Biological Conservation 142 (2009) 2710–2717

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Vital rate sensitivity analysis as a tool for assessing management actions for the desert tortoise

J. Michael Reed [a,*], Nina Fefferman [b,1], Roy C. Averill-Murray [c]

[a] Department of Biology, Tufts University, Medford, MA 02155, USA
[b] DIMACS, Rutgers University, Piscataway, NJ 08854, USA
[c] US Fish and Wildlife Service, Desert Tortoise Recovery Office, 1340 Financial Blvd, #234, Reno, NV 89502, USA

ARTICLE INFO

Article history:
Received 21 January 2009
Received in revised form 10 June 2009
Accepted 25 June 2009
Available online 3 August 2009

Keywords:
Population viability
Adaptive management
Elasticity
Turtle
Head-starting
Translocation

ABSTRACT

Sensitivity analyses of population growth in desert tortoise (*Gopherus agassizii*) have shown no consensus on the limiting vital rate. More importantly, the most sensitive vital rate might not be the most readily manipulated by management, so it begs the question of what actions would be most effective. We compared 13 management alternatives using a vital rate sensitivity analysis that is valid regardless of age structure, and is sensitive to initial population size and time frame, to determine the efforts required for equivalent population growth. We evaluated three time frames, each with five initial population sizes and three initial age distributions. To achieve equivalent population growth, mortality of older females needed to be reduced less than did mortality of other age classes. Similarly, fewer adults needed to be introduced to a population to have the same effect as releasing juveniles, but differences among adult age classes were trivial. A single release (headstarting) required fewer total individuals than did annual releases to achieve the same population growth. Also, the same population growth was more easily achieved when the initial age structure was deficient of young animals. Interestingly, because small tortoises are difficult to survey, some management alternatives could result in increased population size but decreased numbers of countable individuals over short to intermediate (25 years) time frames. Our paper demonstrates an approach to determine what constitutes equivalent management actions for population growth, thus allowing managers to more directly compare expected gains toward population recovery achieved by their resource-allocation decisions.

© 2009 Elsevier Ltd. All rights reserved.

1. Introduction

The desert tortoise (*Gopherus agassizii*) is one of four tortoise species endemic to North America (Ernst et al., 1994). Desert tortoises were listed as Threatened under the US Endangered Species Act because of pervasive threats and population declines across its range (USFWS, 1990, 1994). Unlike some listed species, desert tortoises are threatened by a complex array of interrelated factors such as predators, drought, disease, exotic plant invasion, habitat loss and degradation due to multiple causes, and illegal collection of tortoises (Boarman, 2002; Tracy et al., 2005; USFWS, 2008). To quantify extinction risk of the desert tortoise, and to identify the most effective way to achieve positive population growth, a number of population viability analyses (PVAs) and sensitivity analyses have been conducted (Doak et al., 1994; USFWS, 1994; Heppell, 1998; Wisdom et al., 2000). One use of PVA is parameter sensitivity analysis to identify the vital rate that limits population growth (e.g., Beissinger and Westphal, 1998; Reed et al., 2002). Implementing management actions to increase the most sensitive vital rate, therefore, might be the most effective approach to increasing population size and thus decreasing extinction risk (e.g., Crowder et al., 1994; Reed et al., 1998; Mills et al., 1999; but see Beissinger and Westphal, 1998; Reed et al., 2002).

Prior sensitivity analyses, however, show little consensus on the limiting vital rate for desert tortoise populations, even when analyzing the same life tables. In USFWS (1994) Gilpin did an incomplete sensitivity analysis and concluded that if management efforts were focused on increasing survival rates, one should target young adults because of their relatively high reproductive value. Doak et al.'s (1994) extensive sensitivity analysis showed that survival of large adults most influences population growth. Consistent with these assessments, Heppell (1998) found adult survival to be the most sensitive (elastic) vital rate (vital rates analyzed included fecundity and survival rates of three age classes: juvenile, subadult, adult). Wisdom et al. (2000) did the most thorough sensitivity analysis, looking both at mean vital rate values in simulated elasticity analysis and manipulating mean and variance of vital rates

* Corresponding author. Tel.: +1 1 617 627 3544; fax: +1 1 617 627 3805.
E-mail address: michael.reed@tufts.edu (J.M. Reed).
[1] Present address: Department of Ecology, Evolution and Natural Resources, Rutgers University, 14 College Farm Road New Brunswick, NJ 08901, USA.

0006-3207/$ - see front matter © 2009 Elsevier Ltd. All rights reserved.
doi:10.1016/j.biocon.2009.06.025

to determine the effect on population growth rates. Unlike the majority of published sensitivity analyses, they found that multiple vital rates have similar influences on population growth measures. In the first analysis, there was similar sensitivity among survival rates for young adult, yearlings, early juveniles, late juveniles, and late immatures, and with the transition likelihood from late immatures to sub-adults. In the second analysis, there was similar sensitivity to population growth rate exhibited by survival rates for yearlings, early juveniles, late juveniles, early adults, and transition likelihood into early juveniles, late juveniles, and sub-adults.

A limitation of all these analyses of vital rate sensitivity is that the methods used require stable age distributions for analysis (e.g., Mills and Lindberg, 2002; *cf.* Caughley, 1977). Because there are no desert tortoise populations known to have stable age distributions, populations in these analyses were projected over time until the age distribution was stable. Consequently, these previous sensitivity analyses are for populations that do not exist – or at least are not known to exist. In declining populations there is no reason to believe that stable age distributions would be maintained, particularly if the forces causing population decline are selectively targeting particular ages or sexes (e.g., raven predation on young tortoises (Kristan and Boarman, 2003), or female biased predation rates (Field et al., 2007). An additional limitation of typical (λ-based) sensitivity analyses is that they calculate limitations for long-term population changes and cannot identify or compare alternative actions that allow short-term population goals to be achieved if they differ from long-term management solutions (Fefferman and Reed, 2006).

Fefferman and Reed (2006) developed a vital rate sensitivity analysis (VRSA) that is valid regardless of the age distribution. Because of this, VRSA can be used to contrast alternative short-term and long-term management options to maximize population growth rates. VRSA works the same way as an age/stage-based PVA and involves perturbation of vital rates to look at the effect on the change in population size (ΔN). Here we use VRSA to determine functional equivalence of alternative management activities. That is, we want to determine what change in each vital rate causes equivalent change in population growth. This approach allows flexibility to manage within bounds of management restrictions and situation-specific needs; for example, the most "sensitive" vital rate might be difficult or costly to manipulate. So, our goals are to determine what level of effort different management options affect vital rates equivalently with regard to increasing population size and to determine how these are affected by age structure, population size, and management time frame.

2. Methods

2.1. Desert tortoise life tables

For our initial analyses, we used the life table from Goffs, California, USA. (38°00′N, 97°00′W) (Supplementary Table S1) (Turner et al., 1987). It is one of only two life tables for the desert tortoise of which we are aware, and the only one that we know of that has been used in viability analysis. Unlike earlier analyses, we created an age-based, rather than matrix-based, model. We recognize, however, that it is not practical to target specific ages of desert tortoises for management, so we created age classes on which to focus management activities. Age classes in previous analyses generally agreed on the younger age classes, but differed somewhat on how older ages were classified. Rather than constructing our age classes based on previous studies or standard data categories used by biologists working with the species in the field (Berry, 1984; Doak et al., 1994), especially when vital rates of these "standard" categories can vary geographically (Germano, 1994; Wallis et al., 1999; *cf.* Turner et al., 1987; Doak et al., 1994), we constructed age classes based on a balance of similar vital rates for the life table under consideration, reproductive value, and whether they were uniquely amenable to targeted management action (Fig. 1). We needed to set an age of first reproduction, which can occur between ages 12 and 19 at Goffs, apparently depending on female size and nutrition (Turner et al., 1986; Germano, 1994); we selected our default model value to 15 years old. This resulted in 5 age classes: Stage 1, young juveniles, hatchlings through age 6 (mean midline carapace length [mmc] <91 mm); Stage 2, older juveniles, 7–14 years (mmc = 101–181 mm); Stage 3, young adults, 15–27 years (mmc = 191–222 mm); Stage 4, mid-age adults, 28–52 years (mmc = 222–240 mm); and Stage 5, older adults, >52 years (mmc >240 mm). As with previous models, ours is a female-only model. We do acknowledge that there are other life tables for this species that suggest a shorter life expectancy for desert tortoises (Germano 1994, Curtin et al., 2009), and that there can be other age-size relationships than those we use here. Consequently, we note that our results and expectations will change with other life tables.

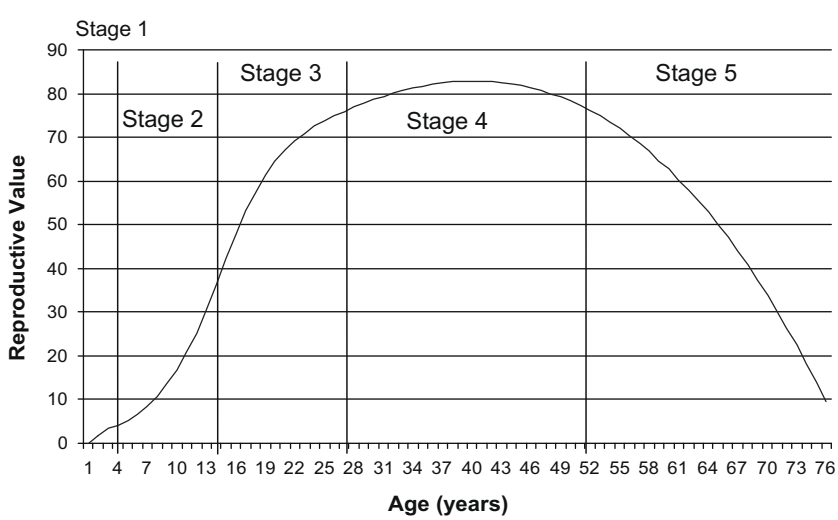

Fig. 1. Plot of reproductive value (V_x) vs. age from the life table in the Supplementary Table S1 (Turner et al., 1987). Combining this life table with previous analyses, we selected our age classes for analysis, and vertical lines depict stage cut-offs.

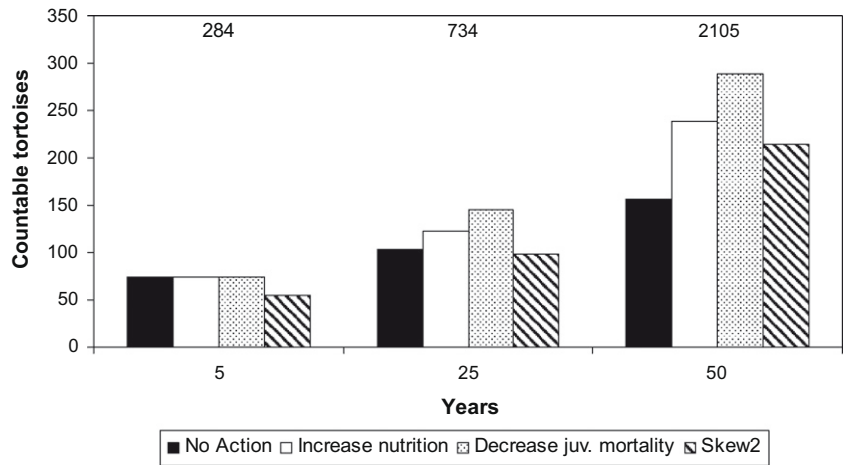

Fig. 2. Number of countable individuals out of the total number of individuals (numbers above bars). These are for the original age structure, for three target years, and $N_0 = 100$ (see Table 2 for details).

We analyzed three different initial age distributions. The first was the stable age distribution (Supplementary Table S1) created from the Goffs data set that has been analyzed in previous viability and sensitivity assessments (Turner et al., 1987). We also created two initial age distributions that mimicked the effects of particular types of threats. The first altered initial age distribution, Alternative 1, simulated an age structure where there has been a catastrophe for young animals such as might be expected from short-term drought (Morafka, 1994). Specifically, in the initial age distribution we reduced Stage 1 by 75%. The second altered initial age distribution, Alternative 2, was imagined to be the result of a catastrophe to adults, such as through disease (Berry, 1997). This age distribution started with a 60% reduction in adult age classes (Stages 3–5). In both scenarios initial population size was maintained by increasing the number of individuals in the age classes in proportion to their post-adjustment frequency. Also, the altered initial age structures did not change the vital rates used in the analyses.

2.2. Management alternatives

Given the number of potential threats to desert tortoises, there are many actions available to resource managers that can affect one or more vital rates. It is not our goal to describe all possible alternatives. Rather, we present 13 scenarios from the perspective of how they affect a particular vital rate. That is, we focus on how a vital rate is improved, rather than on the method a resource manager might use to achieve the improvement. While any benchmark of desired population growth could be used for comparison among scenarios, we selected one scenario, increasing nutrition, as a standard against which to compare the other scenarios. We then asked what would be required of the other management efforts to achieve the same effect in population growth. We selected increasing nutrition because it was the one scenario that we considered that affected more than one vital rate. The scenarios we considered are described in Table 1. Note that the "skews" referred to in two of the scenarios, where decreased mortality occurs across multiple age classes, are the result of an age-preferential effect on who gets helped by a management action, not that the action selectively targets particular ages.

2.3. Vital rate sensitivity analysis

The original VRSA model is a stochastic simulation that can be used to compare the effects of proposed alternative management scenarios (Fefferman and Reed, 2006). In this paper we wanted to determine the degree to which different single vital rates need

Table 1
Management scenarios compared using vital rate sensitivity analysis (VRSA). The first scenario, increased nutrition, is the only scenario where the specific change of the model is set, and it acts as the standard against which other actions are compared. For the other actions, VRSA is used to determine what value "x" (change in survival rate or number of tortoises released) needs to be for the same effect on population growth as achieved by increased nutrition.

Alternative management scenario	Effect on vital rates
Increased nutrition	Decrease age of first breeding to 12 years old, and increase average reproductive success by 15% (i.e., multiply reproductive success by 1.15), but truncated at a maximum of 16 eggs (Mueller et al., 1998)
Decrease juvenile mortality	Increase probability of survival by x% for Stage 1
Decrease all mortality	Increase probability of survival by x% for all stages
Decrease all mortality skew 1 = the older you are, the greater the survival benefit you receive	Increase probability of survival for all stages, skewed towards larger animals; increased from P_i (original survival probability) to $P_i * (1 + x)^i$, where i is age and x is the increase in survival rate; truncated so survival rate did not exceed 1.0
Decrease all mortality skew 2 = easier to survive when younger, harder to survive when older	Increase probability of survival for all stages, skewed towards smaller animals; increased from P_i (original survival probability) to $P_i * (0.2 + (1 + x)^{-i})$
Annual release of head-started juveniles	Annual release of x 7-year old animals (first age of Stage 2)
Annual release of adults	Annual release of x Stage 3–5 animals
Annual release of young adults	Annual release of x Stage 3 animals
Annual release of mid-age adults	Annual release of x Stage 4 animals
Annual release of old adults	Annual release of x Stage 5 animals
Single release, young adults	Single release of x Stage 3 animals at time step 1
Single release, mid-aged adults	Single release of x Stage 4 animals at time step 1
Single release, old adults	Single release of x Stage 5 animals at time step 1

to be changed to achieve the same population growth as was achieved by a particular scenario. To do this, we ran the improved-nutrition scenario stochastically, and then we used the mean population growth achieved (ΔN) as our goal for other scenarios to meet. Specifically, we projected the age structured population by iterative application of the vital rate-based transition matrix, incorporating alterations to reflect management strategies into the relevant vital rates (hence, into the appropriate matrix entries) for each affected year. Improved nutrition can improve clutch sizes, probability of breeding, age to reach reproductive size, and likely survival. For example, egg production at Goffs varied during the 1980s and 1990s with forage availability (Turner et al., 1986; Henen, 1997; Wallis et al., 1999). Improved nutrition can also increase total egg production, but this trait appears to asymptote at about 2 clutches totaling 7–9 eggs per female per year (Wallis et al., 1999; Mueller et al., 1998). Consequently, for this study, we allowed increased nutrition to decrease age of first breeding to 12 years old and to increase average reproductive success by 15% (i.e., multiply reproductive success by 1.15), but we truncated total egg production at a maximum of 16 eggs. We also needed measures of variance in vital rates for the first, nutrition-based population projection. Mean number of eggs produced per tortoise at Goffs across multiple years was 3.4–8.7 ± 1.9–3.1 (SD) eggs (Turner et al., 1986, 1987; Henen, 1997; Wallis et al., 1999). We were unable to find field measures of variance in age-specific survival rates. Consequently, for the model we used a standard deviation of 0.02 around the reported mean survival for each age group and also for the efficacy of all survival related intervention effects.

We ran each alternative scenario in turn as deterministic models. We initially ran each model with a small change in vital rate due to management. We then increased the management-influenced vital rate iteratively until we achieved the same population growth across the target time period as with the improved nutrition scenario. That is, we started with our initial age distribution and vital rates and used repeated application of the unaltered transition matrix to project the population the target number of years. When the scenario involved introducing animals of a particular age class (e.g., through translocation), we distributed individuals uniformly across ages within the age class at the start of the time interval and assumed they shared the same survival and fecundity as residents within the same age class in the population Nussear, 2004; Field et al., 2007. We then increased the intensity of the activity until the observed population growth rate matched that of the improved nutrition scenario.

For each initial age distribution and management scenario, we projected populations for five initial population sizes: 100, 500, 1000, 5000, and 10,000 females. For each initial population size, we evaluated three time frames for population growth comparisons: 5, 25, and 50 years. Because VRSA is designed to maximize growth for a given time period (Fefferman and Reed, 2006), maximizing growth for 5 years did not necessarily give maximum growth to the 25 and 50 year target times. Consequently, we reran each analysis for each target time period. Initial population sizes and time frames for evaluation were intended to mimic a range of likely scenarios to be found in wild populations.

We preferred to model only discrete individuals (Fefferman and Reed, 2006), but this created significant errors at small population sizes. When we distributed individuals across ages within an age group, we commonly were left with partial individuals at each age that were rounded out of the population, creating proportionally large errors in the population growth rates achieved by both the introduction-focused interventions. Consequently, we took two approaches to projecting the populations to help understand the impact of scale. (1) In the first approach, we allowed partial individuals to stay in the population. This avoided the problems associated with rounding, but resulted in masking the effects of initial population size on the relative effectiveness of management scenarios. (2) In the second approach we rounded partial individuals to the nearest whole individual (rather than truncating them). This allowed us to determine the effects of initial population size on alternative management actions.

3. Results

Results from vital rate sensitivity analyses when partial individuals were allowed to stay in the population are shown in Table 2 and Fig. 2. As expected, the effects of increased nutrition on population size increased with the length of the management time frame. Also with longer implementation, the annual effort required for a particular management action to match the population growth achieved by improved nutrition decreases. This was expected because the effects of actions are compounded over time. Comparing across scenarios that manipulated survival rates, decreasing mortality of older females (skew 1) had a greater effect on meeting population growth goals than did decreasing mortality of other age classes. Decreasing mortality of juvenile females required the greatest annual management effect, although this should not be confused with the management effort, which might be unrelated to effect size. These patterns were consistent for all initial age structures.

Comparing scenarios that increased population sizes through the release of individuals (a reminder that we are referring strictly to females), releasing adults had a greater effect on meeting target ΔN values than did releasing juveniles, but the differences in population growth effects caused by releases of the different adult age classes were trivial. For the five-year target window, essentially the same total number of young or mid-age adult females would need to be released by the annual release and single release scenarios. Differences, however, become apparent with longer time frames (25 and 50 years), where a single release during the first year requires fewer animals than does annual releases of animals. This is because the effects of added animals on population growth are staggered over time for the annual releases. In contrast, the total number of females that need to be released for equal population growth tended to be greater for single vs. annual releases of old adults.

Absolute comparisons among management alternatives should be made cautiously across initial age structures, bearing in mind that there are large differences in ΔNs across the initial age structures. For example, it might appear that under Alternative age structure 1, annual head starting is relatively much more effective than under the original age distribution because only 33 animals/year need to be added rather than 73 to match the ΔN caused by increased nutrition. However, the ΔN with the original age structure is 284, while in Alternative 1 it is only 129. One can compare ΔNs, though, for increased nutrition directly across age structures.

Of the alternative initial age structures, population growth due to increased nutrition was by far the lowest for the age structure that had a reduced number of young (Alternative 1 – juvenile deficient). Consistent with this, management actions focusing on adults had the greatest effect on population growth for a given amount of effort for this initial age structure. Otherwise, patterns across time frames and the relative effects of alternative actions on population growth were similar to those found for the original age structure.

Results from vital rate sensitivity analyses when partial individuals are rounded to the nearest entire individual are shown in Supplementary Table S2. Rounding had a significant effect on predicted results, consistently reducing the ΔNs from increased nutrition. The same caution mentioned earlier applies to comparisons across initial population sizes (N_0) of management effective-

Table 2
Results of model simulations where partial individuals were allowed to stay in the population, so initial population size had no effect on the results. Results are presented for three target time frames and three initial age structures: Original, Alternative 1 (reduced number of young), and Alternative 2 (reduced number of adults). The increase in population size (ΔN) due to increasing nutrition is relative to a population where no management action was taken. Subsequent rows show the size of the vital rate change (the value of x in the corresponding scenarios in Table 1) for each alternative that has the same ΔN as observed for the increased nutrition scenario. Parenthetically, we report the number animals of countable size in the target year[a]; for $N_0 = 100$ in year 0, 67 individuals were of countable size[b].

	5 years	25 years	50 years
For the original (Goffs) age structure and $N_0 = 100$, if no action is taken, the number of individuals of countable size[a] would be:	(74)	(103)	(156)
Management action			
Original (Goffs) age structure			
ΔN due to increased nutrition	284[b] (74)	734 (122)	2105 (239)
Decrease juvenile mortality	11.1% (74)	6.5% (145)	5.4% (289)
Decrease all mortality	4.8% (92)	1.8% (158)	1.4% (312)
Decrease all mortality skew 1	0.7% (105)	0.1% (161)	0.2% (315)
Decrease all mortality skew 2	1.4% (55)	1.9% (99)	1.9% (215)
Annual release of head-started juveniles	73 (74)	22 (160)	24 (314)
Annual release of young adults	6 (106)	3 (172)	4 (314)
Annual release of mid-age adults	5 (101)	3 (156)	3 (307)
Annual release of old adults	2 (99)	1 (152)	2 (305)
Annual release of all adult stages	5 (101)	3 (156)	4 (308)
Single release, young adults	28 (96)	70 (162)	126 (308)
Single release, mid-aged adults	25 (93)	56 (159)	119 (312)
Single release, old adults	26 (90)	110 (172)	197 (312)
Alternative initial age structure 1			
ΔN due to increased nutrition	129 (33)	281 (45)	730 (82)
Decrease juvenile mortality	18.3% (33)	7.8% (56)	5.6% (100)
Decrease all mortality	6.0% (44)	2.0% (59)	1.5% (108)
Decrease all mortality skew 1	0.9% (49)	0.1% (59)	0.1% (108)
Decrease all mortality skew 2	1.0% (35)	1.7% (52)	1.8% (72)
Annual release of head-started juveniles	33 (33)	8 (58)	8 (108)
Annual release of young adults	3 (48)	1 (59)	1 (108)
Annual release of mid-age adults	2 (46)	1 (57)	1 (106)
Annual release of old adults	1 (45)	1 (55)	1 (105)
Annual release of all adult stages	2 (46)	1 (57)	1 (106)
Single release, young adults	13 (43)	27 (59)	44 (106)
Single release, mid-aged adults	11 (42)	21 (58)	41 (108)
Single release, old adults	12 (41)	42 (63)	68 (108)
Alternative initial age structure 2			
ΔN due to increased nutrition	216 (46)	528 (88)	1584 (178)
Decrease juvenile mortality	11.3% (46)	6.3% (100)	5.5% (213)
Decrease all mortality	5.4% (59)	1.7% (111)	1.5% (231)
Decrease all mortality skew 1	0.8% (69)	0.1% (115)	0.1% (234)
Decrease all mortality skew 2	1.7% (33)	1.9% (170)	1.9% (168)
Annual release of head-started juveniles	55 (46)	16 (117)	18 (233)
Annual release of young adults	4 (70)	2 (115)	3 (233)
Annual release of mid-age adults	4 (66)	2 (111)	2 (228)
Annual release of old adults	2 (65)	1 (108)	1 (227)
Annual release of all adult stages	4 (66)	2 (111)	3 (229)
Single release, young adults	21 (62)	50 (115)	95 (229)
Single release, mid-aged adults	19 (60)	40 (113)	89 (228)
Single release, old adults	19 (58)	79 (122)	148 (227)

[a] Small tortoises are difficult to survey (e.g., Anderson et al., 2001), which means that not all of the predicted increase in N will be readily surveyed. Consequently, for the first age structure we include the ΔN of animals that are at least Stage 3 (at least 15 years old and mm >190 mm), viewing them as countable. The number of newly countable animals will be those that were already in the population that got sufficiently large, plus added animals that are of countable size or grew to countable size. Note that under some circumstances (like adding adults) that it is possible for the number of newly countable animals to be larger than the ΔN.

[b] Numbers in this table (but not the %s) are scaled values. To get values specific to each initial population size, N_0, multiple value in cell by (N_0/100).

ness when actions are reported as numbers of individuals – the ΔNs change across N_0s. Comparisons of actions that are reported as percents are directly comparable across N_0s. Results from this analysis differ from the previous analysis primarily in the effect N_0 has on the results. As initial population size increases, the magnitude of the effect that actions need to have on the population decreases. This is most readily seen in the scenarios dealing with decreasing mortality because they are presented as percentages. For example, with the original age structure, achieving the target population growth in 5 years requires approximately a 12% decrease in annual mortality after hatching (scenarios "decrease all mortality") if $N_0 = 100$ females, but only a 5% decrease when $N_0 = 10{,}000$ females. Effects across time frames remain relatively constant to slightly increasing for each N_0 in the "skew 2" scenario, however.

For scenarios involving introducing individual tortoises, one can see the same pattern of decreasing effect needed by comparing the proportional increase in the number of animals to introduce to achieve population growth goals across different initial population sizes. For example, the VRSA predicts achieving the 5-year population growth goal by annually releasing 9 head-started females per year when $N_0 = 100$ (9% of N_0) in the original age structure and 372 females per year when $N_0 = 5000$ (only 7% of N_0; Supplementary Table S2). Note also that for this comparison when $N_0 = 100$, the ΔN achieved is 32, while at $N_0 = 5000$ $\Delta N = 1449$.

The effects of initial population size also are apparent in the different age structures and differ by management action. For Alternative 1 (initially deficient in number of young), target ΔN values for different time frames and initial population sizes are larger than for the original age distribution. For management actions that

decrease mortality, the input required for ΔN to meet the population-increase goal in Alternative 1 decreases with increasing N_0, as we found with the original age distribution. For management scenarios involving adding individual tortoises, Alternative 1 and the original age structure also react similarly, with proportionally less effort required for increasing time frames as N_0 increases. Alternative age structure 2, in contrast, generally shows much lower target ΔN values for the different time frames and initial population sizes, but the increased effectiveness with increasing N_0 differs a bit compared with the original age distribution depending on the action implemented (Supplementary Table S2).

4. Discussion

The desert tortoise faces a complex array of threats that act on various life stages or vital rates (Boarman, 2002; Tracy et al., 2005; USFWS, 2008). For example, risk of juvenile tortoise mortality may exceed 50% under certain circumstances due to raven predation (Kristan and Boarman, 2003) or nest depredation (Bjurlin and Bissonette, 2004). In contrast, collection or deliberate killing by humans is more likely to affect survival of adult tortoises as a result of the difficulty in finding juveniles (Morafka, 1994; Anderson et al., 2001). Habitat loss or degradation, such as that caused by roads, off-highway vehicle activity, and excessive grazing, should affect survival of all life stages; however, naturally unpredictable weather in arid environments likely contributes to infrequent recruitment (Morafka, 1994), thereby skewing the effects of these threats toward adults. Peterson (1994) and Longshore et al. (2003) showed adult mortality events associated with drought, but neither had juvenile tortoises in the study. We speculate that juvenile mortality might have been even greater than the documented elevated mortality of adults, thus skewing the age distribution more or less as in Alternative 1. Unfortunately, the relative importance of different threats to the status of most desert tortoise populations is unknown, and limited budgets or other socio-political pressures have led managers to implement recovery actions in an *ad hoc* manner without understanding whether those actions would be the most effective in stemming population declines or in promoting population growth (Tracy et al., 2005; USFWS, 2008).

One calculation we did not attempt was to determine which of the management alternatives is most cost effective. This is because the answer to this question depends on a variety of situation specific factors that include available infrastructure (e.g., is there a head-starting facility available or would you have to build one?), allowable uses of available funds (not all funds can be used for all management activities), public sentiment, management experience of the decision maker, potential availability of volunteers, as well as others. Consequently, what management alternative is best will be situation specific. What our approach provides is a framework for working out the optimal decision.

Vital rate sensitivity analysis is a tool to help compare management alternatives to determine which are most effective at increasing population size (ΔN). This can only be determined by understanding or predicting how a particular action will affect specific vital rates and by analyzing the situation-specific ability of a resource manager to be able to achieve (and afford) each of the alternative goals. This is quite different from previous approaches of sensitivity analysis, which identify the most sensitive vital rate without regard for a manager's ability to manipulate it. Our approach also provides a way to compare management activities that affect vital rates with different units (e.g., it allows comparison of survival rate with number of introduced animals). Using this analysis, we were able to estimate the levels at which management alternatives achieve equivalent results. Since different particular management actions may target the same vital rate, managers must evaluate the success of implementing individual actions or combinations of actions at actually improving that vital rate. For example, fencing highways in an area may be insufficient in reducing adult tortoise mortality if human subsidies for coyotes leads to higher predation levels that counteract the beneficial effect of lower road mortality.

In our analyses we scaled various scenarios to the estimated effect of increasing nutrition. Management actions relevant to increasing nutrition involve promoting native plant biomass production for forage at the expense of non-native, invasive plant biomass (Tracy et al., 2006). This can be done directly through targeted invasive plant management and/or indirectly by limiting land-use activities, such as the creation of new roads and trails (Brooks and Lair, 2005; Boarman and Sazaki, 2006) and grazing (Brooks, 2000; Kimball and Schiffman, 2003), that contribute to the spread and establishment of invasive species. However, climate change and difficulties of invasive plant management may make the application of increasing nutrition of desert tortoises unfeasible at landscape scales (although results of the analysis may be applicable to small-scale treatments within critical populations). Also, as with any modeling analysis, we may have inaccurately predicted the effects of increasing nutrition on desert tortoise vital rates. Even so, our comparative scenarios provide useful information for the relative ability to reach the population growth targets established by the baseline scenario.

For actions specifically designed to reduce desert tortoise mortality, we found that those targeting juveniles require a greater relative reduction in mortality than do those targeting adults, regardless of initial population structure, initial population size, or time frame (Table 2 and Supplementary Table S2). Other types of sensitivity analyses done on long-lived turtles also show little effect of juvenile survival when adult survival is relatively high (e.g., >95%; Congdon et al., 1993; Heppell et al., 1996; Enneson and Litzgus, 2008). Furthermore, effects of actions dedicated to reducing juvenile-specific mortality of desert tortoises (e.g., raven management) would not even be apparent for more than 5 years, making it virtually impossible to evaluate the effectiveness of the action (and predictions of the model) before considerable resources have already been committed. For example, we estimate that the same number of detectable tortoises (in Stage 3 or later) would be present after 5 years under both the increase-nutrition and decrease-juvenile-mortality scenarios as would be if no action was taken at all (Table 2, Fig. 2). Populations under management that decreases mortality skewed toward the smallest stage (skew 2) would actually appear to be decreasing after time intervals of 5–25 years (Table 2). Even though the overall population size is increasing equivalent to the baseline scenario, this would be invisible to managers as a result of the time lag in the primary beneficiaries of such a management regime reaching detectable size. Worse would be a scenario in which the population did not respond as expected, and managers assumed the population was increasing when it was in fact decreasing. In our models, increasing annual survival by less than 1%, weighted toward larger tortoises (skew 1), results in a 42% increase in tortoises of detectable size after 5 years (105 vs. 74 tortoises in Stage 3 or later), while the size distribution evens out relative to other mortality-reducing scenarios after 25 years (Table 2). In this case, focusing on detectable results in the first 5 years has the added benefit of applying a conservative approach for longer time horizons. Of course, incorporating some management dedicated toward improving juvenile survival may increase the long-term effect on population growth by helping to ensure that juvenile survival exceeds the relatively low level necessary when accompanied by high adult survival.

It is important to recall that the results we present are specific to the vital rates used in the analysis. Although the life table in Turner et al. (1987) appears to be the only one used to date in via-

bility and sensitivity analyses (citations in introduction), at least one other life table exists (Karl, 1998), and vital rate data are available from other populations under a variety of environmental conditions (e.g., Mueller et al., 1998; Wallis et al., 1999; Longshore et al., 2003). It is notable that Karl's (1998) life table is substantially different from that of Turner et al. (1987), with a maximum life span of 50 rather than 75 years. Different site specific vital rates and age structures might give qualitatively different results than in our analyses. Likewise, results may differ if vital rate variances differ from the empirical estimates used in our analyses due to effects of narrow periods of estimation in the studies from which we took our estimates relative to tortoise generation times or to effects on vital rate variability under changing environmental conditions.

Implementing actions to reduce specific causes of mortality in threatened wildlife populations is important, but measures to further accelerate growth of depleted populations also may be necessary to avoid stochastic effects of small population size, particularly for species with long generation times such as the desert tortoise. Even though the efficacy of head-starting and translocation has been questioned over the years (Dodd and Seigel, 1991; Frazer, 1992; Heppell et al., 1996; Seigel and Dodd, 2002), recent studies have shown initial success in translocation of desert tortoises to be high (Nussear, 2004; Field et al., 2007). In particular, our tortoise-release scenarios assume that released individuals have the same survival and fecundity of resident tortoises in the population, a result that has been demonstrated in recent translocations of adult desert tortoises (Nussear, 2004; Field et al., 2007). Progress is also advancing in head-starting desert tortoises to life history stages with greater survival (Nagy et al., 2007). Similar to results from scenarios focused on reducing mortality, releasing adults results in increases in detectable tortoises of up to 43%, but annual head-starting of 7-year old (presumably near raven-proof) animals is unlikely to be detectable at the population level after 5 years (Table 2, Fig. 2). A simulated 10-year head-starting program for European pond turtles (*Emys orbicularis*) did not result in increases in the adult population for >10 years (Mitrus, 2005). However, we emphasize that both head-starting and translocation may be valuable in research programs designed to evaluate effectiveness of management actions or to assess the presence of threats by providing statistically suitable numbers of study animals for analysis (Tracy et al., 2005).

Acknowledgements

We thank E. McCoy and K. Field for input on alternative desert tortoise management actions and K. Field and C. Darst for comments on an earlier version of the manuscript. The findings and conclusions in this article are those of the authors and do not necessarily represent the views of the US Fish and Wildlife Service.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.06.025.

References

Anderson, D.R., Burnham, K.P., Lubow, B.C., Thomas, L., Corn, P.S., Medica, P.A., Marlow, R.W., 2001. Field trials of line transect methods applied to estimation of desert tortoise abundance. Journal of Wildlife Management 65, 583–597.

Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62, 821–841.

Berry, K.H. (Ed.), 1984. The status of the desert tortoise (*Gopherus agassizii*) in the United States. Desert Tortoise Council Report to the US Fish and Wildlife Service, Sacramento.

Berry, K.H., 1997. Demographic consequences of disease in two desert tortoise populations in California, USA. In: Van Abbema, J. (Ed.), Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles. New York Turtle and Tortoise Society, New York, pp. 91–99.

Bjurlin, C.D., Bissonette, J.A., 2004. Survival during early life stages of the desert tortoise (*Gopherus agassizii*) in the south-central Mojave desert. Journal of Herpetology 38, 527–535.

Boarman, W.I., 2002. Threats to desert tortoise populations: a critical review of the literature. US Geological Survey, Western Ecological Research Center, Sacramento.

Boarman, W.I., Sazaki, M., 2006. A highway's road-effect zone for desert tortoises (*Gopherus agassizii*). Journal of Arid Environments 65, 94–101.

Brooks, M.L., 2000. Does protection of desert tortoise habitat generate other ecological benefits in the Mojave desert? In: USDA Forest Service Proceedings RMRS-P-15, 3, pp. 68–73.

Brooks, M.L., Lair, B., 2005. Ecological effects of vehicular routes in a desert ecosystem. Report Prepared for the US Geological Survey, Recoverability and Vulnerability of Desert Ecosystems Program. Western Ecological Research Center, Henderson.

Caughley, G., 1977. Analysis of Vertebrate Populations. John Wiley & Sons, Chichester.

Congdon, J.D., Dunham, A.E., Van Loben Sels, R.C., 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7, 826–833.

Crowder, L.B., Crouse, D.T., Heppell, S.S., Martin, T.H., 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. Ecological Applications 4, 437–445.

Curtin, A.J., Zug, G.R., Spotila, J.R., 2009. Longevity and growth strategies of the desert tortoise (*Gopherus agassizii*) in two American deserts. Journal of Arid Environments 73, 463–471.

Doak, D., Kareiva, P., Klepetka, B., 1994. Modeling population viability for the desert tortoise in the western Mojave desert. Ecological Applications 4, 446–460.

Dodd Jr., C.K., Seigel, R.A., 1991. Relocation, repatriation, and translocation of amphibians and reptiles: are they conservation strategies that work? Herpetologica 47, 336–350.

Enneson, J.J., Litzgus, J.D., 2008. Using long-term data and a stage-classified matrix to assess conservation strategies for an endangered turtle (*Clemmys guttata*). Biological Conservation 141, 1560–1568.

Ernst, C.H., Lovich, J.E., Barbour, R.W., 1994. Turtles of the Unites States and Canada. Smithsonian Institution Press, Washington, DC.

Fefferman, N., Reed, J.M., 2006. A vital rate sensitivity analysis that is valid for non-stable age distributions and for short-term planning. Journal of Wildlife Management 70, 649–656.

Field, K.J., Tracy, C.R., Medica, P.A., Marlow, R.W., Corn, P.S., 2007. Return to the wild: translocation as a tool in conservation of the desert tortoise (*Gopherus agassizii*). Biological Conservation 136, 232–245.

Frazer, N.B., 1992. Sea turtle conservation and halfway technology. Conservation Biology 6, 179–184.

Germano, D.J., 1994. Growth and age at maturity of North American tortoises in relation to regional climates. Canadian Journal of Zoology 72, 918–931.

Henen, B.T., 1997. Seasonal and annual energy budgets of female desert tortoises (*Gopherus agassizii*). Ecology 78, 283–296.

Heppell, S., 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 1998, 367–375.

Heppell, S.S., Crowder, L.B., Crouse, D.T., 1996. Models to evaluate headstarting as a management tool for long-lived turtles. Ecological Applications 6, 556–565.

Karl, E.A., 1998. Reproductive strategies, growth patterns, and survivorship of a long-lived herbivore inhabiting a temporally variable environment. Ph.D. Thesis, University of California, Davis.

Kimball, S., Schiffman, P.M., 2003. Differing effects of cattle grazing on native and alien plants. Conservation Biology 17, 1681–1693.

Kristan, W.B., Boarman, W.I., 2003. Spatial pattern of risk of common raven predation on desert tortoises. Ecology 84, 2432–2443.

Longshore, K.M., Jaeger, J.R., Sappington, J.M., 2003. Desert Tortoise (*Gopherus agassizii*) survival at two eastern Mojave Desert sites: death by short-term drought? Journal of Herpetology 37, 169–177.

Mills, L.S., Lindberg, M.S., 2002. Sensitivity Analysis to Evaluate the Consequences of Conservation Actions. In: Beissinger, S.D., McCullough, D.R. (Eds.), Population Viability Analysis. University of Chicago Press, Chicago, pp. 338–366.

Mills, L.S., Doak, D.F., Wisdom, M.J., 1999. The reliability of conservation actions based on elasticity analysis of matrix models. Conservation Biology 13, 815–829.

Mitrus, S., 2005. Headstarting in European pond turtles (*Emys orbicularis*): does it work? Amphibia–Reptilia 26, 333–341.

Morafka, D.J., 1994, Neonates: missing links in the life histories of North American tortoises. In: Bury, R.B., Germano D.J. (Eds.), Biology of North American Tortoises. National Biological Survey, Fish and Wildlife Research 13, Washington, DC, pp. 161–173.

Mueller, J.M., Sharp, K.R., Zander, K.K., Rakestraw, D.L., Rautenstrauch, K.R., Lederle, P.E., 1998. Size-specific fecundity of the desert tortoise (*Gopherus agassizii*). Journal of Herpetology 32, 313–319.

Nagy, K.A., Hillard, L.S. Dickson, S.D., Morafka, D.J., 2007. Head-starting desert tortoises: irrigation and yearling releases at Edwards Air Force Base. In: Desert Tortoise Council Symposium, Abstract.

Nussear, K.E., 2004. Mechanistic investigation of the distributional limits of the desert tortoise, *Gopherus agassizii*. Ph.D. Thesis, University of Nevada, Reno.

Peterson, C.C., 1994. Different rates and causes of high mortality in 2 populations of the threatened desert tortoise *Gopherus agassizii*. Biological Conservation 70, 101–108.

Reed, J.M., Elphick, C.S., Oring, L.W., 1998. Life-history and viability analysis of the endangered Hawaiian stilt. Biological Conservation 84, 35–45.

Reed, J.M., Mills, L.S., Dunning Jr., J.B., Menges, E.S., McKelvey, K.S., Frye, R., Beissinger, S., Anstett, M.-C., Miller, P., 2002. Emerging issues in population viability analysis. Conservation Biology 16, 7–19.

Seigel, R.A., Dodd Jr., C.K., 2002. Translocation of amphibians: proven management method or experimental technique? Conservation Biology 16, 552–554.

Tracy, C.R., Averill-Murray, R., Boarman, W.I., Delehanty, D., Heaton, J., McCoy, E., Morafka, D., Nussear, K., Hagerty, B., Medica, P., 2005. Desert Tortoise Recovery Plan Assessment. Report to US Fish and Wildlife Service, Reno, Nevada.

Tracy, C.R., Nussear, K.E., Esque, T.C., Dean-Bradley, K., Tracy, C.R., DeFalco, L.A., Castle, K.T., Zimmerman, L.C., Espinoza, R.E., Barber, A.M., 2006. The importance of physiological ecology in conservation biology. Integrative and Comparative Biology 46, 1191–1205.

Turner, F.B., Hayden, P., Burge, B.L., Roberson, J.B., 1986. Egg production by the desert tortoise *Gopherus agasizii* in California. Herpetologica 42, 93–104.

Turner, F.B., Berry, K.H., Randall, D.C., White, G.C., 1987. Population ecology of the desert tortoise at Goffs, California, 1983–1986. Report to Southern California Edison Company No. 87-RD-81.

US Fish and Wildlife Service, 1990. Endangered and threatened wildlife and plants: determination of threatened status for the Mojave population of the desert tortoise. Federal Register 55, pp. 12178–12191.

US Fish and Wildlife Service, 1994. Desert tortoise (Mojave population) Recovery Plan. US Fish and Wildlife Service, Portland, Oregon.

US Fish and Wildlife Service, 2008. Draft revised recovery plan for the Mojave population of the desert tortoise *(Gopherus agassizii)*. US Fish and Wildlife Service, California and Nevada Region, Sacramento. California.

Wallis, I.R., Henen, B.T., Nagy, K.A., 1999. Egg size and annual egg production by female desert tortoises (*Gopherus agassizii*): the importance of food abundance, body size, and date of egg shelling. Journal of Herpetology 33, 394–408.

Wisdom, M.J., Mills, L.S., Doak, D.F., 2000. Life-stage simulation analysis: estimating vital rate effects on population growth for species conservation. Ecology 81, 628–641.