are imprecise due to a variety of factors. Financial limitations mean that sampling trips to islands are infrequent (e.g., every 5–10 yr, with some populations only surveyed once, often >20 yr ago). Likewise, personnel with experience in handling and detecting tuatara are often limited. It is often assumed that if a tuatara island is free of mammalian predators, then it harbors a healthy population of tuatara. However, these are also the populations that are suggested as sources for translocations, and when population estimates are unavailable, assessing the impact of a translocation on the population dynamics of a potential source island is impossible.

Using mark–recapture and the Lincoln–Peterson estimator, small islands could be visited by a few volunteers for a short period of time (3–4 nights) and surveyed at night for a minimal number of person-hours (e.g., 2 hr/night, depending on habitat and island size), during reasonable weather conditions (e.g., $>10^\circ$ C, light wind, with medium–high humidity, not following a drought or during a full moon). January to April would be the ideal sampling months because females would not be away from their burrows nesting, and temperatures would likely be warm enough to maximize tuatara activity. On larger tuatara islands, a smaller survey area could be designated and used for population estimates and then extrapolated across the island. Because the spatial structure of tuatara is stable over the short term (Moore et al. 2009), there would be little immigration or emigration from the survey area throughout the duration of a sampling trip. Lincoln–Peterson estimates may be more difficult on islands where habitat heterogeneity is extreme, and in these cases a better solution may be to perform small surveys in a range of habitat types and average them across the island. At the very least, extrapolation could provide a rough estimate of population size. A longer sampling trip is beneficial for increasing the precision of the estimate (as CIs tighten with more data; Table 1), but 3 days appears to be sufficient. However, caution is needed if attempting to estimate an accurate sex ratio (simply using counts) with only 3 days of data because this could result in a false bias toward males (because they may have a higher capture probability because they spend more time above ground or are more conspicuous to observers).

Stress and behavioral disturbance from handling have been cited as reasons why mark–recapture is not an appropriate method for tuatara (Cassey and Ussher 1999). However, collecting additional data (e.g., blood samples, health and parasite checks, body-size measurements) is often desirable, particularly for populations that are infrequently surveyed or that are sources for translocations, so handling is likely to occur even without marking. The mark–recapture method we highlighted requires only limited marking, and no knowledge of individual identity or the days on which individuals were first marked. Surveys and population estimates such as these can be conducted by virtually anyone, and no specialist training is needed. However, prior experience with tuatara does increase detection and capture ability, and it is beneficial to have personnel with searching and handling experience, and at least one experienced researcher or manager leading the field surveys.

Management Implications

The Lincoln–Peterson estimator does have its limitations and is not the solution for every situation. Ideally, with large islands and data sets, a more robust and complex estimator that can account for differences in behavior and sex should be used. However, we suggest that for basic population monitoring of small tuatara populations, the Lincoln–Peterson estimator is a vast improvement over the count-based catch per unit effort methods that are currently used.

We advocate evaluating our technique for other species that are cryptic, fossorial, or whose activity depends on climatic conditions (e.g., many reptiles and amphibians). We suggest that simple population estimators should not be overlooked in favor of more complex analytical techniques, even for species whose biology appears to violate the assumptions of these estimators. Translocations are already occurring for many of these species, which may provide appropriate, nondestructive opportunities to assess utility of mark–recapture and the Lincoln–Peterson estimator.

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