

CAN MODELING IMPROVE ESTIMATION OF DESERT TORTOISE POPULATION DENSITIES?

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Abstract. The federally listed desert tortoise (*Gopherus agassizii*) is currently monitored using distance sampling to estimate population densities. Distance sampling, as with many other techniques for estimating population density, assumes that it is possible to quantify the proportion of animals available to be counted in any census. Because desert tortoises spend much of their life in burrows, and the proportion of tortoises in burrows at any time can be extremely variable, this assumption is difficult to meet. This proportion of animals available to be counted is used as a correction factor (g_0) in distance sampling and has been estimated from daily censuses of small populations of tortoises (6–12 individuals). These censuses are costly and produce imprecise estimates of g_0 due to small sample sizes. We used data on tortoise activity from a large ($N = 150$) experimental population to model activity as a function of the biophysical attributes of the environment, but these models did not improve the precision of estimates from the focal populations. Thus, to evaluate how much of the variance in tortoise activity is apparently not predictable, we assessed whether activity on any particular day can predict activity on subsequent days with essentially identical environmental conditions. Tortoise activity was only weakly correlated on consecutive days, indicating that behavior was not repeatable or consistent among days with similar physical environments.

Key words: activity modeling; detectability; distance sampling; *Gopherus agassizii*; monitoring; neural network modeling; power analysis.

INTRODUCTION

In 1991, desert tortoise (*Gopherus agassizii*) populations distributed north and west of the Colorado River were listed as “threatened” under the Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1990). The recovery plan for this species recommended monitoring the effectiveness of management actions by assessing population sizes for one tortoise generation (25 years). One criterion to delist this species is to demonstrate a statistically significant upward or stable trend in population size over a 25-year time period (U.S. Fish and Wildlife Service 1994).

Range-wide monitoring of population densities of desert tortoises was initiated in 1996, using stratified random transects in all 14 Desert Wildlife Management Areas (DWMAs) contained within the six Recovery Units (Appendix; U.S. Fish and Wildlife Service 1994, Anderson et al. 2001). Population densities within DWMAs have been calculated using “distance sampling” calculations (Anderson et al. 2001, Buckland et al. 2001) as

$$D = \frac{n}{l \times w} \times \frac{1}{P_a \times g_0} \quad (1)$$

where D is the estimated density of animals, n is the

number of animals observed on transects, l is the total length of the transect walked, and w is the width of the transect. In addition, this equation uses two functions to estimate how many animals are missed during the sampling as a function of (1) their distance from the transect (detectability, P_a ; see Plate 1), and (2) their availability to be encountered by an observer (g_0). Tortoises are frequently unavailable to be sampled because tortoises are cryptic and make extensive use of underground shelters.

Desert tortoises spend much of the year in burrows even during the active season (Woodbury and Hardy 1948, Nagy and Medica 1986, Bulova 1994), and usually only the proportion of the tortoise population that is above ground is sampled. This can lead to a violation of a critical assumption of the distance sampling technique, namely, that all animals on the line are found (Anderson et al. 2001, Buckland et al. 2001). Aboveground availability (g_0) is currently estimated by monitoring the proportion of radiotelemetered animals ($N = 6$ –12) that are visible to observers at several sites within the desert tortoise recovery units (Anderson et al. 2001).

The goals of this study were: to identify the level of precision necessary to statistically detect trends in tortoise populations; to explore the error in density estimates that could be induced by estimating g_0 from observing small focal populations; and to explore the extent to which modeling g_0 using a suite of environmental conditions could improve estimates of g_0 .

Manuscript received 13 December 2005; revised 24 May 2006; accepted 30 May 2006. Corresponding Editor: J. Van Buskirk.

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MATERIALS AND METHODS

Power analysis

To get an estimate of the precision necessary to satisfy the first U.S. Fish and Wildlife Service delisting criterion we conducted a power analysis to estimate the statistical power to detect growth in populations at different growth rates and with different degrees of error in the density estimates over a 25-year period. The power analysis used computer simulations (Link and Hatfield 1990) of population growth for populations with a constant average growth rate. Simulated growth rates ranged from 1% to 5% annual growth in increments of 1% (Hatfield et al. 1996), and coefficients of variation for the density estimates ranged from 5% to 100% in increments of 5% for each subsequent analysis.

Populations were simulated to grow at a specified average growth rate starting with 1000 individuals, and a population size was generated for each time step that was randomly modified according to a specified coefficient of variation. Thus, a population of N_{t+1} at time $(t + 1)$ was calculated as a product of the population one year prior (N_t) multiplied by the discrete population growth rate (λ). Variation was then added to the resulting population estimate (N_t) by drawing a number from a random-normal distribution with a mean of N and a specified coefficient of variation (CV):

$$N_{t+1} = N_t \times f(\lambda, CV). \quad (2)$$

We simulated population size over 25 years and then regressed the resulting annual population sizes against time. Statistical power was determined from the proportions of 1000 simulations of population growth with each set of population parameters (λ and CV) that were significant with an alpha of 0.05 (Hatfield et al. 1996).

Source of data for calculating g_0

Approximately 150 adult desert tortoises were tracked weekly at one site near Las Vegas, Nevada, USA (Appendix). The tortoises were located approximately between 04:00 and 16:00, which generally bounded the daily activity times of tortoises. These animals were monitored over a three-year period (1997–1999) using hand-held radiotelemetry receivers (e.g., Telonics TR-2, Mesa, Arizona, USA). Radio transmitters (AVM models G3, SB2, or SB2-RL) were attached to tortoises in a manner similar to that described in Boarman et al. (1998). The body of the transmitter was attached (with epoxy) to the first costal scute, usually on the left side of the animal, to provide the best positioning of the antenna. The antenna was then affixed (with epoxy) to the center of each costal scute from front to rear, wrapping around the back of the animal and continuing forward on the opposite side. Silicone caulk was used to secure the antenna in the scute margins while allowing for growth of the animals (Boarman et al. 1998). All

tortoises were numbered with a paper tag covered with clear epoxy, and the carapaces were notched on the marginal scutes by creating a small groove using a triangular file (Cagle 1939).

When tortoises were located, the date, time, and the microhabitat of the animals were recorded. We categorized the microhabitats into four general categories: in the open, under vegetation, in a pallet (a shallow shelter that does not completely cover the tortoise, Bulova 1994), or in a burrow. To approximate availability we further categorized each microhabitat as above ground (i.e., under vegetation or in the open), or below ground (i.e., in a burrow or a pallet) and calculated the proportion of animals above ground.

Environment

A weather station recorded environmental and operative temperatures (T_e ; Bakken et al. 1985) at a central location at the study site. Operative temperatures represent an estimated potential body temperature if the animals were to achieve a steady state under current environmental conditions (Tracy 1982, Bakken et al. 1985, O'Connor et al. 2000). Operative temperatures were measured using painted cast aluminum models of both juvenile (carapace length [CL] = 80 mm), and adult-sized (CL = 240 mm) tortoises placed in full sun and in shaded microhabitats (Zimmerman et al. 1994). The amount of solar radiation was measured using a pyranometer (model number LI-200SA, LI-COR, Lincoln, Nebraska, USA). Wind speed was measured at a height of 1 m from the surface with a cup anemometer (model number 03101, Campbell Scientific, Logan, Utah, USA). Air temperatures were measured at 10, 20, and 40 cm above the ground with shielded thermocouples (Christian and Tracy 1985). Soil temperatures were measured at the substratum surface, and at 10, 20, and 70 cm below the surface. All thermocouples were 24-gauge type k (Omega Engineering, Stamford, Connecticut, USA). Data were recorded using a CR-10X datalogger with an AM416 multiplexer (Campbell Scientific, Logan, Utah, USA).

Average and variance of g_0 with sample size

We wanted to determine the possible error in the estimates of the proportion of tortoises above ground and available to be censused as a function of sample size. To do this we used the microhabitat locations that we categorized as above or below ground for 376 observations of ~120 tortoises from 24 May 1999 to 18 June 1999. Animals that were found either in the open or under vegetation were classified as above ground, and animals that were in a burrow or a pallet were classified as below ground. Samples of these 376 observations ranging from 3 to 150 observations were drawn randomly, and the average and standard deviation of the locations were calculated. This was repeated with 100 random draws (with replacement) of observations at each sample size.

TABLE 1. Sensitivity analyses of the input variables to the results of the Artificial Neural Network model.

Inputs to model	Influence on g_0
Maximum of large T_e in shade	0.027
Maximum of surface temp. in shade	0.020
Average of large T_e in sun	0.021
Average of T_{air} (20 cm) in shade	0.017
Maximum of small T_e model in sun	0.016
Average of small T_e model in sun	0.014
Average soil temp. (-30 cm) in sun	0.013
Minimum of small T_e model in shade	0.013
Average of large T_e model in shade	0.009
Average of soil temp. (-10 cm) in sun	0.007
Average of small T_e model in shade	0.006
Average soil temp. (-70 cm) in sun	0.005
Minimum of small T_e model in sun	0.005
Maximum of large T_e model in sun	0.003
Maximum of surface temp. in sun	0.002
Average of T_{air} (40 cm) in sun	0.002
Average of wind speed (m/s)	0.001
Average of T_{air} (40 cm) in shade	0.001

Notes: Air and soil temperatures are expressed in centimeters above or below the surface. The sensitivity analysis was performed by running the model with each input value set at one standard deviation above and below its mean, and measuring how much the output varied. The influence on the predicted proportion of animals active (g_0) is the standard deviation of each output divided by the standard deviation of each input. Operative temperature is represented by T_e , and air temperature is represented by T_{air} .

We fitted a power function to the curve created by the standard deviations of the measurements ($y = 0.5479x^{-0.5678}$), and the first derivative of the fitted function ($dy/dx = -0.3111x^{-1.5678}$) indicated the number of samples at which relatively little change occurred in the reduction of the standard deviation as sample sizes increased.

Model of g_0

We used an Artificial Neural Network (ANN) to model daily tortoise activity (g_0) as a function of 18 site-specific environmental variables recorded by the weather station. The environmental variables that we used as inputs included: daily values of maximum solar radiation, rainfall, average wind speed, and minimum, maximum, and average temperatures of air, soil, and operative temperature (T_e) models (Bakken et al. 1985). The model was constructed from 334 days of input using 65% of the data for training, 25% for cross-validation, and 10% for testing the network. Specifically, the neural network was a back-propagating network consisting of one hidden layer of four processing elements and one hidden layer, using Tan-h transfer functions, with a momentum-learning-rate of 0.7 per epoch (Principe et al. 2000). We used weight decay to allow model inputs to drop out of the model when they did not contribute to the prediction of g_0 . The network was constructed using NeuroSolutions for Excel (Version 4.2, Neuro Dimension, Gainesville, Florida, USA). This software normalized inputs prior to running the model.

The relative influence of different inputs to the model was quantified by sensitivity analyses of each variable on the predicted outcome (Table 1). The sensitivity analysis consisted of running the model with each normalized input value set at one standard deviation above and below its mean, and measuring how much the output varied. The standard deviation of each output was then divided by the standard deviation of each input.

Repeatability of g_0

To assess the repeatability of tortoise activity across time, we chose consecutive pairs of days from three years of observations with the criterion that the difference between the maximum operative temperature of the first and second day was not $>5^\circ\text{C}$. The proportions of tortoises active on the first and second days were then regressed against one another to indicate the repeatability of percentage activity for the tortoise population on similar days.

RESULTS

Power analysis

Coefficients of variation of $>12\%$ around a growth rate of 1% per year would not allow enough statistical power (i.e., 0.8) to detect the trend over a 25-year period (Fig. 1). To achieve similar power for 2%, 3%, 4%, and 5% annual growth rates the coefficients of variation of the population estimate would need to be less than or equal to $\sim 25\%$, 35%, 45%, and 55%, respectively.

Microhabitat use

The proportions of animals that were found in underground microhabitats (pallets and burrows) during the part of the day when tortoises are active over the three-year study period ranged from 60% to 75% (Fig. 2). In addition, the numbers of animals found in different microhabitats differed among years ($\chi^2 = 324.3$, $df = 6$, $P < 0.0001$). Tortoises used burrows much more than the other three microhabitats (Fig. 2).

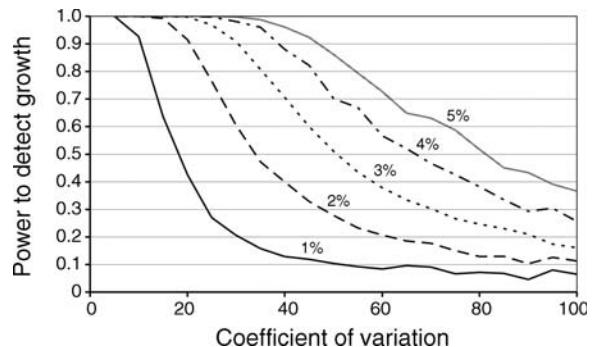


FIG. 1. Power to detect different growth trends in annualized population growth rates as a function of the coefficient of variation of the density estimates. Curves represent the power to detect different population growth rates from 1% to 5% growth.

The proportion of animals active varied annually, seasonally, weekly, and daily (Fig. 3). For example, high levels of spring activity in April and May of 1998 were not as great in either 1997 or 1999. The period of activity in the fall of 1997 (roughly October), was qualitatively higher than that seen in either of the other two years. The variation in daily activity was not consistent throughout the season, or among years. For example, the variation in the proportion of animals active during spring in 1997 was greater than that for 1998. In all years, tortoises were generally more active during the morning hours.

Average and variance of g_0 with sample size

Sample size had a large influence on the precision of the estimates of g_0 . With a sample size of 100, the proportion of animals active was very similar to the average of the population of 150 tortoises. However, as would be expected, the variance of the estimates was greater for smaller sample sizes. The reduction in the variance of the estimates of activity was not linearly related to the number of samples. A power function was fitted to the curve created by the standard deviations of the means with an explained variance of 97%. The rate of change of standard deviation (where the first derivative of the power function fit to the standard deviations approached 0) indicates that with at least 20–30 animals the variance in the estimate of g_0 became nearly a constant at a low value. The sample size required to achieve a coefficient of variation in the estimate of g_0 (let alone other sources of variation implicit in the sampling technique) of <12% (see previous power analysis) was ~95 animals. This implies that focal populations may never be of sufficient size to estimate g_0 precisely.

Neural network model

The neural network model of tortoise activity yielded a significantly correlated estimate of modeled g_0 and measured g_0 ($F_{1,82} = 58.3$, $P < 0.0001$), but explained only 42% of the variance in g_0 . This level of explained variance corresponded to a CV of ~57% (by taking the RMSE/mean of the response variable), which would occlude trends in growth rates of >5% per year. The input variables to the model to which the outputs were most responsive included the maximum daily temperature of the large T_c model, the surface temperature in a shaded microhabitat, and the daily average of the large T_c model in the sunny microhabitat (Table 1).

Repeatability

Activity of tortoises on consecutive days with similar climate was significantly correlated. However, this correlation explained only 29% of the variance ($r = 0.54$) indicating that behavior may not be repeatable at the population level.

DISCUSSION

The foremost criterion for desert tortoise populations to be delisted requires that there be a statistically

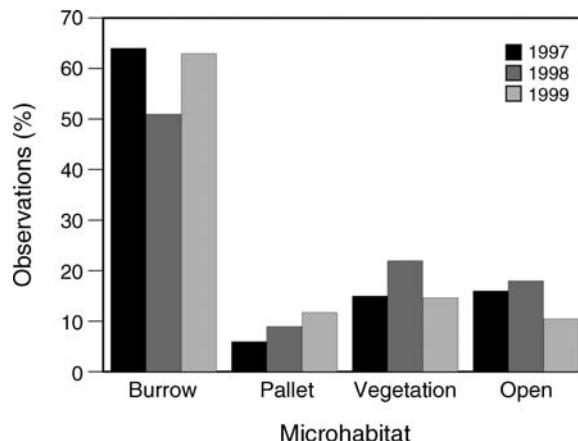


FIG. 2. Percentage of observations of ~150 free-ranging desert tortoises in three field seasons during the daytime hours at Bird Spring Valley, in southern Nevada. Tortoises were categorized as (1) in a burrow, (2) in a pallet, (3) under vegetation, or (4) in the open.

significant upward or level trend in population size over a 25-year period (U.S. Fish and Wildlife Service 1994). The maximum reasonable population growth rate for tortoise populations has been estimated to be ~1% per year under ideal reproductive conditions (U.S. Fish and Wildlife Service 1994), albeit population declines can occur at rates up to 30% in a single year (Longshore et al. 2003). Our power analysis indicated that to detect a trend over a 25-year time period with a 1% annual growth rate, the coefficient of variation about the density estimates would have to be 12% or less.

Current estimates of population density from range-wide transect sampling for desert tortoises for the years 2001 through 2005 have coefficients of variation that range from 9.5% to 56.2%, depending on the year and area sampled (U.S. Fish and Wildlife Service 2006). With this magnitude of variation, tortoise populations would have to increase at rates of at least 4% per year to detect an upward trend in a 25-year period with sufficient power (Cohen 1988). With such low potential growth rates and the high variance in population density estimates reported from the range-wide monitoring program, this criterion may be intractable.

Another important result from this analysis is that it applies not only to the detection of increasing trends, but also decreasing ones. Thus, tortoise populations could decline at a rate of up to 4% per year, and that trend would still not be distinguishable from populations with no statistical trend at all. Clearly more precise density estimates are necessary to make sound decisions regarding the recovery and conservation of this species, as the error present in the current sampling method is exceedingly high (Gerrodette 1987, Taylor and Gerrodette 1993, Freilich et al. 2005).

The difficulties of sampling desert tortoises for population densities largely result from the fossorial habits of the species (Freilich et al. 2000). Tortoises

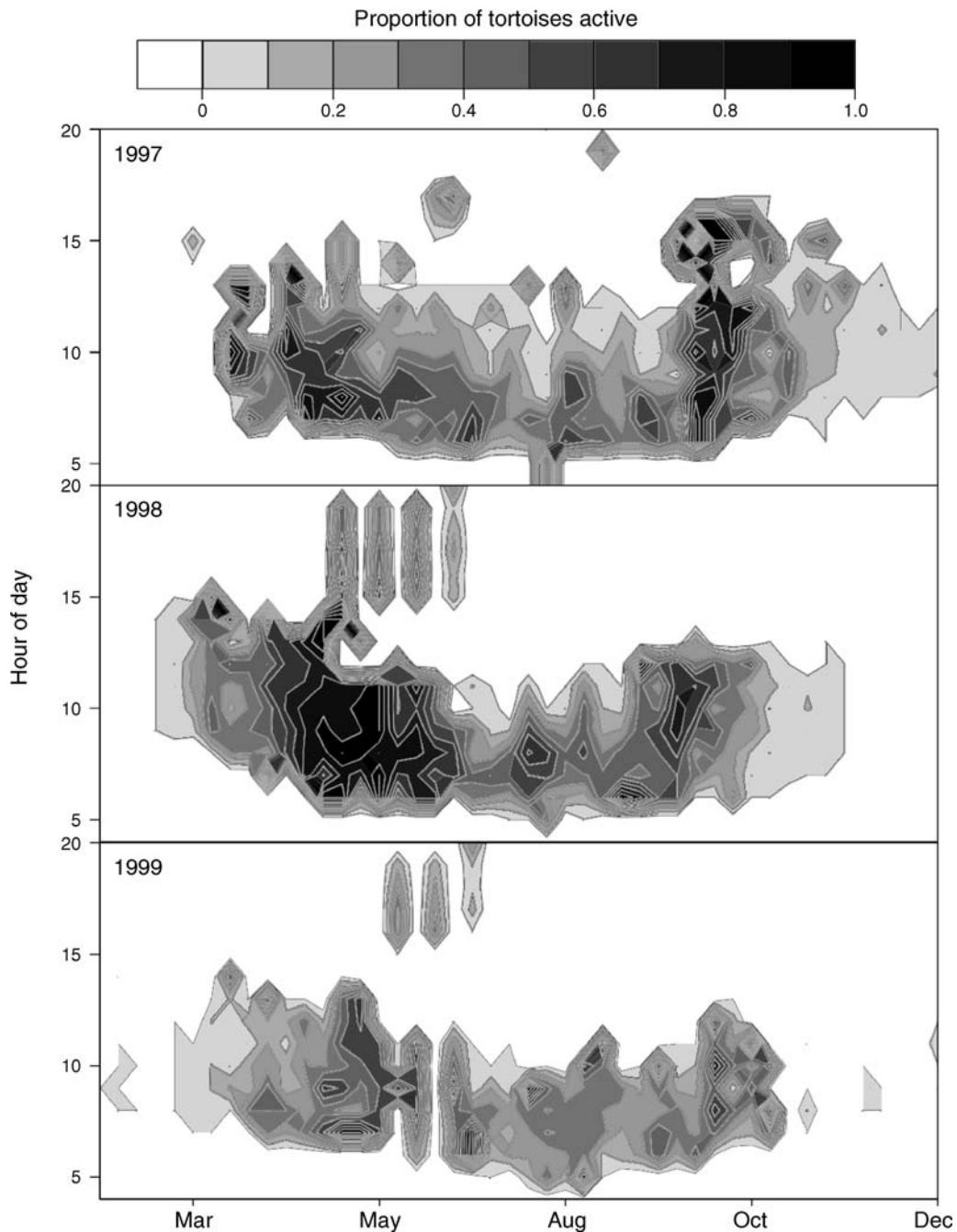


FIG. 3. The proportion of animals active for each hour of the day calculated from daily tracking of 150 tortoises at Bird Spring Valley, Nevada. The proportion of tortoises active is denoted by the darkness of the color, where gray colors indicate low levels of activity, and black denotes high levels of activity. The white background indicates times when animals were not sampled by radiotelemetry.

spend much of the year in underground burrows (Figs. 1 and 3; Woodbury and Hardy 1948, Nagy and Medica 1986, Bulova 1994), and the patterns of tortoise activity vary annually, seasonally, and daily (Fig. 3; Duda et al. 1999, Freilich et al. 2000, Anderson et al. 2001), yet none of this variance is accounted for in estimates of g_0 for population density estimates of tortoises. This is

critically important because an improperly calculated g_0 will impart significant error to density estimates. Both of the modifiers to the density estimation equation (P_a and g_0) are influenced by tortoise activity and the mechanisms determining patterns of activity (Eq. 1). The precision of the detectability estimate (P_a) calculated by distance sampling is largely influenced by the



PLATE 1. A desert tortoise that covered itself with sand seeking shade under a shrub. Photo credit: K. Nussear.

numbers of animals encountered on transects. A sample must include at least 60–80 animals to estimate P_a with adequate precision using distance sampling (Buckland et al. 2001). To achieve sample sizes of 60–80 desert tortoises the established monitoring protocols have included animals found on the surface, as well as those in burrows. However, the animals in burrows are currently treated in the same way statistically as animals on the surface. Specifically, the probability of detecting burrows as a function of distance from the line, and the detectability of tortoises in those burrows have not been evaluated, but are assumed to be the same as detecting an animal on the surface. Additionally, estimates of the proportion of animals above ground (which should equal g_0 in the strictest sense) are influenced by the sample size of focal populations, and by the times of year that tortoises are sampled (Fig. 3).

In some years there may be so few tortoises active that the number of animals encountered on transects will be low, and thus the precision of the estimate of P_a will be low (e.g., Fig. 3, 1999). In other years, there may be high variability in the proportion of animals active as a function of the week of the year or time of day during the sampling period (e.g., Fig. 3, spring of 1997). These mechanisms create an inherent lack of precision in the estimation of the availability of animals to be sampled, and this error will be incorporated into the estimates of tortoise density in unknown magnitudes.

Focal observations of 8–10 tortoises per site have been used to infer g_0 during the sampling period. If focal populations are used, the number of animals included in the sample is important to the precision and accuracy of the g_0 estimate. Monte Carlo simulations of g_0 measured from a population tracked by radiotelemetry of ~150 animals indicate that the sampling error associated with samples of 8–12 animals (the number of focal animals used in many of the focal sites) may lead to errors in the estimation of g_0 as high as 50%. Additionally, even if the focal populations are increased to 20 or 30 animals, the variance in the estimates of g_0 resulting from “snapshot” monitoring of focal animals remains as high as 25% (in this analysis). Indeed, a population of ~100 tortoises would be required to achieve a coefficient of variation for g_0 alone that was 12%. Thus, precise estimates of g_0 may require large focal groups that would be prohibitively costly, and may not reduce the error in the estimation of g_0 sufficiently to increase the precision of annual density estimates to acceptable levels.

We modeled the proportions of animals active on a given day as a function of several environmental variables related to the biophysical environment of desert tortoises using an Artificial Neural Network as one possible approach to create a more cost effective and precise means of estimating g_0 . Several other factors, such as forage availability, are likely to be important to quantifying tortoise activity; however the biophysical parameters that we included are likely to

define the thermal environment, which has been demonstrated to influence activity strongly (Zimmerman et al. 1994, Hillard 1996). This model had a high level of variance around the mean predictions. In fact, the amount of variation explained by our model is roughly equivalent to that expected using small focal populations to estimate g_0 . Thus, our initial model does not create an improvement over using focal animals to estimate g_0 .

To test the precision with which it is possible to model g_0 , we examined the repeatability of population level activity estimates, under similar environmental conditions by analyzing the proportion of tortoises that were active on consecutive days. Despite similar environmental conditions, the proportion of tortoises active on consecutive days was only weakly correlated. This indicates that the behavior of tortoises is not especially predictable based upon environmental variables alone. This may place limitations on our ability ever to model tortoise activity at the population level.

While our example highlights an approach to modeling activity as a surrogate for availability of desert tortoises, there are many animals that frequently have a reduced availability or observability (i.e., $g(0) < 1$) to sampling efforts. Examples in the literature include those from a variety of species, including cetaceans (Skaug et al. 2004), birds (Hone and Short 1988), large herding herbivores (Jachmann 2002), kangaroos (Pople et al. 1998), sea turtles (Gómez de Segura et al. 2006), lizards, and snakes (Rodda and Campbell 2002). For animals typically censused using areal surveys this is an especially relevant topic. Frequently, efforts to estimate availability/visibility involve modeling aspects of the animal's behavior; such as surfacing intervals in whales and sea turtles (Skaug et al. 2004, Gómez de Segura et al. 2006); differences in coloration of individuals, or herd behavior due to daily or seasonal differences in temperature, and detectability in large mammals (Bayliss and Giles 1985, Hill et al. 1985, Jachmann 2002). Our approach stems from examining the behavior of the population as a function of key environmental drivers of behavior (Zimmerman et al. 1994).

We think the need for modeling approaches extends beyond studies using transect methods to survey for an organism. For example, prior to 1999, survey efforts for desert tortoises consisted of a score of permanent study plots located throughout the Mojave that were surveyed, and densities were estimated using mark-recapture techniques. These surveys took place using a 30-day marking phase, and a 30-day recapture phase (Berry 1986). Over a 60-day time period, tortoise behavior, and the resulting availability of these animals is likely to change. Seasonal changes in behavior will influence the precision of the density estimates as a smaller proportion of the population is available for sampling (Williams et al. 2001), and could also violate the equal catchability assumptions of capture-recapture analysis if there are seasonal differences in activity

among different members of the population (e.g., genders or size classes).

We think that understanding the effects that behavior and the resulting observability of an animal is important to the methods that we use to estimate their population sizes or densities. This is an important factor to consider when designing and implementing survey studies, and this importance extends beyond studies that use distance to estimate population parameters.

ACKNOWLEDGMENTS

E. T. Simandle, J. P. Hayes, S. H. Jenkins, R. W. Marlow, R. A. Wirtz, and two anonymous reviewers provided helpful comments on earlier versions of this paper. This research was funded by the Clark County Multiple Species Habitat Conservation Program, and the Biological Resources Research Center at the University of Nevada, Reno. K. E. Nussear was supported by a Pre-Doctoral Fellowship from the Redlands Institute, University of Redlands, during this study.

All experiments using animals were conducted according to IACUC guidelines (University of Nevada IACUC Protocols A98/99-29 and A95/96-28).

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APPENDIX

A map of transects surveyed during the 2001 season and the field site for behavioral observations (*Ecological Archives* A017-021-A1).