with comments on other Mexican species. Milwaukee Pub. Mus., Contrib. Biol. Geol. 20:1–15.
———. 1982. Reproductive cycles in tropical reptiles. Occas. Pap. Nat. Hist. Univ. Mus. Univ. Kansas 96:1–53.
———, AND R. W. HENDERSON. 1973. A new anole (Reptilia: Iguanidae) from southern Veracruz. J. Herpetol. 7:125–128.
GIANNASI, N., R. S. THORPE, AND A. MALHOTRA. 1997. Introductions of *Anolis* species to the island of St. Lucia, West Indies: Testing for hybrids using multivariate morphometrics. J. Herpetol. 31:586–589.
GUYER, C. 1988a. Food supplementation in a tropical mainland anole, *Norops humilis*: Demographic effects. Ecology 69:350–361.
———. 1988b. Food supplementation in a tropical mainland anole, *Norops humilis*: Effects on individuals. Ecology 69:362–369.
———, AND J. M. SAVAGE. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). Syst. Zool. 35:509–531.
———, AND ———. 1992. Anole systematics revisited. Syst. Zool. 41:89–110.
HOWARD, A. K., J. D. FORESTER, J. M. RUDER, J. S. PARMELEE, JR., AND R. POWELL. 1999. Natural history of a terrestrial Hispaniolan Anole: *Anolis barbouri*. J. Herpetol. 33:702–706.
JENSSEN, T. A. 1970. Ethoecology of *Anolis nebulosus* (Sauria, Iguanidae). J. Herpetol. 4:1–38.
LOSOS, J. B. 1996. Dynamics of range expansion by three introduced species of *Anolis* lizards on Bermuda. J. Herpetol. 30:204–210.
MARTTZ, M. F., AND R. M. DOUGLAS. 1994. Shape quantization and the estimation of volume and surface area of reptile eggs. J. Herpetol. 28:281–291.
NIETO-MONTES DE OCA, A. 1994. Rediscovery and redescription of *Anolis schiedii* (Wiegmann)(Squamata: Polychridae) from central Veracruz, Mexico. Herpetologica 50:325–335.
———. 1996. A new species of *Anolis* (Squamata: Polychrotidae) from Chiapas, Mexico. J. Herpetol. 30:19–27.
RAMÍREZ-BAUTISTA, A. 1995. Demografía y reproducción de la lagartija arborícola *Anolis nebulosus* de la Región de Chamela, Jalisco. Tesis Doctoral [PhD Dissertation], Facultad de Ciencias, Universidad Nacional Autónoma de México, México. 160 pp.
———, AND L. J. VITT. 1997. Reproduction in the lizard *Anolis nebulosus* (Polychrotidae) from the Pacific coast of México. Herpetologica 53:423–431.
RZEDOWSKI, J. 1981. Vegetación de México. Editorial Limusa, México. 432 pp.
RUIBAL, R., R. PHILIBOSIAN, AND J. L. ADKINS. 1972. Reproductive cycle and growth in the lizard *Anolis acutus*. Copeia 1972:509–518.
SCHOENER, T.W. 1968. The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. Ecology 49:704–726.
———, AND G. G. GORMAN. 1968. Some niche differences in three Lesser Antilles lizards of the genus *Anolis*. Ecology 49:819–830.
———, AND A. SCHOENER. 1971a. Structural habitats of West Indian *Anolis* lizards I. Lowland Jamaica. Breviora. Mus. Comp. Zool. 368:1–53.
———, AND ———. 1971b. Structural habitats of West Indian *Anolis* lizards II. Puerto Rico uplands. Breviora, Mus. Comp. Zool. 375:1–39.
SECRETARIA DE GOBERNACION Y GOBIERNO DEL ESTADO DE PUEBLA. 1988. Los Municipios de Puebla. *In*: Enciclopedia de Los Municipios de México, Puebla. México. Bol. Soc. Bot. Méx. 59:35–58.
SELBY, S. M. 1965. Standard Math Tables, 14th ed. Chemical Rubber Co., Cleveland, Ohio.
SMITH, H. M. 1968a. A new pentaprionid anole (Reptilia: Lacertilia) from the Pacific slopes of México. Trans. Kansas Acad. Sci. 71:195–200.
——— 1968b. Another new lizard from México of the *schiedii* group of *Anolis*. Southwest. Nat. 13:368–370.
——— 1968c. Two new lizards, one new, of the genus *Anolis* from México. J. Herpetol. 2:143–146.
———, AND D. R. PAULSON. 1968. A new lizard of the *schiedii* group of *Anolis* from México. Southwest. Nat. 13:353–372.
VILLASEÑOR, J. L., P. DÁVILA, AND F. CHIANG. 1990. Fitogeografía del Valle de Tehuacan-Cuicatlán. Bol. Soc. Bot., Méx. 50:135–149.
VITT, L. J., AND H.J. PRICE. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. Herpetologica 38:237–255.
———, P. A. ZANI, AND R. D. DURTSCHE. 1995. Ecology of the lizard *Norops oxylophus* (Polychrotidae) in lowland forest of southeastern Nicaragua. Can. J. Zool. 73:1918–1927.

TECHNIQUES

Herpetological Review, 2002, 33(4), 271–274.
© 2002 by Society for the Study of Amphibians and Reptiles

Distance Sampling of Forest Snakes and Lizards

GORDON H. RODDA
USGS Midcontinent Ecological Science Center
Fort Collins, Colorado 80525, USA
e-mail: Gordon_Rodda@usgs.gov

and

EARL W. CAMPBELL
Ohio State University Cooperative Fish and Wildlife Research Unit
Present address: U.S. Fish and Wildlife Service, Honolulu, Hawaii 96850, USA
e-mail: 76130.312@compuserve.com

How does one test the validity of a population enumeration technique? Most validation studies perform "soft" validation; they attempt either to correlate the counts from two or more methods (Fitch 1992) or to compare the economic costs, difficulty, time requirements, or non-economic costs of carrying out selected methods (Strong et al. 1993). Soft validation does not establish the accuracy of a method. "Hard" validation, in which population estimates are checked against the true values, is obviously desirable, but it is always difficult to do and might be impossible for some systems. Hard validation studies involving reptiles or amphibians are rare and usually involve the artificial stocking of a bounded plot (Henke 1998; Rose and Armentrout 1974).

Distance sampling is a relatively new technique (Buckland et al. 1993) that has gained considerable favor for certain herpetological sampling problems (Akin 1998; Thompson et al. 1998), but has yet to be subjected to hard validation tests for reptiles or amphibians. As with strip transect searches (Duellman 1987), distance sampling involves searching for animals within a certain distance from a transect centerline, but it differs from strip transects in requiring the measurement (or estimation) of the perpendicular distance from the centerline to each detected animal. Whereas strip transect searches make the implicit assnmption that detection is complete for animals within the strip, distance sampling reqnires only that all animals *near the centerline* be detected. The distribution of sighting distances to animals off the centerline is used to model detectability in the vicinity of the centerline, but it is only the centerline density estimate that is used and extrapolated to the habitat at large.

Because the centerline density is extrapolated to the overall habitat, it is essential that the centerline conditions be representative of the habitat. Strip transects make a similar assumption about the representativeness of the entire strip, but the corresponding distance sampling assumption is more problematic in that the centerline of many transects is a road or trail, hardly representative of adjacent habitat. In addition to having different ground cover

and animal use patterns than surrounding habitat, trails in forested areas are associated with light gaps that alter the density and form of vegetation (hence visibility, basking opportunities, etc.). To be truly representative, a distance sampling centerline must be placed randomly in relation to animal position and habitat heterogeneity. These strictures dictate that trails or roads should not be followed, but this is impractical in most forested habitats.

The other key assumptions of distance methodology are that each animal is counted only once and that the perpendicular distance from the animal to the centerline is estimated without error and prior to any movement of the animal towards or away from the centerline/observer. Depending on the study species, these assumptions would not be troublesome for many reptiles and amphibians.

Distance sampling seems ideally suited for the many species of amphibians and reptiles that are rarely seen or hard to capture, because marking, recapture, or handling of animals is not required. One can sum rare detections over many sampling occasions, and there is no minimum number of detections needed for a sampling occasion to be useful. There is no uncertainty about the size of the area sampled, and one obtains an absolute population density estimate that is insensitive to habitat structure, species, or the capabilities of the searcher (Rodda 1993). The key disadvantages of distance sampling for reptiles and amphibians are that one *must* detect 100% of the animals on the unbiased centerline and that detections must be gathered over an amount of time and space sufficient to accumulate an adequate sample size. Thus one might have difficulty using distance sampling to answer a question such as, "Do rainbow snakes reach peak density in a particular wetland in May?"

We conducted a hard validation study of distance sampling for forest geckos and snakes on Guam. We compared the estimates produced by distance sampling to true local gecko densities based on subsequent total removal of all animals and vegetation from sealed 10 x 10 m plots (Rodda et al. 2001). For brown treesnakes (*Boiga irregularis*), we compared distance sample estimates to densities based on mark-recapture estimates that we had in turn validated in adjacent fenced 1-ha plots by comparing mark-recapture estimates to total removal of all snakes (Campbell 1996). The gecko comparison was done sequentially, as the total removal method alters vegetation and therefore could not be carried out concurrently with the distance sampling.

Methods.—We searched for forest geckos and snakes in a 6.5-ha patch of tangantangan (*Leucaena leucocephala*) forest north of the grenade range at Northwest Field, Andersen Air Force Base, Guam (N 13.6373–13.6399; E 144.8616–144.8643), 19 January 1993 to 29 November 1994. Within this patch were four 1-ha plots circumscribed by trails and penetrated by three parallel internal transect trails spaced 25 m apart. Sighting of forest squamates was facilitated because all searching was done at night when the many small leaflets of the dominant tree, *Leucaena leucocephala*, fold closed (mean percentage of tree basal area due to the species *L. leucocephala* = 61%, N = 7 removal plots). The forest canopy in this area is very low (mean = 5.4 m, N = 7 removal plots) and is unusually open (mean distance to daytime disappearance of a human = 15.7 m, N = 1000). Mean forest canopy cover was 69% (N = 7 removal plots). Because of this naturally incomplete canopy, creation of the transect trails did not greatly alter forest structure. Negligible movement towards or away from the observer was noted in sighted animals, which were illuminated by spotlight.

Distance estimates were obtained by two experienced observers who periodically checked sighting distance estimates against measured distances (a telescoping rod marked at 0.1 m intervals was extended perpendicularly from transect centerline to the sighting point). They walked each transect five times quarterly, for a total of 36.2 km of transect searched on both sides of the trail/centerline. Results from other transects (in manipulated or snake-controlled plots: Campbell 1996) were not included in the distance validation data presented here. Sightings > 4 m from the transect centerline were extremely sparse and were not used in the analysis. Because of uncertainty about the species identity of small geckos, all gecko species were pooled. Based on known identities (96% of sighted geckos were identified to species), the majority (88%) of these sightings were *Hemidactylus frenatus*, the remainder *Lepidodactylus lugubris*. It is possible that some individuals of *Gehyra mutilata* were present; none was definitely sighted, though one was found in a removal plot. The only other sighted squamate was the brown treesnake, *Boiga irregularis*. Snakes were analyzed separately from geckos.

Conventional distance analytical methods (Buckland et al. 1993) were used, with cut points for distance caregories set at 0, 1, 2, 3, and 4 m (i.e., sightings grouped in the ranges 0–1.0 m, 1.01–2.00 m, etc.). Alternate cut points were investigated but did not appreciably affect density estimates. Model selection was guided by program DISTANCE; alternate models provided nearly identical density estimates. Estimated sighting distances were pooled over time for the four 1-ha study plots, providing sample sizes of effort (36.2 km), samples (4 plots), and observations (1853 geckos and 51 snakes).

Absolute population density measurements, by total removal, were obtained using the methods described by Rodda et al. (2001). Briefly, canopy separation and ground-level aluminum flashing were used to prevent the movement of lizards into or out of the sample plots while the vegetation was removed and all vertebrates identified, measured, and weighed. Plots were selected on the basis of representative canopy coverage and plant species composition. Four 5 x 5 m plots and one 10 x 10 m plot within the area surveyed using distance methods were censused 16 Feb–14 May 1995. Four 10 x 10 m additional samples from the same area were censused 28 Jan–11 Feb. 1999. Because the two series produced nearly identical mean gecko densities (3350/ha v. 3450/ha), these were pooled for comparison to distance estimates.

Mark-recapture was used only for snakes, following the methods described in Campbell (1996) and using program MARK (White and Burnham 1999). Through saturation removal of snakes from fenced plots, Campbell demonstrated that the true snake density was well within the 95% confidence limits of mark-recapture estimates made with this method on these plots at the time this work was carried out. Briefly, we captured brown treesnakes using snake traps (Rodda et al. 1999) and hand capture over six 15–22 day periods simultaneous with the distance sampling. All captives were double marked using PIT tags and paint markings. Exploration of the resulting capture history matrices with various open population models consistently indicated a best model (selected on the basis of Akaike's Information Criterion) that varied capture probability, p, in accordance with snake snout-vent length

(small snakes were less frequently captured), but with capture probability and apparent survivorship, ϕ, constant over time. "Apparent survivorship" quantifies the probability of a snake dying or moving permanently out of a study plot between daily trapping occasions. Emigration so measured was high enough (2.5–17.5%/day) to preclude analysis with closed mark-recapture models. Snake abundance in each plot was estimated as size-stratified n-bar/p-hat, where n-bar is the mean number of captures/day and p-hat is the maximum likelihood estimator of mean capture probability. Density was estimated by dividing estimated abundance by each plot's nominal trap grid area (1 ha). Twenty-four venues (four plots by six time periods) provided density estimates, but ten of these involved plots for which the snake density had been manipulated. The fourteen density estimates from unmanipulated plots were averaged for comparison to the oue distance estimate obtained concurrently.

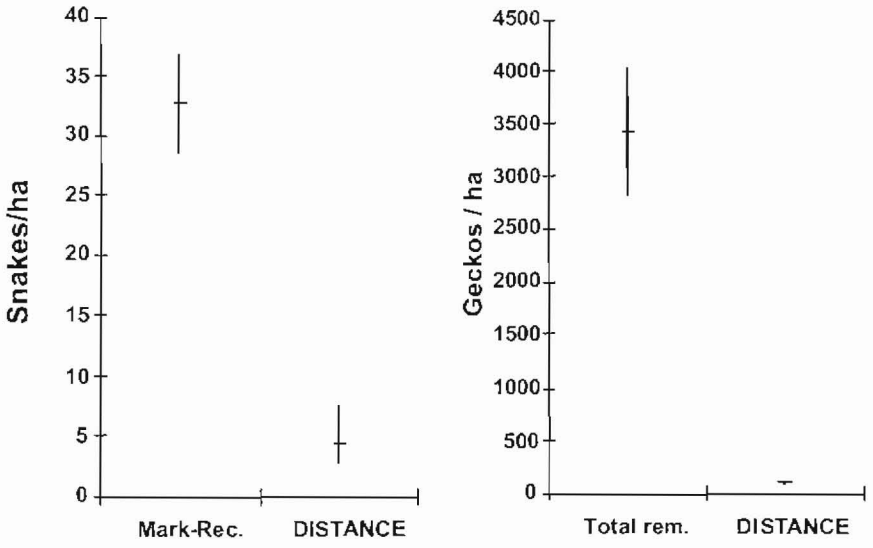

FIG. 1. Distance sampling estimates for brown treesnakes, *Boiga irregularis*, and geckos (*Hemidactylus frenatus*, *Lepidodactylus lugubris*, and *Gehyra mutilata*) on Guam in relation to mark-recapture (snakes) or total removal estimation (geckos). Distance estimates show maximum likelihood estimate with 95% confidence intervals. The other values are mean +/- SE.

Results.—The detection distances analyzed by DISTANCE showed the expected smooth decline with increasing distance from the transect centerline (geckos: 721, 602, 390, and 140; snakes: 29, 21, 7, and 9) and had excellent model goodnesses of fit (geckos: $\chi^2 = 0.71$, df = 1, P = 0.4; snakes: $\chi^2 = 1.39$, df = 1, P = 0.24). For both data sets, the selected model used the uniform key and cosine adjustment. However, the density estimate obtained for geckos was 100.1 geckos/ha (95% CL: 85.6–117.1), whereas the mean density estimate obtained by direct count (total removal) averaged 3416.7 geckos/ha (SE = 608). Thus the disrance estimate for geckos was low by a factor of about 34 (Fig. 1). The distance density estimate for snakes was 4.4/ha (95% CL: 2.6–7.4), whereas the validated mark-recapture population estimates (N = 14) averaged 32.7/ha (SE = 4.0). Thus the distance estimate for snake density was low by about a factor of 7 (Fig. 1).

The gecko species composition estimated from sighted individuals was overwhelmingly *Hemidactylus frenatus* (88%), whereas subsequent total removal censuses indicated that less than half of the gecko individuals present (46%) were of that species. The majority (52%) were *Lepidodactylus lugubris*.

Discussion.—Does the discrepancy in gecko species composition between visual sightings (88% *Hemidactylus*) and census results (46%) reflect detecrion differences among gecko species or were geckos misidentified or often not-identified to species during visual searches? The percentage of unidentified geckos (4.1%) was small relative to the total sample, indicating that the large discrepancy could not be made up by more complete identification of geckoes sighted. The two observers gave virtually identical percentages of *Hemidactylus* in their visual samples (87.3 v. 87.7%), suggesting that few identifications were in error. It is likely, however, that detection differed between these species. *Lepidodactylus* is found mainly in foliage, where visibility is reduced, whereas *Hemidactylus* is most often found in more visible sites on branches, limbs, and trunks. Thus we expected that detection would be more complete for *Hemidactylus*. If one assumes that all visual identifications were correct and that the proportional representation of unidentified species was the same as for the identified geckos, the distance estimate for *Hemidactylus* would be 88/ha (CL 75–103/ha), which underestimated the true value of 1572/ha low by a factor of about 18. If one combines the small uncertainty associated with species identification with the distance sample confidence limits, the *Hemidactylus* uncertainty ranges 72–104/ha, implying an error factor of 15–22 fold. The corresponding values for *Lepidodactylus* are 12/ha (CL 10–14/ha), which underestimated the true density of 1777/ha by a factor of about 148. Adding in the identification uncertainty broadens the total uncertainty range for this species' estimate to 10–18/ha, implying an error factor of 98–181.

The population density estimates provided by DISTANCE in this case were severely biased in comparison to higher validity methods. As evidenced by the different gecko species composition of the contrasted methods, the bias was different for different species even within the same guild and body size range. Before concluding that distance sampling is inappropriate for this system, however, it is desirable to question possible sources of error in the higher validity methods. Each method makes assumptions, but the following seem to us to have the greatest likelihood of error.

Open mark-recapture analysis assumes negligible individual heterogeneity in capture probability. If this assumption is invalid for brown treesnakes, the true population densities would be higher than reported here, and the estimated bias of the distance estimates would be greater.

Open mark-recapture analysis also assumes the absence of either trap happiness or trap shyness. The existence of trap happiness would exacerbate the apparent bias of distance sampling for snakes, whereas trap shyness would have the opposite effect. Note that the mouse attractant used in the snake traps could not be eaten by captured snakes, so trap happiness would not be expected. In

closed model analysis of brown treesnake trap captures we have detected only limited evidence of either type of behavioral response (Rodda and Dean-Bradley, unpubl. data), suggesting that the observed difference between mark-recapture and distance sampling is not attributable to trap shyness.

The small sample plots used for total removal population density estimation might have been non-representative. The selection criteria seem unbiased, and extensive glueboard surveys and visual searches failed to document any evidence of non-representation. We expect that only random bias would be produced by failure of this assumption.

Which distance assumptions might be invalid? The use of trails rather than randomized unimproved transects for distance sampling centerlines violates a key method assumption, that transects be placed randomly in relation to habitat. In this specific case, the transect "centerline" is a 2-m wide band spanning the trail. If squamate sighting rates were lower on trails than when walking cross-country through the forest, our use of trails could produce the observed bias. It is our experience, however, that sighting rates are not higher when walking cross country through the forest on Guam, but drop to near zero, because of visual interference by vegetation. Furthermore, if trails have any effect on the distribution of these species we would expect that heliophilic squamates would seek out the sides of trails, as the light gaps created by trails produce more vegetation of a suitable height and these provide more basking and foraging opportunities. Thus, our expectation was that use of trails for transect centerlines would bias distance estimates upwards, not downwards as observed.

Violation of the assumption that all squamates present on the centerline were detected most likely produced the observed bias. It seems likely to us that vegetation concealed many active squamates, and that inactivity of others would account for their unavailability for detection. Intensive visual searches of brown treesnakes in finely-gridded areas on Guam produce an average detection probability of < 9% (usually < 5%; Rodda et al., unpubl. data). If one can see only 9% (or less) of the snakes that are present in a forest, it is unrealistic to expect distance sampling to produce unbiased estimates of forest squamate population density. Because of the ubiquitousness of visual barriers in a forest, we suggest that distance sampling is unlikely to be valid for absolute densities of forest vertebrates detected exclusively by sight.

Does the discrepancy in gecko species composition between visual sightings (86% *Hemidactylus*) and census results (46% *Hemidactylus*) reflect detection differences among gecko species, or were visually-sighted geckos unidentified or misidentified frequently enough to account for the discrepancy? The percentage of unidentified geckos (4.1%) was small relative to the number identified; this could not account for the discrepancy. Misidentification cannot be unequivocally ruled out, but we believe that the primary cause of the discrepancy is the different microhabitats used by these geckos: *Lepidodactylus lugubris* is found mainly in foliage, where visibility is reduced relative to the branch/trunk sites preferred by *Hemidactylus frenatus*.

Also, if detection on the centerline is not 100% and differs among species, distance estimates cannot be used as an index of abundance when comparing species. For example, the distance estimator for *Hemidactylus frenatus* cannot be compared to that for *Lepidodactylus lugubris*, even if used only as an index of abundance. However, it might be possible to make temporal comparisons within a single species. Validation studies among different seasons, species, and habitats would be needed to determine if the ratio of undercounting is consistent enough for distance sampling to have utility as a single species index.

Acknowledgments.—Craig Clark was a cornerstone of support for all of the field work involved in this project. We were also ably assisted by Jay Graham, Matt Reid, Tom Fritts, Thomas Sharp, Grant Beauprez, Todd Mabee, Stan Kot, and numerous appreciated volunteers. The Department of Defense Legacy Program and the U.S. Department of the Interior's Office of Insular Affairs provided financial support. Andersen Air Force Base (H. Hirsch) provided access to field sites. Ken Burnham, Gary White, and David Anderson provided superlative training on the software used for the analyses. Kathy Dean-Bradley, Tony Tucker, Teri Kman, and Jimi Gragg suggested improvements to the manuscript.

Literature Cited

Akin, J. A. 1998. Fourier series estimation of ground skink population density. Copeia 1998:519–522.

Buckland, S. T., D. R. Anderson, K. P. Burnham, and J. L. Laake. 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London. 446 pp.

Campbell, E. W., III. 1996. The effect of Brown Tree Snake (*Boiga irregularis*) predation on the island of Guam's extant lizard assemblages. Unpub. Ph.D. dissert. Ohio State Univ., Columbus, Ohio. 91 pp.

Duellman, W. E. 1987. Lizards in an Amazonian rain forest community (Peru): Resource utilization and abundance. Nat. Geogr. Res. 3:489–500.

Fitch, H. S. 1992. Methods of sampling snake populations and their relative success. Herpetol. Rev. 23:17–19.

Henke, S. E. 1998. The effect of multiple search items and item abundance on the efficiency of human searchers. J. Herpetol. 32:112–115.

Rodda, G. H. 1993. Where's Waldo (and the snakes)? Herpetol. Rev. 24:44–45.

———, E. W. Campbell, III, and T. H. Fritts. 2001. A high validity census technique for herpetofaunal assemblages. Herpetol. Rev. 32:24–30.

———, T. H. Fritts, C. S. Clark, S. W. Gotte, and D. Chiszar. 1999. A state-of-the-art trap for the Brown Treesnake. *In* G. H. Rodda, Y. Sawai, D. Chiszar, and H. Tanaka (eds.), Problem Snake Management: the Habu and the Brown Treesnake, pp. 268–305. Cornell Univ. Press, Ithaca, New York.

Rose, F. L., and D. Armentrout. 1974. Population estimates of *Ambystoma tigrinum* inhabiting two playa lakes. J. Anim. Ecol. 43:671–676.

Strong, D., B. Leatherman, and B. H. Brattstrom. 1993. Two new simple methods for catching small fast lizards. Herpetol. Rev. 24:22–23.

Thompson, W. L., G. C. White, and C. Gowan. 1998. Monitoring Vertebrate Populations. Academic Press, San Diego, California. 365 pp.

White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46 Supplement:120–138.