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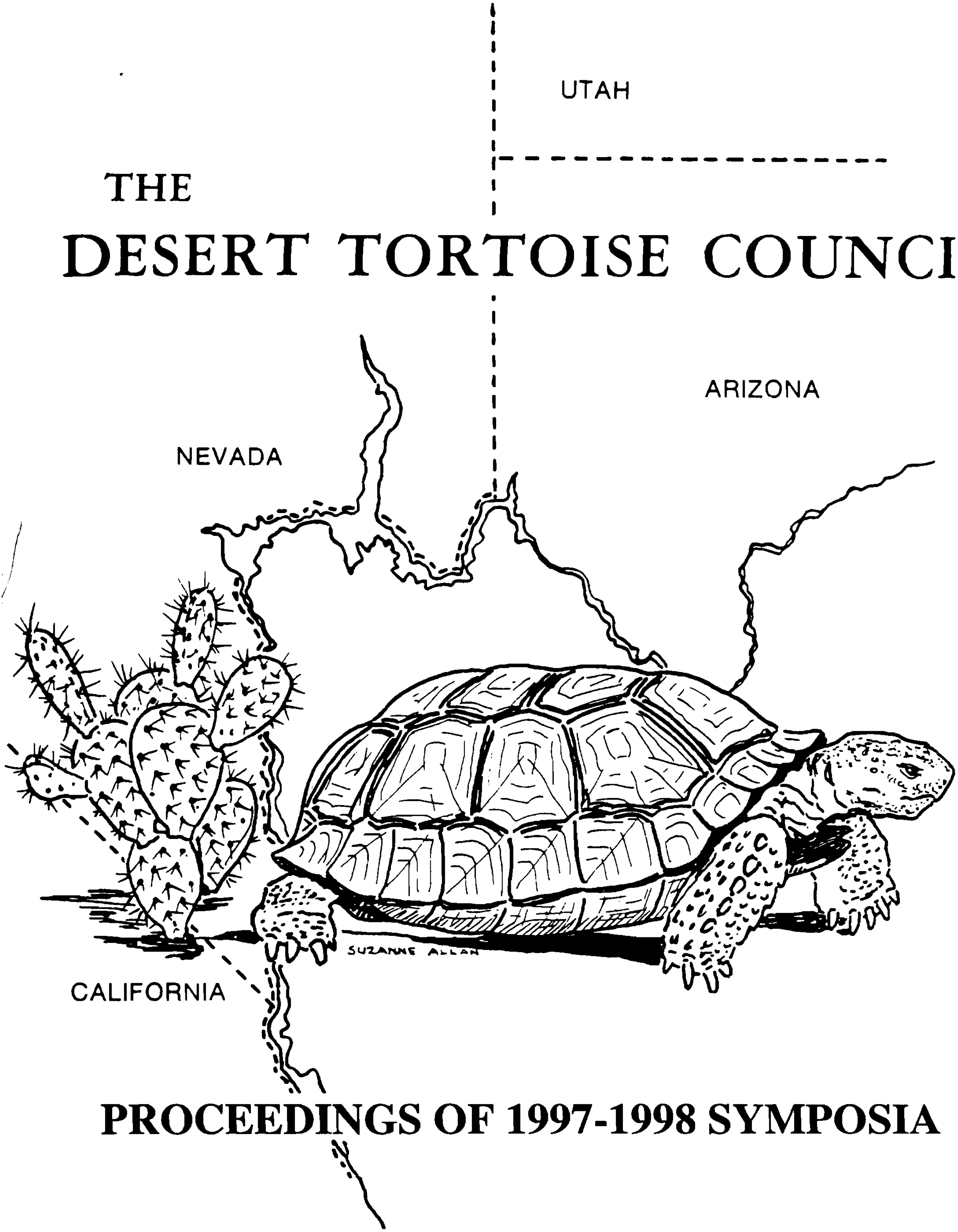

PROCEEDINGS OF 1997-1998 SYMPOSIA

DESERT TORTOISE COUNCIL
PROCEEDINGS OF THE 1997 & 1998 SYMPOSIA

A compilation of reports and papers presented at the twenty-second and twenty-third annual symposia of the Desert Tortoise Council
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Monitoring Tortoise Populations in the Sonoran Desert: A Power Analysis

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Abstract— **Using power analysis, I estimated the ability to detect trends in desert tortoise populations in the Sonoran Desert of Arizona. Regression of data from three monitoring plots surveyed from 1990 through 1994 showed no detectable trend at two of the plots. Retrospective power analyses using Program MONITOR revealed little power to detect trends at these sites, given the available data. Prospective analyses also indicate that little power exists to detect trends in tortoise abundance as surveys are currently conducted. Power to detect trends in abundance increases with survey interval and total number of surveys. For a given level of temporal (among survey) variation in abundance estimates, power increases with initial population size. At a given initial population size, power increases as temporal variation in estimates decreases. However, small, locally distributed populations appear to have smaller sampling variation than larger populations, so the power to detect a given proportional level of decline in small populations may be greater than detecting the same level of decline in large populations. Reducing temporal variation by increasing the accuracy and precision of abundance estimates will improve the ability to detect population declines. Short-term monitoring programs are only likely to detect catastrophic population declines. A long-term commitment to repeated surveys is necessary to detect relatively small, but important, declines.**

The Mojave Desert population of the desert tortoise is listed as threatened by the U. S. Fish and Wildlife Service (USFWS, 1990), and the tortoise is considered a species of special concern throughout Arizona (Arizona Game and Fish Department [AGFD], 1996). Therefore, monitoring trends in desert tortoise abundance is an important conservation and management issue. The recovery plan for the Mojave population, in its first delisting criterion, states that "as determined by a scientifically credible monitoring plan, the population within a recovery unit must exhibit a statistically significant upward trend or remain stationary for at least 25 years" (USFWS, 1994). The plan also recommends that monitoring be continued after delisting to ensure population stability. Additionally, the Arizona Interagency Desert Tortoise Team considers a statewide monitoring program a priority in managing the Sonoran Desert population in Arizona (Murray and Dickinson, 1996).

Distance sampling (Buckland et al., 1993) has recently been identified as the preferred method for estimating tortoise densities and trends throughout the Mojave Desert (Technical Advisory Committee, memorandum to Desert Tortoise Management Oversight Group, 1998), but efforts to monitor tortoise abundance have traditionally centered around permanent plot techniques (Berry, 1984). Plot methods remain important for demographic analyses, including the estimation of local population growth rates and studies of population regulating mechanisms. Whether surveys focus specifically on identifying population status or other ecological questions, managers need to know something about the accuracy and precision of their trend estimates to know how reliable their surveys are in revealing trends (Harris, 1986). They must know the power of their monitoring design to detect trends in abundance or density over time. What is a sufficient number of samples; how precise must estimates be; what is the probability of detecting a trend, if one is present (Gerrodette, 1987)? This paper investigates the power of detecting population trends on monitoring plots in the Sonoran Desert of Arizona.

Materials and Methods

Three tortoise populations were surveyed for five consecutive years from 1990–94: Eagletail Mountains, Maricopa County, Arizona; Granite Hills, Pinal County, Arizona; and Little Shipp Wash, Yavapai County, Arizona. Each population was surveyed with modified 2.6-square-km, 60-day monitoring plot methods (Shields et al., 1990; Hart et al., 1992; Woodman et al., 1993, 1994, 1995). Abundance of tortoises ≥180 mm straight midline carapace length (MCL) was estimated with the Lincoln-Petersen method (Pollock et al., 1990). Except for the first year of survey, abundance was estimated using the number of tortoises captured in the previous year as the "mark" sample and the number of tortoises captured in the current year as the "recapture" sample (*op. cit.*). I conducted analyses for both the number of tortoises captured (counts) each year and annual abundance estimates to compare temporal variation between the two measures. The number of tortoises captured in any given year depends largely on environmental conditions of that year, so count data might be expected to be quite variable depending on the weather during surveys. If statistical assumptions are met, abundance estimates might be less variable from year to year, since they are based on ratios of recaptures to first captures and not on the total number captured.

I estimated the percent annual change in each population as the slope of linear regression results after $\log_e$-transforming the data. Trends were considered significantly different from zero if the 95% confidence interval of the slope did not include zero. I then conducted retrospective power analyses (Thomas, 1997) with Program MONITOR (Gibbs, 1995) to determine the probability of detecting trends in abundance at the three populations. The 1990 tortoise count (or abundance estimate) and observed standard deviations served as initial values for the analysis.

Table 1. Numbers of tortoises ≥180 mm MCL found (Count) and estimated abundance (Lincoln-Petersen estimates) at three monitoring plots in Arizona, 1990–94; standard deviation in parentheses. Data from Shields et al., 1990; Hart et al., 1992; and Woodman et al., 1993, 1994, 1995.

Population	Year	Count	Estimate
Eagletail Mountains	1990	29	31
	1991	26	30
	1992	22	29
	1993	22	30
	1994	25	30
	Mean	24.8 (2.95)	30.0 (0.71)
	CV (%)	11.9	2.4
Granite Hills	1990	33	68
	1991	49	63
	1992	45	60
	1993	55	90
	1994	60	69
	Mean	48.4 (10.33)	70.0 (11.77)
	CV (%)	21.3	16.8
Little Shipp Wash	1990	68	85
	1991	67	79
	1992	76	107
	1993	81	107
	1994	61	97
	Mean	70.6 (7.89)	95.0 (12.73)
	CV (%)	11.2	13.4

I also conducted a prospective power analysis to examine conditions for maximizing trend detection. I used simulations with Program MONITOR to investigate the effects of 1) initial population size, 2) temporal variation in abundance estimates within plots, 3) the number of surveys conducted (3–6) and over which a potential trend may be investigated, and 4) the interval between surveys (1–6 yrs) on the power to detect trends in abundance. After initial simulations, I fixed survey interval at four years. Variables 1 and 2 are intrinsic to specific populations under study, so I used baseline abundance and variation (standard deviation) data from the three populations listed above to set realistic bounds on the simulations.

For both sets of power analyses with Program MONITOR, I specified two-tailed significance tests and replicated each simulation 1000 times. I assumed annual population change to be proportional to abundance, so I used the exponential model; the linear model produces similar results (Gibbs, 1995; unpubl. data). Due to the conservation implications of failing to detect negative trends, I set $\alpha=0.10$ instead of $\alpha=0.05$ to increase power (i.e., decrease the Type II error rate of incorrectly concluding there is no trend when one does in fact exist).

RESULTS

An average of 24.8 (±2.95 [1 SD]) tortoises ≥180 mm MCL were found at the Eagletail Mountains, 48.4 (±10.33) at the Granite Hills, and 70.6 (±7.89) at Little Shipp Wash (Table 1). Estimated abundance for each population was 30.0 (±0.71), 70.0 (±11.77), and 95.0 (±12.73) tortoises, respectively (Table 1). Trends of counts and abundance estimates differed significantly from zero only for the number of tortoises marked at the Granite Hills (Table 2; Fig. 1).

Power to detect meaningful trends, given the observed variance and initial population sizes, was generally poor for count data at all

Table 2. Regression results for marked tortoises (log$_e$-transformed counts) and log$_e$-transformed estimated abundance at three monitoring plots in Arizona, 1990–94. Asterisk indicates trend significantly different than zero at α=0.05.

Population	Slope	*P*-value	95% C.I.	r^2
Eagletail Mountains				
Counts	-0.05	0.2391	-0.15-0.06	0.39
Abundance	-0.01	0.4442	-0.03-0.02	0.19
Granite Hills				
Counts	0.13	0.0236	0.01-0.25*	0.81
Abundance	0.04	0.5054	-0.13-0.21	0.15
Little Shipp Wash				
Counts	-0.00	0.9493	-0.13-0.13	0.00
Abundance	0.06	0.2067	-0.06-0.18	0.43

three populations and acceptable for estimated abundances only at the Eagletails (Fig. 2). For count data, power was acceptable ($\geq$80%) only for detecting an increasing trend of 10% at the Eagletail Mountains. The power to detect a decreasing trend in tortoise counts between 1990 and 1994 was <67% in all cases and was exceptionally low at the Granite Hills ($\leq$20%). Power to detect trends as low as 3–4% based on Lincoln-Petersen estimates exceeded 90% at the Eagletail Mountains but was still poor (<60%, even for trends as large as 10%) at the Granite Hills and Little Shipp Wash.

As expected, power to detect population trends increases with number of surveys conducted (Fig. 3). Power also increases for a given number of surveys as the interval between surveys increases (Fig. 4), because longer time spans from first to last survey result in larger absolute changes in population size. For a given level of temporal variation in abundance estimates (or counts), power to detect trends is greater for larger populations (Fig. 5), but power decreases for populations of a given size as temporal variation increases (Fig. 6). This can result in greater power to detect trends in small populations with precise year-to-year abundance estimates, such as at the Eagletails (Table 1), than in large populations with more variable estimates (Fig. 7). Detecting population declines is also more difficult than detecting increases of the same magnitude for small populations (i.e., those already close to zero; Fig. 5) or when abundance estimates are highly variable (Figs. 6–7).

Discussion

The general simulation results of this study are consistent with well-known properties of trend power analysis. Trends are more "detectable" for larger effect sizes (i.e., degree of change), in longer studies, with more samples, and with more precise abundance estimates (Harris, 1986; Gerrodette, 1987; Taylor and Gerrodette, 1993). If we were primarily interested in detecting trends in a specific direction (e.g., detecting declines in abundance), power could be increased by specifying one-tailed tests (Gerrodette, 1987).

The retrospective analyses further indicate that the data collected to date, even on relatively intensively surveyed plots, are inadequate to detect anything less than a catastrophic decline in tortoise abundance. It is important to note that *a posteriori* estimates of power are meaningful only relative to effect sizes hypothesized to be biologically significant (Hayes and Steidl, 1997). Hayes and Steidl (1997) also pointed out that determining whether the confidence interval around the estimated slope encompasses a biologically significant change can provide more meaningful information than *a posteriori* power analyses about hypothesis tests that were not rejected. Of course, any decline, however small, that ultimately leads to extirpation or extinction is biologically significant, and it is difficult to determine in advance what level of decline in any given year could lead to extirpation of a population (Reed and Blaustein, 1997). For example, 5% declines at both the Granite Hills and Little Shipp Wash populations (based on abundance estimates) are undetectable with the existing data (Table 2).

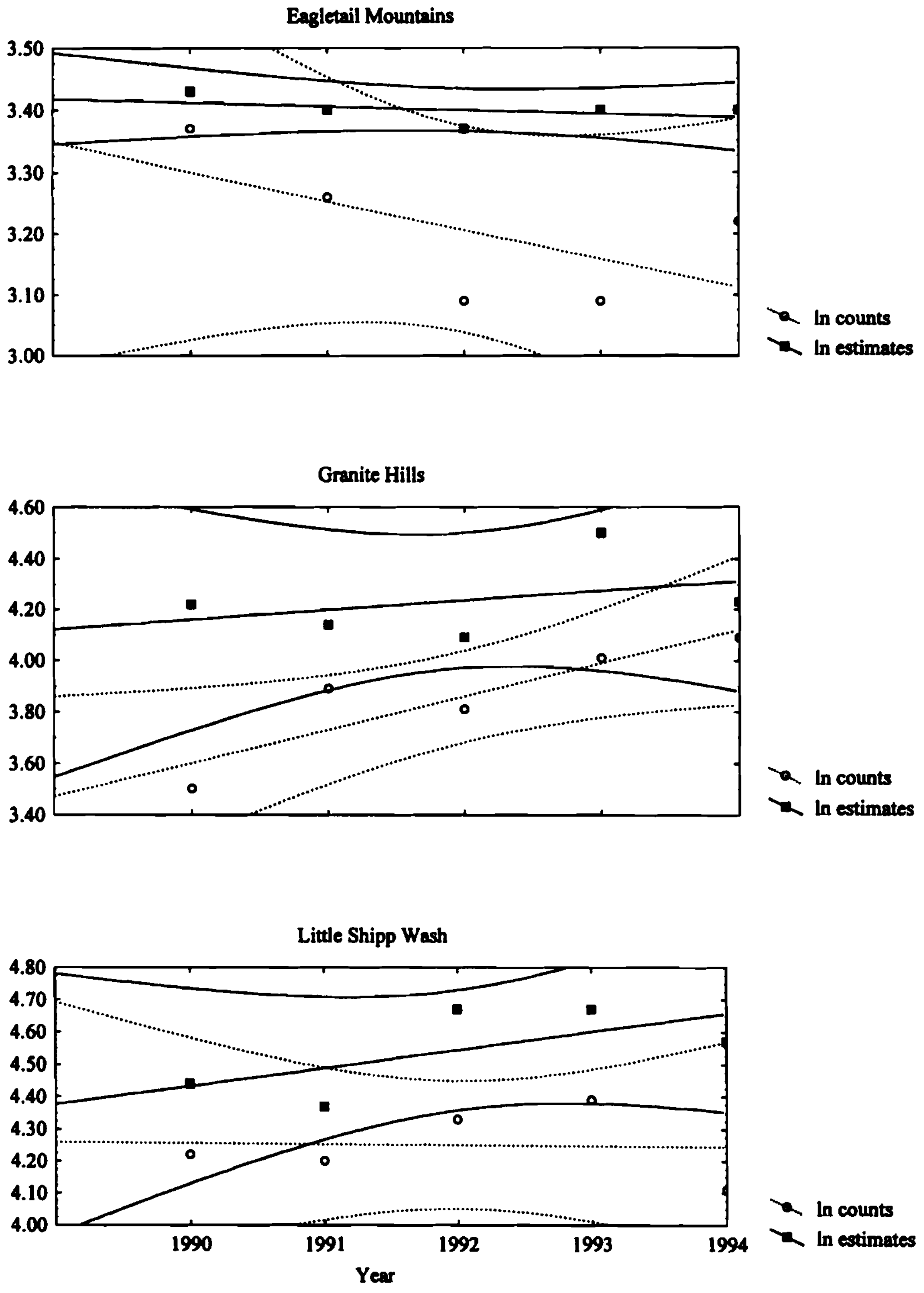

Fig. 1. Linear regression (with 95% confidence bands) of $\log_e$-transformed counts and abundance estimates at three monitoring plots in Arizona.

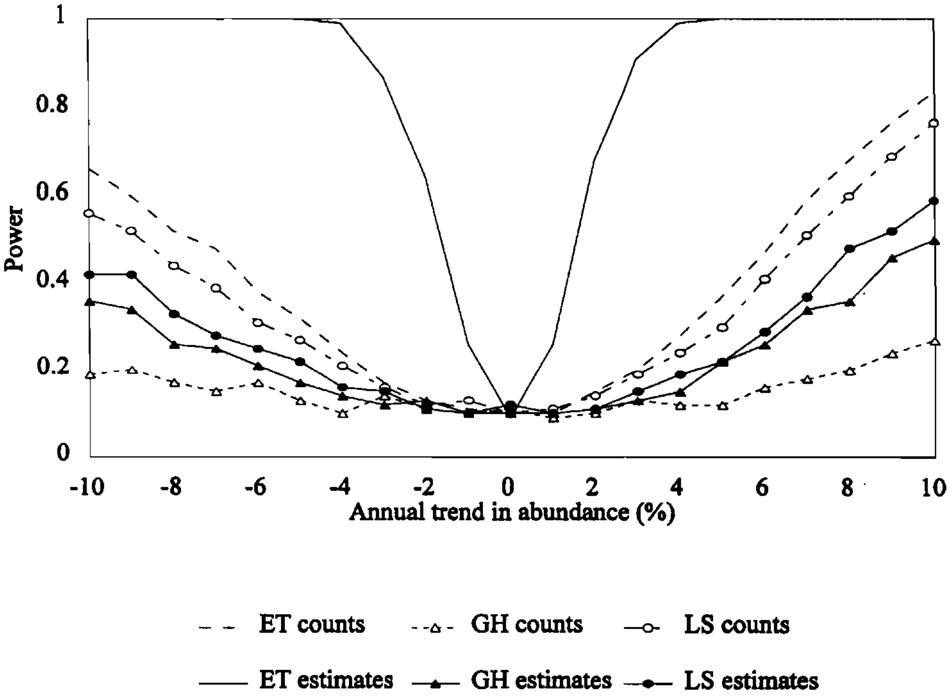

Fig. 2. Power to detect trends in counts and abundance estimates at three monitoring plots surveyed in Arizona from 1990 to 1994. ET=Eagletail Mountains, GH=Granite Hills, LS=Little Shipp Wash.

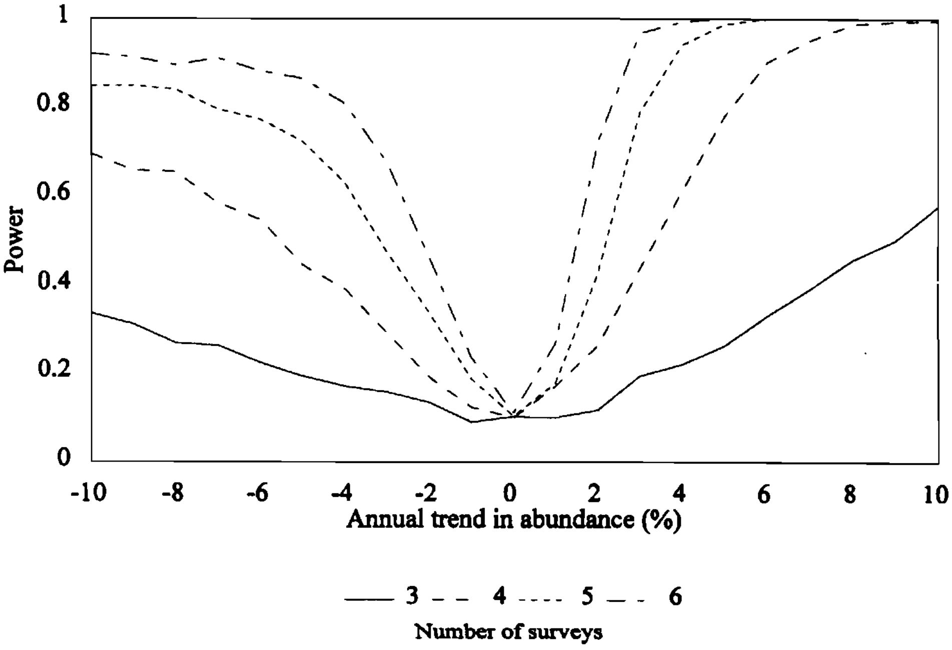

Fig. 3. Effect of the number of surveys on the power to detect linear trends in abundance. Simulations were conducted for an initial population of 100 individuals (N_0=100), surveyed at an interval of every four yr (i=4), and with abundance standard deviation (SD)=15.

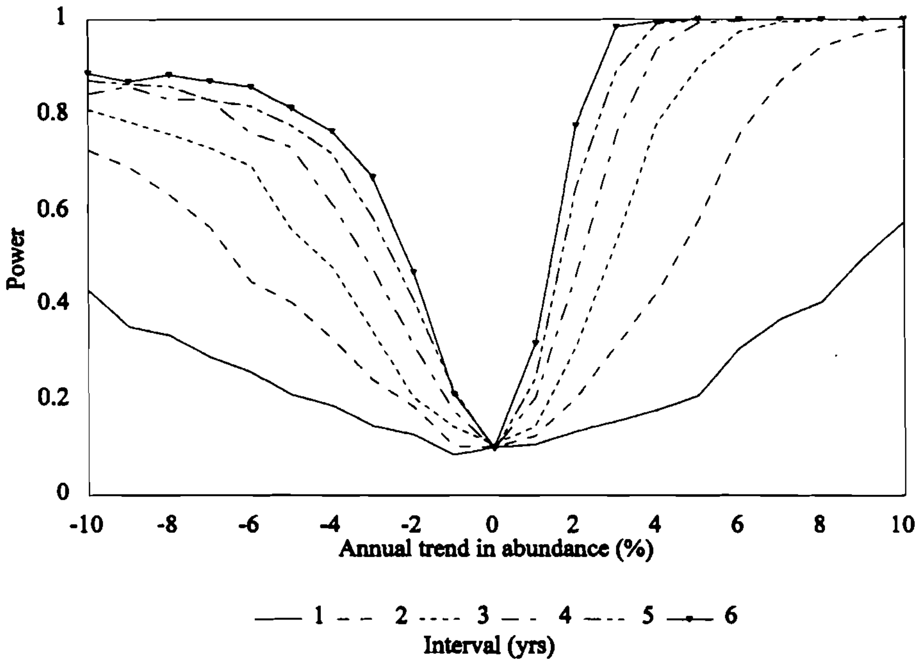

Fig. 4. Effect of survey interval on the power to detect linear trends in abundance; N_0=100, population surveyed five times (t=5), SD=15.

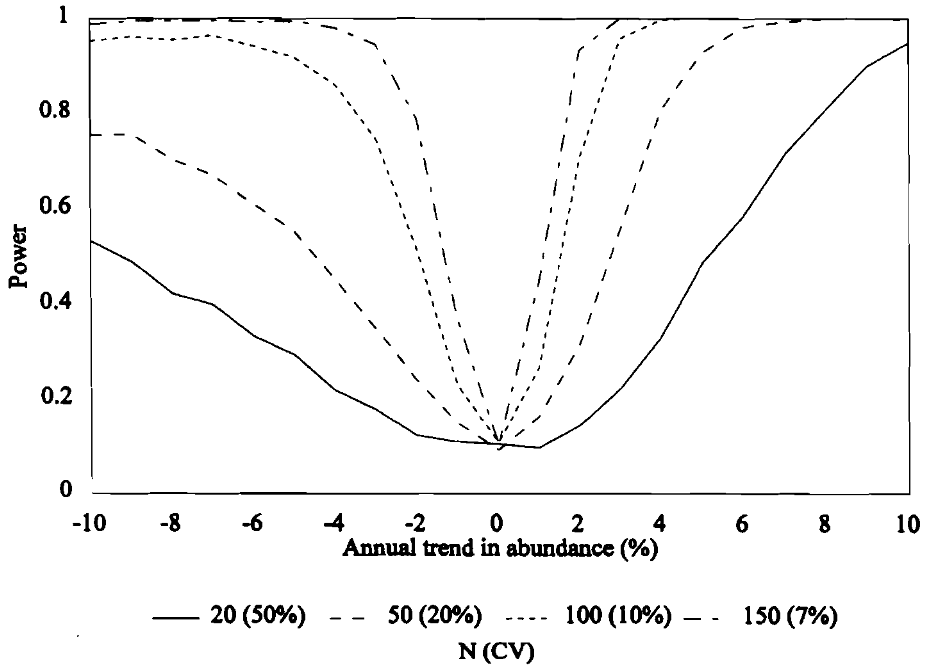

Fig. 5. Effect of initial population size on the power to detect linear trends in abundance; t=5, i=4, SD=15.

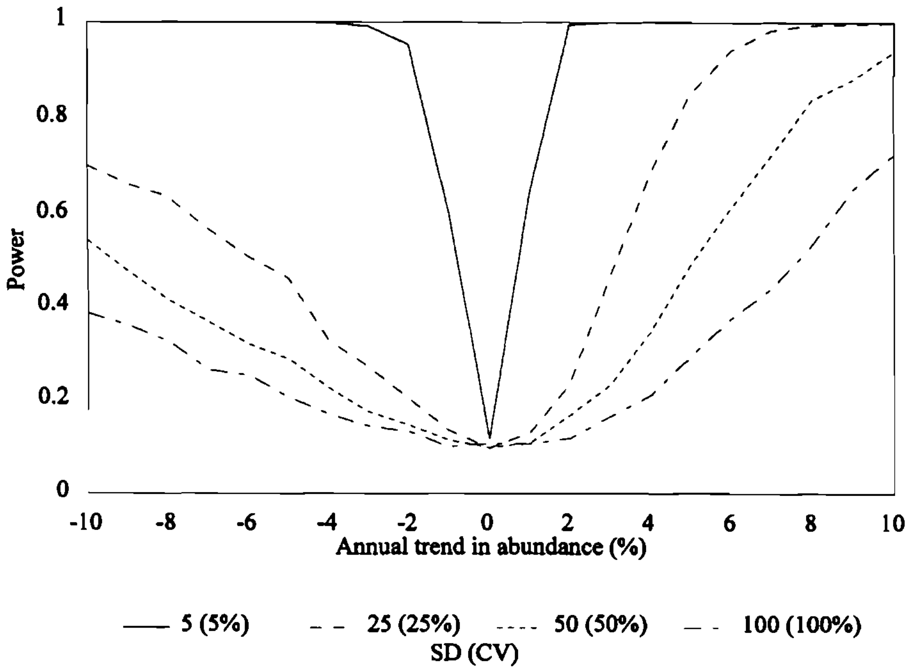

Fig. 6. Effect of temporal variation on the power to detect linear trends in abundance; N_0=100, t=5, i=4.

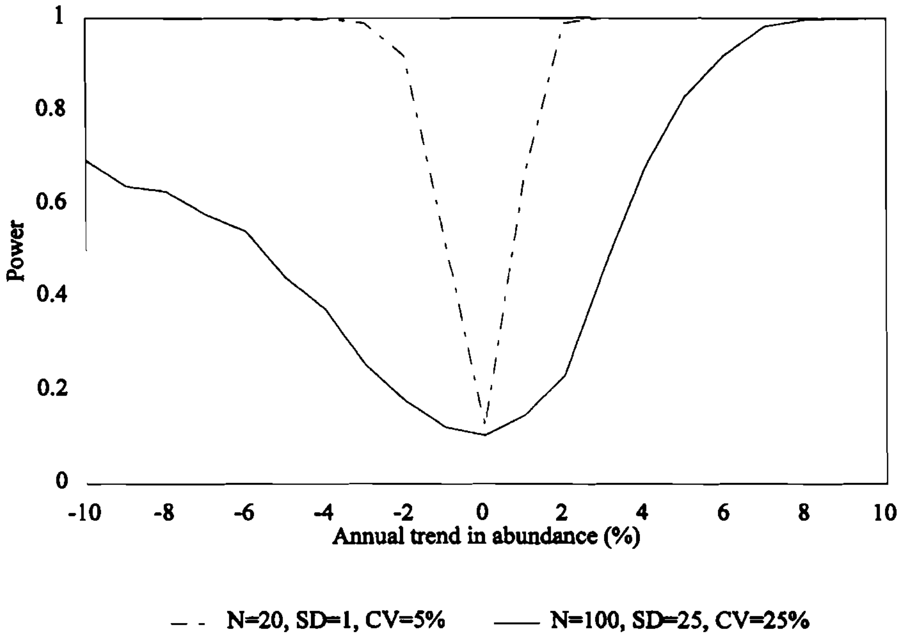

Fig. 7. Effect of relative survey precision (coefficient of variation, CV) on the power to detect linear trends in abundance; t=5, i=4.

This is double the level of decline considered by the USFWS in determining recovery goals (e.g., population numbers and size of reserves) for the Mojave population (USFWS, 1994). Developing matrices or graphs illustrating different levels of power achieved with different study designs and variables provides a more useful approach than subjectively choosing a "biologically significant" trend level; this technique provides managers with information needed to determine the effort required to detect changes (Reed and Blaustein, 1997) and can highlight areas on which to focus in improving monitoring study designs.

An important step to improve the power to detect trends in tortoise abundance is to minimize the temporal variation in counts or abundance estimates as much as possible. This variation has two components: environmental variation and sampling variation. In two of the three populations, variation of count data exceeded that of abundance estimated by the Lincoln-Petersen method (Table 1). Population dynamics of long-lived animals, such as the desert tortoise, are characterized by damped variation in population growth rates; therefore, variation in population estimates mainly reflects measurement error instead of environmental variability (Gerrodette, 1987). Count data include both measurement (i.e., sampling) error and environmental variation. The degree of variation in abundance estimates from the three reference plots may be overly optimistic, however. Since the abundance estimates were calculated using one year as the "mark" sample and the subsequent year as the "recapture" sample, the estimates are not independent of each other and temporal variation is underestimated, making trend estimates less reliable (Harris, 1986). Yearly abundance estimates must be independent to maximize the chance of detecting population trends. Unfortunately, the data at these monitoring plots were not collected in such a way to accurately estimate abundance within years.

Simulations modeling the effects of variation and population size (Figs. 5–7) indicate that a focussed survey effort, which may produce more recaptures and more precise abundance estimates, can improve the power to detect trends by reducing the coefficient of variation of the abundance estimates. Standard 2.6-square-km plots in Sonoran Desert habitats typically include much area not used by tortoises, even for relatively large populations (Murray, 1993). Surveys restricted to the primary areas of tortoise distribution have been successful in recapturing a high proportion of tortoises within each year (e.g., the Eagletail Mountains; Woodman et al., 1993, 1994, 1995). If we applied this technique to other populations, excluding areas where few or no tortoises are usually found, field workers could systematically search the plots repeatedly to produce abundance estimates for the core populations on each plot within each survey year. This should accomplish two things: additional recaptures obtained from focussed, repeated search efforts will result in more precise abundance estimates, and each estimate will be independent of others from survey to survey.

Finally, a long-term commitment to monitoring tortoise populations is necessary if we want to develop a clear understanding of desert tortoise population dynamics, especially if we want to detect anything less than a catastrophic decline. Power is negligible if we only survey a population two or three times, and small trends are difficult to detect under the best of circumstances. Managers must be aware of the potential implications of an inconsistent monitoring effort for long-lived species such as the desert tortoise. Although power increases as the interval between surveys increases (Fig. 4), this must be balanced against the fact that power decreases dramatically as the number of surveys decreases (Fig. 3). If the survey interval is too large, gradual declines over several years may not be detected until a significant absolute decline in abundance has already occurred, and catastrophic declines (such as that at the Maricopa Mountains; Shields et al., 1990) might not be recognized as such, reducing our ability to identify and correct the cause of the decline. I recommend a survey interval of four to five years over at least 20 years to confidently identify the trend status of desert tortoise populations in the Sonoran Desert of Arizona.

Acknowledgments— This paper is the result of the hard work of several biologists who conducted the monitoring plot surveys in Arizona from 1990 to 1994 and whose work is cited below. The USFWS, U. S. Bureau of Land Management, and AGFD (Heritage Fund and Nongame Checkoff) have contributed significant funding to tortoise monitoring efforts as well as to the completion of this paper. The comments of L. Allison and J. Howland greatly improved earlier drafts of this manuscript.

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A Demonstration of a Spatially Dynamic Model of a Desert Tortoise Population

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Abstract— **A series of modeling techniques have been developed for creating dynamic landscape simulations (DLS). To demonstrate the techniques, we developed a DLS of a desert tortoise (*Gopherus agassizii*) population (a Federally listed threatened species) at Fort Irwin, California, which has been the Army's National Training Center since 1979. We demonstrate how these modeling techniques could be used to assess the impacts of military training at Fort Irwin across time and space on desert tortoises and their habitat.**

Recently, efforts in computer-based simulation have been directed towards developing spatially explicit models, but the spatial distribution and complexity of land characteristics makes it difficult to analyze and simulate a landscape as a whole. Partitioning a landscape into small but connected parcels makes it possible to work with patches of land that can be treated as homogeneous for certain analyses. Our approach seems especially useful for developing spatially explicit models for endangered species on military lands.

Our results of this model evaluate the potential effects of military training on desert tortoises and their habitat. These results are not intended to provide land managers with detailed predictions of specific impacts, but do demonstrate the feasibility of using this modeling approach to develop landscape-level simulations

Computer-based simulation modeling is becoming an increasingly important tool for government. It can provide insights into species-habitat relationships, patterns of habitats in space and time, and the effects of impacts on animal populations and their environments (Turner et al. 1995). Recently, efforts have been directed towards developing spatially explicit models (Turner et al. 1995), but the spatial distribution and complexity of land characteristics makes it difficult to analyze and simulate a landscape as a whole. Partitioning a landscape into small but connected parcels makes it possible to work with patches of land that can be treated as homogeneous for certain analyses (i.e., gridded landscape models). This approach seems especially useful for developing spatially explicit models for endangered species on military lands.

Our model is one of a series of models that have been developed to study the processes involved with building dynamic landscape simulation (DLS) models. We continue to learn how to enhance and improve these types of models. In this model, we attempted to assess the impacts of military training across time and space on desert tortoises (*Gopherus agassizii*) and their habitat.

The desert tortoise was designated as federally threatened in the Mojave Desert in 1990. Its has a patchy distribution over very large areas which makes population density estimates difficult to obtain. And it is a long-lived animal that does not reproduce until an age of about 15 years, making it highly susceptible to perturbations in the environment.

We used the previously developed desert tortoise model (Westervelt et al. 1997) to evaluate the potential response of tortoise density and habitat suitability to changes in the intensity, location, and timing of military training. This study serves as a scientific investigation of the sensitivity of the developed model to these simulated variations. It is

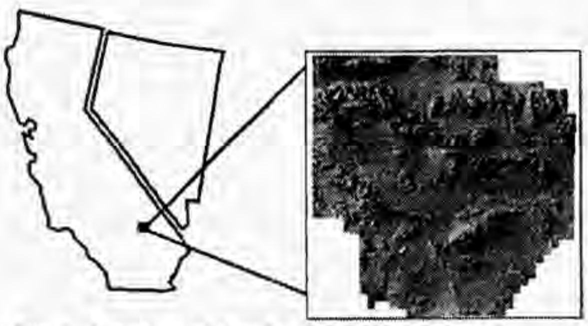

Fig. 1. Location of Fort Irwin, California.

not intended to provide land managers with absolute predictions of the response of tortoise density or habitat to different land management approaches. At best, the results could be viewed as suggestive of the trends that might be expected as training intensity is changed both temporally and spatially. Our objective was to evaluate the model's ability to predict results of various military training activities. Our results should be verified through the observations of land managers and controlled field experiments.

MATERIALS AND METHODS

Fort Irwin is located midway between Los Angeles, California and Las Vegas, Nevada in the center of the Mojave Desert (Fig. 1). It is approximately 260,000 hectares with elevations of 390–1865 m. Temperatures in the summer range from 35–46°C while in winter range from -7–5°C. The precipitation is low with only approximately 6–8 cm annually. Since 1979, Fort Irwin has been the National Training Center for the Army, providing a large training area for force-on-force military training. The desert tortoise, a federally threatened species, occurs within the boundary of Fort Irwin and throughout the Mojave Desert ecosystem

We divided the Fort Irwin landscape into 1 km^2 grid cells, with a total of 3249 cells representing the entire area. The basic processes or cell model ran in each cell with only the initialization values differing among cells. The model simulated changes through time using mathematical equations. The state of any given cell was a function of its state in the previous time step, the state of adjacent neighbors in the previous time step, and external weather factors.

The cell model created by Westervelt et al. (1997) was developed as four major submodels: climate (including soil moisture and temperature), vegetation, tortoise population dynamics, and tortoise dispersal movements. We developed a fifth submodel to incorporate military training into the simulation model.

The simulation model used modeled tortoise populations over a 250–year time period. Parameters of the model were altered to show what might happen under a variety of conditions. Each set of parameters was manipulated and evaluated in a separate submodel. Each submodel had a 1–month time step which accommodated seasonal changes within the landscape such as weather patterns, tortoise nesting and egg-laying seasons, and vegetation growth cycles. All simulations were initiated in January (time step 0).

We used a grid cell size of 1 km^2 because desert tortoises have home ranges that extend up to 1 km^2 (Krzysik 1994). The dispersal of tortoises in the model was represented by movement from one grid cell to a neighboring cell in any of the 4 cardinal directions.

Only females were modeled because we assumed a sex ratio of 1:1 (see Berry 1976). Luke (1990) and Doak et al. (1994) found that the rate of population growth relies largely on the survival of large adult females. We obtained the total tortoise population on our simulated landscape by doubling the total number of female tortoises.

A brief discussion of each submodel follows. However, more specifics about the model and data used in the model can be found in Westervelt et al. (1997).

Climate submodel— The purpose of this submodel was to determine monthly soil moisture, monthly surface temperature, and to estimate water available to tortoises. The approach they used allowed each month's mean temperature to vary within the appropriate historical values according to a normal distribution (Westervelt et al. 1997). Additionally they adjusted temperature for physical conditions (i.e., slope and elevation), determined evapotranspiration from the Thornthwaite model (Thornthwaite 1948), and estimated infiltration and runoff of precipitation (Westervelt et al. 1997).

Vegetation submodel— The purpose of this submodel was to determine vegetative cover and estimate available food. The approach they used estimated the total vegetative cover of a given cell, estimated seasonal changes in aerial cover using logistic equations, and determined community composition of annuals and perennials (Westervelt et al. 1997).

Tortoise population dynamics submodel— The purpose of this submodel was to identify impacts of human activity and habitat quality on tortoise population dynamics. The approach they used captured demographic changes by subdividing the population into 5 life history stages (eggs, hatchlings, juveniles, adults, and elders). They simulated population dynamics by incorporating transitions between life history stages, reproduction, and mortality of tortoises (Westervelt et al. 1997).

Tortoise dispersal movements submodel— The purpose of this submodel was to simulate immigration, emigration, and costs associated with dispersal, as well as to investigate connectivity among subpopulations (Westervelt et al. 1997). Emigration was determined by conditions in the home cell. Emigration took place if conditions in 1 of the 4 adjacent cells were better than the home cell. The direction of dispersal was toward the adjacent cell with the best relative conditions. Their submodel did not allow the dispersal of eggs or hatchlings.

Training impacts submodel— The purpose of this submodel was to determine the indirect impacts of military training on tortoise populations. Based on available literature (Krzysik 1994), we assumed that indirect impacts of training (e.g., disturbance of vegetation and compaction of soil) were more significant than direct impacts (e.g., getting crushed by a vehicle) so we modeled only indirect impacts. Indirect impacts, including vegetation destruction and increased soil compaction, caused by off-road vehicles have detrimental effects in desert environments (Bury et al. 1977; Adams et al. 1982; Webb et al. 1986). Since we did not have data indicating the impacts of military training on tortoise habitat, we assumed military training caused impacts similar to off-road vehicles.

As a surrogate for a detailed map of training locations, we developed a soil compaction map from elevation data, by assuming that the most severe soil compaction occurs at lower elevations (Krzysik 1994). The indirect impact of training on tortoises was captured as a map of training intensity. The soil compaction map we generated had values ranging from 4 to 17 kg/cm². We divided these values into 3 categories, representing different training level intensities (4.0–9.0 kg/cm² = low training; 10.0–14.0 kg/cm² = moderate training; 15.0–17.0 kg/cm² = high training).

We associated the training level intensities with different levels of tracked-vehicle-days per month (TVD/month). These values were determined from training data in Krzysik (1994; 1–475 TVD/month = low training; 476–1189 TVD/month = moderate training; 1190–1666 TVD/month = high training).

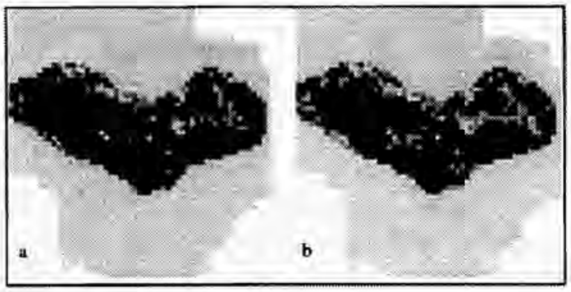

Fig 2. Surrogate soil compaction map (a) used to create training intensity map (b) for Fort Irwin, California. Lighter shades within the heart-shaped area indicate low compaction and low training intensity, while darker shades indicate high compaction and high training intensity. No soil compaction or training occurred on the remaining portion of the landscape.

We created a training intensity map by reclassifying our soil compaction map based on the above values (Fig. 2). We changed the training intensity both temporally and spatially in our model simulations.

Westervelt et al. (1997) developed the simulation model which applied to each cell with a graphical programming language, STELLA II (High Performance Systems, Inc. 400 Lyme Road, Suite 300, Hanover, NH 04755). This desktop modeling tool uses icons and schematics, linked with equations, as the mechanism to build the equations upon which the model is based.

To apply the simulation model across multiple cells, STELLA II equations were translated into C++ programs by the Spatial Modeling Environment (SME; version 2; Maxwell and Costanza 1994 and 1995). SME applies the same functions used in the single-cell STELLA II model, but it runs them within each cell of the landscape and generates output data layers. In other words, SME allows the model and all its functions to run dynamically in each cell across the Fort Irwin landscape and transfers information between cells.

We created the initialization maps for the simulation model in the GIS program, Geographic Resource Analysis Support System (GRASS; USACERL 1993). Output data from SME were written to GRASS data layers.

The spatial data used for the climate submodel included average monthly available water content (AWC) generated by using a deterministic run of the climate submodel. Vegetation maps were derived from Land Condition Trend Analysis (LCTA) transect data using a back-propagation neural network (Wu and Westervelt 1994). Tortoise density maps were obtained from transect data collected by Krzysik (1991, 1994) using a back-propagation neural network (Westervelt et al. 1997). Topography data were acquired from digital elevation models (DEM) which were used to derive slope and aspect maps. Westervelt et al. (1997) provides more specifics regarding these spatial data.

RESULTS

We simulated each of 7 different training scenarios 100 times, with each run capturing changes over 250 years. The results are the mean values for tortoise populations over the 100 runs. The scenarios differed in how vegetation and tortoise density input maps were derived as well as in training intensity maps. We altered the model for each scenario by changing input maps and model parameters. Model algorithms, time steps, spatial extent, and resolution were not changed between scenarios.

We intended this research to identify trends in tortoise density due to environmental responses to simulated changes in training intensity. We caution that relative, rather than absolute, differences among scenarios should be compared.

Scenario 1: Neural network baseline— In scenario 1, we ran the model with no new training after time step 0 to simulate changes in vegetation and tortoise density expected in 250 years. This run essentially simulated the recovery of the landscape from previous impacts. This also provided us with a final debugging of the model to ensure that all submodels were working as intended.

The initialization map for tortoise density was derived from tortoise transect data (Krzysik 1994) and the vegetation initialization map was derived from LCTA transect data using a back-propagation neural network analysis (Fig. 3). See Wu and Westervelt (1994) for more information on back-propagation neural network analyses and see Westervelt et al. (1997) for more information regarding the derivation of these maps.

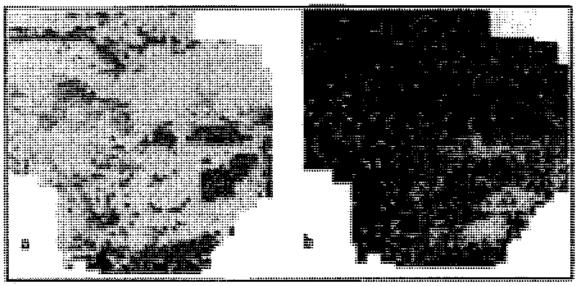

Fig. 3. Initialization maps for desert tortoise density (a) and vegetation cover (b) used in scenario 1 for Fort Irwin, California. These maps were created using a back-propagation neural network analysis by correlating ground truth data with satellite imagery. Lighter shades indicate low tortoise density or less vegetative cover, while darker shades indicate high tortoise density and more vegetative cover.

Initially, tortoises were distributed across the landscape at moderate densities with higher concentrations along the southern boundary, while more vegetative cover occurred in the northwest portion of Fort Irwin (Fig. 3). This approach produced an adequate representation of tortoise densities and vegetative cover at Fort Irwin, which we used to initialize the model (A. Krzysik, pers. comm.).

After running the model 100 times, we averaged the results. They showed tortoises spatially distributed in highly concentrated patches across Fort Irwin (Fig. 4). Woodman et al. (1986) found "core" areas where tortoise densities were higher than surrounding areas. Furthermore, Woodman

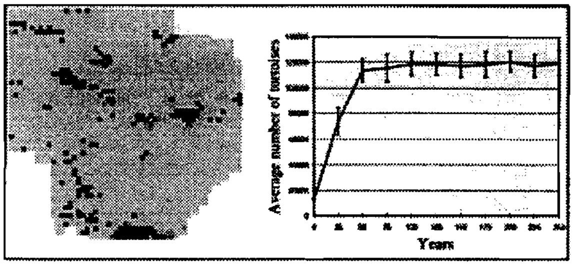

Fig. 4. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 1 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 1. Scenario 1 used the back-propagation neural network analysis to derive initialization maps for tortoise density and vegetative cover (see Fig. 3). No new training occurred in the model after time step 0. Darker shades indicate higher tortoise densities.

et al. (1986) and Krzysik (1994) found a large tortoise concentration near the southern boundary of Fort Irwin, which is similar to our tortoise density maps at time 0 and 250 years (Figs. 3 and 4). Nicholson et al. (1980) found a similar pattern of tortoise densities on the China Lake Naval Weapons Center, San Bernardino County, California, with small pockets of high tortoise densities. Tortoises populations are naturally clumped on the landscape (Krzysik 1994).

Even though tortoises were distributed in patches, their density asymptotically increased over the 250 years. This might be expected given no additional training after time step 0 which allowed the landscape to recover from previous impacts. Our results showed that tortoises concentrated in areas that had good vegetative cover. The tortoises may have been moving away from unsuitable habitat as opposed towards good habitat (Gibbons 1986).

The simulated vegetative cover after 250 years differed little from the carrying capacity map (Fig. 5). In the model, we assumed vegetation could not exceed carrying capacity, instead vegetation densities fluctuated just below carrying capacity.

The habitat suitability index developed for tortoises in the model appeared to decrease over time (Fig. 6). Habitat suitability was a function of the percentage of green vegetation available to tortoises for consumption and the percentage of total vegetative cover. Over time, the increase in tortoise densities caused greater amounts of green vegetation to be consumed and decreased the habitat suitability index.

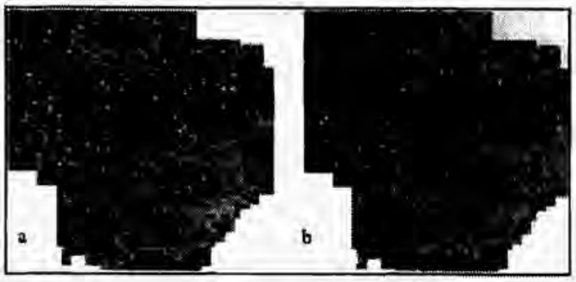

Fig. 5. The average percent aerial cover of vegetation after running scenario 1 for 250 years (a) and the carrying capacity of vegetation (b) at Fort Irwin, California. The average was obtained from 100 simulations of scenario 1. No new training occurred in the model after time step 0. Darker areas represent higher densities of vegetative cover.

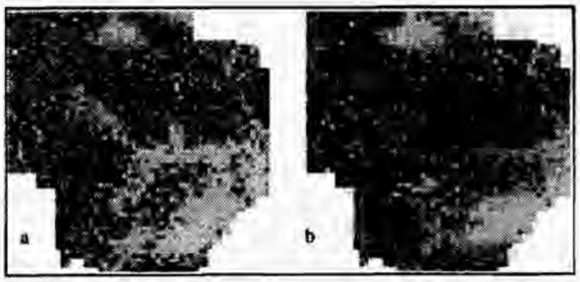

Fig. 6. The average index of habitat suitability for desert tortoises after running scenario 1 for 250 years at Fort Irwin, California for time 0 (a) and time 250 years (b). The average was obtained from 100 simulations of scenario 1. No new training occurred in the model after time step 0. Darker shades represent habitat better suited for tortoises.

Scenario 2: New baseline— We ran this simulation to establish a new baseline for scenarios 3–7. We used the maps for tortoise density and vegetation cover from the end of scenario 1 (Figs. 4 and 5a, respectively) as the initialization maps for this scenario. We attempted to simulate a landscape that had recovered from training after 250 years and could be used as the initialization landscape for the remaining scenarios, which included training impacts. By using the output from scenario 1, we effectively removed confounding effects of past training impacts which allowed us to fairly assess the impacts of future training.

In scenario 1, the tortoise population stabilized and throughout scenario 2 that population level

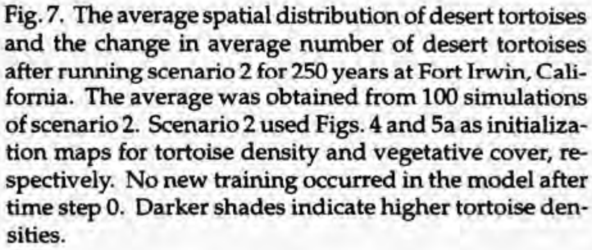

Fig. 7. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 2 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 2. Scenario 2 used Figs. 4 and 5a as initialization maps for tortoise density and vegetative cover, respectively. No new training occurred in the model after time step 0. Darker shades indicate higher tortoise densities.

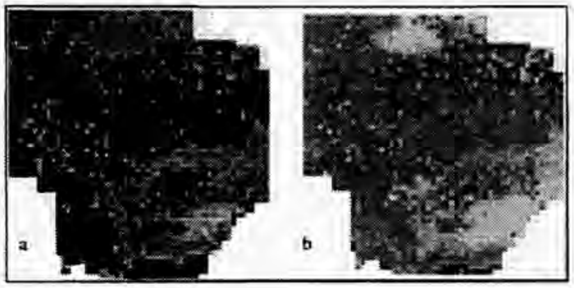

Fig. 8. The average percent aerial cover of vegetation (a) and average index of habitat suitability (b) for desert tortoises after running scenario 2 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 2. Figs. 5a and 6b show the average percent aerial cover of vegetation and index of habitat suitability, respectively, of time 0 for scenario 2. No new training occurred in the model after time step 0. Darker shades represent higher densities of vegetative cover (a) and habitat better suited for tortoises (b).

was maintained (Fig. 7). Furthermore, the spatial distribution of tortoises across Fort Irwin remained relatively constant: tortoise densities within cells changed only in response to environmental stochasticity (Fig. 7).

In scenario 2, the initialization map for vegetation (Fig. 5a) was very close to carrying capacity and the vegetation changed very little over the next 250 years (Fig. 8a) Furthermore the habitat suitability remained relatively constant (Fig. 8b). The results of this scenario indicated that a stable point was reached in the model and that the simulated landscape had recovered fully from training.

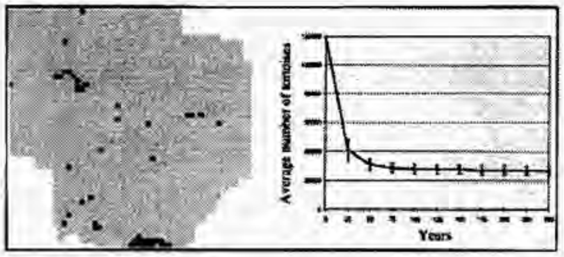

Fig. 9. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 3 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 3. Scenario 3 used Figs. 4 and 5a as initialization maps for tortoise density and vegetative cover, respectively. On a monthly basis, a low level of training occurred in the model after time step 0. Darker shades represent higher tortoise densities.

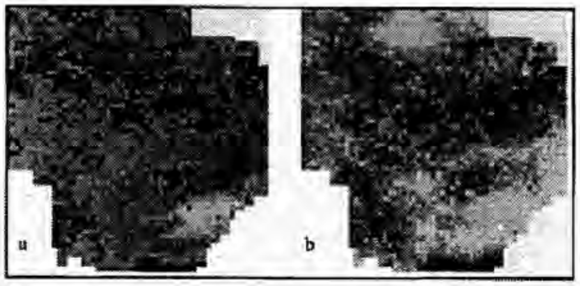

Fig. 10. The average percent aerial cover of vegetation (a) and average index of habitat suitability (b) for desert tortoises after running scenario 3 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 3. Figs. 5a and 6b show the average percent aerial cover of vegetation and index of habitat suitability, respectively, of time 0 for scenario 3. No new training occurred in the model after time step 0. Darker shades represent higher densities of vegetative cover (a) and habitat better suited for tortoises (b).

Scenario 3: Low training intensity— In this and the following scenarios, we evaluated the ability of the simulation model to respond to varying training intensities. In this scenario, we used a low level of training intensity (237.5 TVD/month) at each time step (i.e., monthly) across all of Fort Irwin. The initialization maps for tortoise density and vegetation were the same used for scenario 2 (Figs. 4 and 5a, respectively).

Our results show that the tortoise population did not recover from the training impacts, but stabilized at a lower value (Fig. 9). Tortoises became restricted to a few small patches which contained high densities. Less vegetative cover was available for tortoises after 250 years (Fig. 10) because the vegetation was unable to recover from monthly training events. The impact of low intensity training was also evident in the habitat suitability index which decreased over time (Fig. 10).

Scenario 4: Training varied temporally— In this scenario, we examined the responses of tortoises and vegetation to seasonal- rather than sustained-training activities. Tortoises display seasonal patterns by hibernating during November–February and breeding and laying eggs during March–October (Luckenbach 1982). We incorporated these seasonal patterns into the training activities. While seasonal training activities were based on tortoise activities, we did not include direct impacts of training on tortoises (e.g., being crushed in their burrows) into the model.

However, the indirect impacts of training oc-

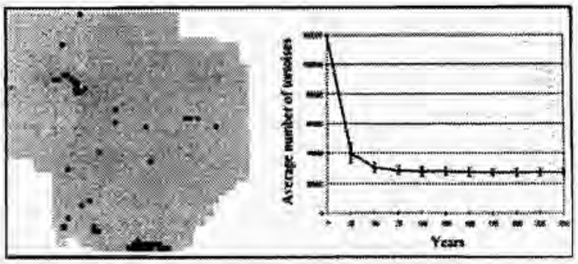

Fig. 11. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 4 for 250 years for Fort Irwin, California. The average was obtained from 100 simulations of scenario 4. Scenario 4 used Figs. 4 and 5a as initialization maps for tortoise density and vegetative cover, respectively. Temporal variation of training occurred during Scenario 4. Darker shades represent higher tortoise densities.

curring on a seasonal basis were expected to allow vegetation to recover from impacts and result in increased habitat suitability for tortoises. The egg-laying and nesting season is a critical time for tortoises and adequate vegetative cover maybe especially important at these times (Krzysik 1994).

We used the same initialization maps for tortoise density and vegetation that we used for scenario 2 (Figs. 4 and 5a, respectively). Training occurred at each time step (monthly), but training intensity was moderate (832.5 TVD/month) during November–February and low (237.5 TVD/month) during March–October over all of Fort Irwin.

Our results indicated that the tortoise population asymptotically decreased and became very patchily distributed across the landscape (Fig. 11). The aerial cover of vegetation and habitat suitability also decreased (Fig. 12). These results were very similar to the results of scenario 3a (constant low intensity training) which suggested that tortoises and vegetation were able to withstand periodic moderate training, but not constant moderate training (see scenario 3b) throughout the year. The low level of training during March–October allowed the vegetation adequate time to recover, which indirectly allowed tortoise populations to remain stable. In short, seasonal military training caused the tortoise population to decline initially, but it stabilized after the first 50 years.

Scenario 5: Training varied spatially— In the previous scenarios, training occurred with similar intensity in all cells across Fort Irwin. However, training likely occurs at different intensities across the installation with approximately 64% of the total installation available for military training (Goran et al. 1983). In this scenario, we attempted to capture spatial variation in training intensity. Three training intensity levels were assumed to occur only in the lower elevations toward the center of our simulated landscape (Fig. 2b). No training occurred on the remaining portion of the landscape. The three levels of training intensity were low (237.5 TVD/month), moderate (832.5 TVD/month), and high (1428 TVD/month). We used the same initialization maps for tortoise density and vegetative cover that were used for Scenario 2 (Figs. 4 and 5a, respectively). Training occurred at each time step (i.e., monthly), and varied spatially based on the training map (Fig. 2b). We did not include temporal variation in this scenario.

Results of this scenario indicated that the tortoise population asymptotically decreased, but the amount of decline was much less than found in previous scenarios (Fig. 13). Spatially, tortoises did not occur where training occurred. Vegetation and habitat suitability also decreased (Fig. 14), but not to the same extent as found in previous scenarios. Both the vegetation and habitat suitability were impacted in areas where training occurred, but appeared to do well outside of those areas. This suggested that areas with suitable tortoise habitat which were restricted from training exercises supported tortoises for long periods of time.

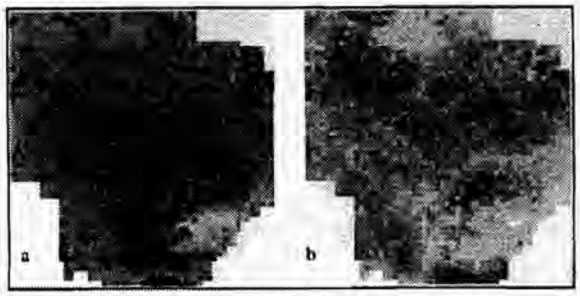

Fig. 12. The average percent aerial cover of vegetation (a) and average index of habitat suitability (b) for desert tortoises after running scenario 4 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 4. Figs. 5a and 6b show the average percent aerial cover of vegetation and index of habitat suitability, respectively, of time 0 for scenario 4. Temporal variation of training occurred during scenario 4. Darker shades represent higher densities of vegetative cover (a) and habitat better suited for tortoises (b).

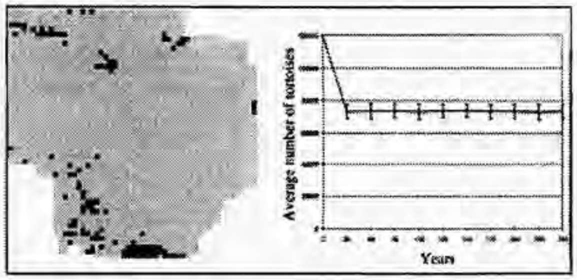

Fig. 13. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 5 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 5. Scenario 5 used Figs. 4 and 5a as initialization maps for tortoise density and vegetative cover, respectively. Spatial variation of training occurred during scenario 5. Darker shades represent higher tortoise densities.

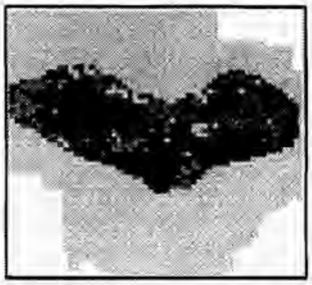

Fig. 15. The training intensity map for scenario 6, Fort Irwin, California. Training was excluded from the most lightly shaded areas. The moderately shaded areas were subject to low training intensity while the darkest areas indicated moderate training intensity.

Scenario 6: Training varied temporally and spatially— Realistically, military training at Fort Irwin likely occurs at different intensities over both time and space. To simulate such variation in intensity, we modified Scenario 5 to include only 2 training intensities (low and moderate) for each of the 2 seasons identified in Scenario 4 (Fig. 15). We used the same initialization maps for tortoise density and vegetative cover that were used for Scenario 2 (Figs. 4 and 5a, respectively). Thus, training occurred at each time step (i.e., monthly), but varied spatially.

Our results indicated that the tortoise population decreased, but not to the same extent as in previous scenarios (Fig 18). Spatially the tortoises did not occur where training occurred. Woodman et al. (1986) found high tortoise densities near areas with high training impacts, but each were spatially mutually exclusive. The aerial cover of vegetation and habitat suitability decreased in scenario 6, but not to the same extent as in previous scenarios (Fig. 17). Results of this scenario were very similar to those of Scenario 5, suggesting that the spatial variation in training intensity had a stronger influence on tortoise populations than did temporal variation. Thus, our model predicted that the effects of temporal and spatial variation in training intensity on tortoise population dynamics were not additive.

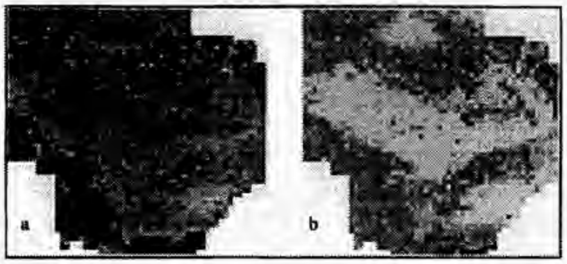

Fig. 14. The average percent aerial cover of vegetation (a) and average index of habitat suitability (b) for desert tortoises after running scenario 5 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 5. Figs. 5a and 6b show the average percent aerial cover of vegetation and index of habitat suitability, respectively, of time 0 for scenario 5. Spatial variation of training occurred during scenario 5. Darker shades represent higher densities of vegetative cover (a) and habitat better suited for tortoises (b).

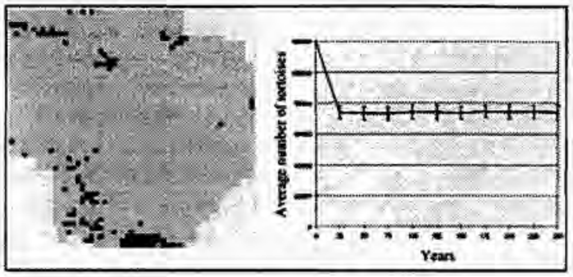

Fig. 16. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 6 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 6. Scenario 6 used Figs. 4 and 5a as initialization maps for tortoise density and vegetative cover, respectively. Spatial and temporal variation of training occurred during scenario 6. Darker shades represent higher tortoise densities.

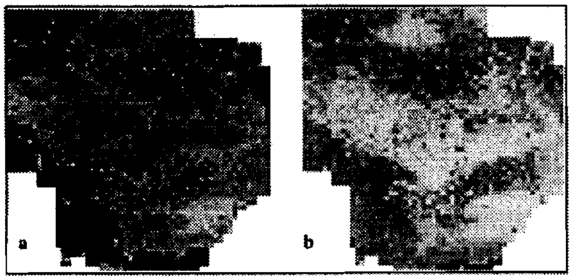

Fig. 17. The average percent aerial cover of vegetation (a) and average index of habitat suitability (b) for desert tortoises after running scenario 6 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 6. Figs. 5a and 6b show the average percent aerial cover of vegetation and index of habitat suitability, respectively, of time 0 for scenario 6. Spatial and temporal variation of training occurred during scenario 6. Darker shades represent higher densities of vegetative cover (a) and habitat better suited for tortoises (b).

Comparisons among scenarios 1–6— To compare the results of all scenarios, we determined the percent difference between the average tortoise population in year 250 for different pairs of scenarios (Table 1). Our results showed only a 2% difference between the final tortoise populations in scenarios 1 and 2, indicating that a steady state in the model was obtained at the end of Scenario 1 and maintained throughout Scenario 2. This suggested that the landscape had recovered from past impacts. Comparisons between the final tortoise population in Scenario 2 (no training) with scenarios 3–6 (with training) indicated that simulated military training impacted tortoise dynamics. However, some training scenarios impacted tortoises far more or less than others.

Table 1. Percent difference between the average desert tortoise population (females only) in year 250 for different pairs of scenarios run with the model, Fort Irwin, California. Scenarios are (1) neural network baseline, (2) new baseline, (3) low intensity training, (4) training varied temporally, (5) training varied spatially, and (6) training varied temporally and spatially.

Scenarios	2	3	4	5	6
1	+2	-78	-78	-39	-38
2		-78	-78	-40	-40
3			+1	+64	+64
4				+63	+64
5					+1

Our simulations indicated that low intensity training had a much smaller effect on the tortoise population than did moderate intensity training. Further, periodic moderate intensity training (Scenario 4) had similar effects to constant low intensity training (Scenario 3a), suggesting that timing of training can influence tortoise populations. Temporal variation in training intensity likely would have had even greater effects on tortoises if direct effects had been incorporated into the model, due to the seasonal differences in tortoise activities.

Spatial variation of training resulted in lower impact on the tortoise population than did most other scenarios. Scenario 6 represents the most realistic training scenario since it incorporates both timing and location of training. Results of this scenario indicated that impacts on tortoises may be minimized by altering the timing, location, and intensity of training. Additional data on patterns and timing of training are needed for future modeling efforts.

Scenario 7: Potential tortoise reintroduction— In this scenario, we used the model to determine if areas on Fort Irwin might serve as locations for potential reintroduction of tortoises. In all our previous scenarios, tortoises occur in certain areas of Fort Irwin, but not others. This pattern held throughout all simulations, perhaps, because of limited movement away from initial locations into suitable habitat. We wanted to determine if there were additional areas on the simulated landscape that were suitable for tortoises but remained unoccupied in previous scenarios.

We used the initialization map for vegetation from time 250 years of Scenario 1. Each cell across the Fort Irwin landscape was initialized with the maximum number of tortoises that occurred in Scenario 1 at 250 years (415 female tortoises/km^2). The total number of tortoises on Fort Irwin in this scenario was artificially high, but we wanted to see where on the landscape tortoises would occur after running the scenario for 250 years. We ran this simulation with no new training after time 0, allowing tortoises to move around on the landscape without any impacts from training.

Our results (Fig. 18) indicated a dramatic drop in the tortoise population in the first 25 years. Since

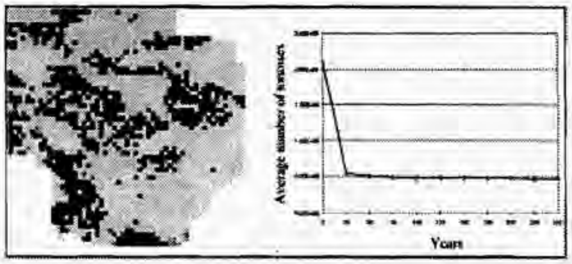

Fig. 18. The average spatial distribution of desert tortoises and the change in average number of desert tortoises after running scenario 7 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 7. Scenario 7 used Fig. 5a as the initialization map for vegetative cover. Each cell across the landscape was initialized with the maximum number of tortoises that occurred in scenario 1 at time 250 years. No new training occurred in the model after time step 0. Darker shades represent higher tortoise densities.

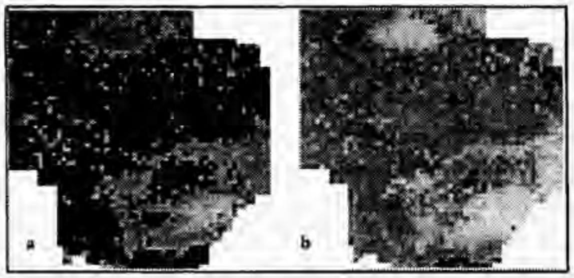

Fig. 19. The average percent aerial cover of vegetation (a) and average index of habitat suitability (b) for desert tortoises after running scenario 7 for 250 years at Fort Irwin, California. The average was obtained from 100 simulations of scenario 7. Figs. 5a and 6b show the average percent aerial cover of vegetation and index of habitat suitability, respectively, of time 0 for scenario 7. Darker shades represent higher densities of vegetative cover (a) and habitat better suited for tortoises (b).

there were no impacts incorporated into this scenario, the drop was attributed to an artificially large number of tortoises that the landscape could not support. After the initial drop, the population stabilized at a higher level than in previous scenarios. Comparison of these results (Fig. 18) with the results of Scenario 2 (Fig. 7) indicated areas in which tortoises could be supported, but do not currently occur. Thus, errors in the initialization map for tortoise density which was used to initialize the other scenarios may have influenced our results.

The vegetation and the habitat suitability index results (Fig. 19) were very similar to the results of scenario 2 (Fig. 8). This was expected since there was no new training after time 0.

Even though our model indicated potential reintroduction sites on Fort Irwin, additional criteria need to be considered prior to pursuing a tortoise reintroduction. Berry (1986) suggested that relocation sites should be at least 14 km in diameter to permit dispersal and introduction sites should be in areas where tortoises were recently extirpated to ensure suitable habitat exists. Further research is needed to determine if the areas indicated in our model meet these criteria.

DISCUSSION

Desert tortoises are a long-lived species with a low reproductive rate making them vulnerable to perturbation (Woodman et al. 1986). They are dependent on perennial shrubs for cover and burrow sites. Because tortoises are vulnerable to impacts on their environment, it is valuable to have a model that can gauge the effects of impacts on their population density and habitat.

We developed a dynamic landscape simulation (DLS) model to evaluate potential effects of military training on desert tortoises and their habitat at Fort Irwin, California. While we did not expect results to provide land managers with detailed predictions of specific impacts, we wanted to demonstrate the feasibility of using this modeling technique to develop landscape-level simulation models.

We believe DLS models are applicable to the management of threatened and endangered species. Often, a major factor in a species decline is habitat loss and fragmentation over the species range. DLS models developed at the landscape-level could provide new management techniques for threatened and endangered species survival. Our modeling approach (developing a single-cell model, initializing it with GIS maps and then running the model to simulate changes across the landscape) proved successful for desert tortoises at Fort Irwin. We believe this approach can be used to develop future, realistic models for other species and landscapes.

While models can aid in the synthesis of many parts into a whole, modeling cannot be substituted for field experimentation (Salwasser 1986, Conroy et al. 1995). Future model development should include obtaining more accurate tortoise dispersal and military training data. Furthermore, additional simulation scenarios could be conducted to determine if there are optimal spatial and temporal patterns for different levels of military training, which will minimize impacts on tortoises and vegetation.

Land managers must not expect models to make decisions for them or to provide them with a perfect version of a real-world system (Chalk 1986). For modeling technology to reach its full potential in threatened and endangered species management, researchers and managers must work together. This will aid researchers in understanding the needs of managers and will provide managers with a sense of ownership in the models they use (Chalk 1986).

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Competition Between *Bromus madritensis rubens* and Native Desert Annuals in the Northern Mojave Desert

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Abstract— ***Bromus madritensis rubens*** **invaded the Mojave Desert in the early 1900's and now dominates the winter annual population through much of the middle elevations. On the Nevada Test Site two *Bromus* removal experiments were performed to see if native species' populations would rebound. In the first experiment, when *Bromus* was selectively harvested from small quadrats early in the growing season, the native annual average weight was increased, but not to a statistically significant degree. There was no effect in the succeeding year. In the second experiment, 100 m^2 plots were sprayed with a grass-specific herbicide (fluazifop) where *Bromus* was dense. Again, native population densities increased where Bromus was reduced, but results were not statistically significant for several years. In three plots the weight of natives per square meter increased significantly in one, the density of natives increased in two, and number of species per quadrat increased significantly in two. The high spatial and temporal variability of native annual populations was a serious impediment to demonstrating that *Bromus* was reducing native populations. However, certain species appeared more severely affected. In shaded conditions under shrubs *Cryptantha pterocarya* and *Phacelia vallis-mortae* seemed more seriously inhibited. Larger annual species increased on sprayed plots, and may (as *Bromus*) require the more fertile soil under shrubs to mature. Those species included *Rafinesquia neomexicana, Chaenactis stevioides* and *Malacothrix glabrata.* Future experiments should focus on particular species, in particular habitats, and should continue for long time periods.**

Bromus madritensis rubens is a weedy grass introduced into the Pacific Northwest (Hickman 1993), probably early in the nineteenth century. It invaded the Mojave Desert in the early twentieth century (Hunter 1991). It thrives in the somewhat richer soils and shadier habitats under shrubs in the Mojave Desert, and where present it makes up a large portion of the winter annual populations (Brooks 1997). It does not dominate on sandy soils or lower elevations, where another introduced grass, *Schismus arabicus*, is similarly abundant (Brooks 1997). Because *Bromus madritensis rubens* grows in high densities the question naturally arises, does it affect the growth and survival of the many native winter annual species which have similar habits?

Winter annuals in the northern Mojave Desert germinate with rains between October and February and flower and fruit from mid-March through early May. Impressive displays of wildflowers result from rains totaling about 25 mm in October, given moderate rains through the rest of winter (Beatley 1974). Those conditions occurred on the Nevada Test Site in 1967 and 1973, but not since. Nevertheless, some winter annuals grow nearly every year, and populations vary greatly with germination conditions and total rainfall (Tevis 1958a, b).

Mojave Desert annual populations have been studied by several researchers, notably Frits Went in the 1930's, 40s and 50's, primarily in Joshua Tree and Death Valley National Monuments (Went 1942, 1948, 1949; Went and Westergaard 1949; Juhren et al. 1956); Janice Beatley in the 1960s and early 1970s on the Nevada Test Site (Beatley 1966a, 1966b, 1967, 1969a, 1969b) ; and T. L. Ackerman during International Biological Program studies at Rock Valley on the Nevada Test Site from 1970 through 1976 (Turner 1972, 1973, 1975, 1976; Turner and McBrayer 1974). I monitored annual plant populations on the NTS from 1987 through 1994 (Hunter and Medica 1989; Hunter 1994a, b, c, 1995) as part of a biological monitoring program supported by the U.S. Department of Energy. A number of other researchers have made observations on desert annuals for short periods on other sites, often in studies on animal diets (e.g. Tevis 1958c; Ohmart 1980; Karl 1981; Knight 1983).

Interpreting the available historical data is difficult, as researchers worked generally in different locations, with different techniques, and, most importantly, with constantly varying weather. Winter annuals as a group vary from zero density in some years to high densities following a series of good years. A wet spring following several years of drought may result in low densities but unusually good growth (Turner and McBrayer 1974). Germination conditions can favor different species in different years, depending on temperatures and timing of precipitation (Juhren et al. 1956). Species richness varies with size of study area(s) and the environmental complexity. For example, on the IBP Validation Site Zone 20 in Rock Valley, an area of about .46 km^2, Ackerman found about 55 species in 1973. During BECAMP studies in 1993 we found 33 species on a 0.001 km^2 area. Beatley's data are from sampled areas totaling 5 m^2, inside a 100 X 100 foot plot (929 m^2). These differences in weather, techniques, and study site combine to make comparisons of winter annual population data very complex.

Given these complexities, it was not possible to clearly associate historical changes in annual populations with a particular cause, such as competition by *Bromus*. We therefore attempted to examine this competition on small areas, using *Bromus* removal as an experimental manipulation.

MATERIALS AND METHODS

Work was done on the Nevada Test site, an area of approximately 3500 km^2 in southern Nevada. Considerable historical work was done in Rock Valley (116° 5′ W long., 36° 45′ N lat.), hence studies were begun in that valley in 1984. Twenty *Larrea tridentata* shrubs in a small area of Rock Valley between plots C and D (French et al. 1974) were selected. The locations were chosen to have significant *Bromus madritensis rubens* densities and convenient access to the shaded north side of the shrub. Small metal stakes were used to mark two corners of 25 x 25 cm quadrats under the north side of the shrub. Another quadrat was placed in the center of the nearest bare area between shrubs. On January 6, 1984 all *Bromus* were pulled by hand from ten randomly selected shrub and the paired bare quadrats, leaving any native species. On April 16th and 17th the quadrats were revisited, and native annuals and any remaining or newly germinated *Bromus* were harvested. Harvested annuals were placed in small paper envelopes and allowed to air dry, then weighed. The same quadrats were harvested again April 25, 1985, without removing the *Bromus* early in the growing season. The object in 1984 was to determine if native annual sizes increased in the absence of *Bromus*, and in 1985 to see if the 1984 harvest reduced *Bromus* or increased native species' populations the succeeding year. The treatment was applied only one year because the quadrats were thought to have a large edge effect, i.e. the dense *Bromus* at the quadrat edges was thought to be competing with the natives inside.

The second experiment was begun in 1989. Four pairs of circular 100 m^2 plots were marked with lawn flashing, leaving one to five meters between the two plots. One pair was in Rock Valley about 20 meters from Beatley's plot 3 (116° 11.32′ W, 36° 41.2′ N); one was in West Mercury Valley on an area cleared of shrubs by burrowing rodents (gophers and kangaroo rats primarily) (116° 7.2′ W, 36° 38.1′ N); one was in Frenchman Flat near Beatley Plot 23 (115° 59.2′ W, 36° 48.8′ N); and one in Yucca Flat near the BECAMP YUF001 baseline plot and Beatley Plot 46 (116° 5.0′ W, 37° 0.0′ N).

The Rock Valley and Yucca Flat sites were similar. Both were of loamy-rocky soils with mature shrub populations. *Bromus* was concentrated at the edges of low shrubs with reduced populations of smaller plants in the open, desert pavement areas.

Mercury Valley soils were loamy, but the site was disturbed by burrowing animals and soils were uniform and thoroughly mixed. *Bromus madritensis rubens* was denser under the sparse suffrutescent shrubs occupying the site. In years of sufficient rainfall *Bromus* was spread densely across the whole plot, not just shaded areas. In Frenchman Flat, which had sandy soil, the sparse *Bromus* was primarily associated with shade on the north sides of the creosotebushes (*Larrea tridentata*).

There were too few winter annuals to spray until 1992, when one randomly selected plot of each pair was sprayed in early March with the grass-specific herbicide Ornamec® (fluazifop-P-butyl(R)-2[4[[5-triflouromethyl-2-pyridinyl]oxy]phenoxy-propanoate]) where *Bromus* concentrations were significant, i.e. primarily at the edges of shrub canopies. In 1993 the Rock Valley and Yucca Flat plots were sprayed similarly (March 22), and the Frenchman Flat plot was hand weeded (20 *Bromus* were found). The Mercury Valley plot was not sprayed in 1993, as it was erroneously expected to have a low density based on 1992 results. In 1994 the Mercury Valley and Rock Valley Plots were sprayed

March 14, and the Frenchman Flat plot again hand-weeded.

Annuals were censused by harvest from 20 0.025 m^2 randomly placed quadrats. All included annuals were harvested, separated by species, dried and weighed. In 1994, 25 random quadrats were harvested. The Rock Valley and Yucca Flat plots were censused in May 1995 with 25 quadrats, and the Mercury Valley plot with 10 quadrats. After harvesting the quadrats, the whole 100 m^2 area was examined, and a rough tally was made for species not recorded in the quadrats. (Because only the larger plants were seen on those searches, the data are not a good indicator of actual density, but indicate rough proportions of the larger members of the population.) If plants were randomly distributed the minimum detectable density in quadrats would have been 2.0 per m^2 (1.6/m^2 with 25 quadrats).

Results

Harvested Bromus— Harvesting *Bromus madritensis rubens* from quadrats in early January 1984 resulted in a reduced density of *Bromus* and a reduced size per plant of the remaining *Bromus* (Table 1). The presence of *Bromus* in all of the harvested quadrats indicated that new plants germinated after January 6 and before the April 16 census. Density under shrubs was reduced by harvest from 1109/m^2 to 189/m^2. However, final density of natives under shrubs was just 34/m^2 in both harvested and control quadrats, so *Bromus* still dominated the harvested quadrats. In open areas harvest did not affect final density. The sum of January (harvested) plus April densities on harvested bare quadrats averaged 130±9/m^2 (95% confidence limits), but final densities were 46±4 on harvested and 42±4 on controls, indicating either new germination on harvested quadrats, mortality on control quadrats, or both.

Bromus weight per plant was significantly reduced under shrubs by harvest, from 24 down to 11 mg ($P<0.001$, Mann Whitney Test), suggesting the later-germinating plants had less time to grow. There was no significant difference in bare quadrats, though *Bromus* weight per plant averaged slightly lower on harvested quadrats (9 vs 12 mg).

Density of all native species was low on all quadrats, and did not differ between *Bromus*-harvested and control quadrats, either under shrubs or in the open. Weights per plant were highly variable, partly due to the species mix and partly to normal variation within species. The most common harvested species, *Chorizanthe brevicornu*, occupied six of 20 harvested quadrats (3 each bare and under shrubs), and 4 of 20 control quadrats. Although weights per plant were somewhat higher on harvested quadrats under shrubs than in bare quadrats, when pooling all native species, the effect was marginally non-significant ($P<0.10$, Mann Whitney).

The same quadrats, when censused in 1985, showed no effects of the 1984 harvest. There were

Table 1. Densities of *Bromus madritensis rubens* and pooled native species on harvested and control quadrats in Rock Valley, 1984. *Bromus* was harvested January 6, and all plants present were harvested and weighed (dry, by species) in April.

	HARVESTED				CONTROL			
	SHRUB		BARE		SHRUB		BARE	
	Jan 6	Apr 16	Jan 6	Apr 16	Jan 6	Apr 16	Jan 6	Apr 16
Densities, n/m^2 ± 95% CL								
Bromus	1461±74	189±7	130±9	46±4	1417±42	1109±40	50±3	42±4
Natives	–	34±2	–	10±1	–	34±2	–	18±2
***Pectocarya* spp.**	–	5±2	–	6±1	–	16±5	–	11±5
Dry Weights per plant, mg ± 95% CL (n)								
Bromus		11.4±3.7		9.0±4.8		23.6±5.3		11.7±5.3
All Natives		279±303		88±75		41±26		70±67
***Pectocarya* spp.**	–	35±10 (4)	–	99±60 (4)	–	21±16 (5)	–	113±164 (2)

Table 2. Densities and weights per plant in 1985 on Rock Valley quadrats harvested in 1984 and control quadrats for *Bromus madritensis rubens* and pooled native species.

	SHRUB		**BARE**	
	Harvested	**Control**	**Hervested**	**Control**
Densities, n/m^2 ± 95% CL				
Bromus rubens	544 ± 283	474 ± 251	43 ± 18	37 ± 14
All natives	168 ± 70	173 ± 104	118 ± 80	75 ± 51
Dry Weights per plant, mg ± 95% CL				
Bromus rubens	30 ± 8	33 ± 14	15 ± 7	9 ± 5
All natives	26 ± 22	17± 9	4 ± 2	12 ± 7

no differences between *Bromus* densities on the harvested versus control quadrats, nor was there a difference in size of the native plants inhabiting the harvested quadrats (Table 2).

Herbicide Plots: Bromus *population fluctuations*— Results on the four herbicide treated plots were different at each location, and quite complex. First, it must be noted that the first two years of the herbicide study were affected by a severe drought, in which almost no winter annuals germinated below 5000 feet elevation (Hunter 1994a). During this time seeds were exposed to high surface temperatures and the absence of surface cover led in sandy areas to some surface ablation and deposition under shrubs. An idea of the natural *Bromus* population fluctuations during the period of study can be seen in Table 3, results of monitoring on plots within 100 m of the four herbicide-treated plots.

The primary factor influencing *Bromus madritensis rubens* population density was clearly rainfall, i.e. germination conditions. The three sites with large populations varied in concert with precipitation, though only in Rock Valley were densities significantly linearly correlated with rainfall (n=6, r=0.84, $p<0.05$, F test). After the severe drought of 1989–1990, however, there was evidence the seed banks were reduced. Thus, the 1992 populations with 200 mm of rain were much lower than the 1987 populations with 136 mm, and the 1993 populations with 257 mm were below the 1988 values with 203 mm.

Biomass patterns were similar (Table 4), though biomass correlated somewhat better with rainfall than did average densities. Linear correlations between biomass and rainfall were significant in both Rock Valley and Mercury valley ($p<0.05$). (Correlations were done with local rainfall, not presented here.) Note that in Frenchman Flat neither population densities nor biomass production recovered to 1988 levels following the drought (Tables 3, 4). In the other three valleys population and biomass recovered to 1988 values by 1995.

Seed production may be estimated from a regression line reported for *Bromus madritensis rubens* in Hunter (1995) (seeds/m^2 =533 X g/m^2 + 2.22). In some cases it is clear that seed production could not account for the following year's density of *Bromus*. Examples are the jumps in Rock Valley from 1991 to 1992, and 1994 to 1995, and the jump in Mercury Valley from 1992 to 1993 (Tables 3,4).

Table 3. *Bromus madritensis rubens* population fluctuations (n/m^2 ± 2SE) and precipitation (Rock Valley, September - April, mm) at four monitoring sites adjacent to the four herbicide-treated/control plot pairs, 1987 through 1995. * = data from herbicide control plots.

Year	Precipitation	Rock Valley	Yucca Flat	Frenchman Flat	Mercury Valley
1987	136	754 ± 596	–	48 ± 70	–
1988	203	2034 ± 1264	1872 ± 1112	258 ± 300	3550 ± 732
1989	18	0	0	0	0
1990	31	16 ± 32	0	0	4 ± 4
1991	83	60 ± 40	64 ± 70	2 ± 4	52 ± 36
1992	200	294 ± 227	106 ± 111	2 ± 4	76 ± 62*
1993	257	1964 ± 1027	884 ± 472	26 ± 27	3104 ± 2638*
1994	64	40 ± 46	106 ± 94	8 ± 9	414 ± 323*
1995	238	1173 ± 338*	742 ± 331*	–	568 ± 369*

Table 4. *Bromus madritensis rubens* biomass fluctuations (g/m^2 ± 2SE) and precipitation (Rock Valley, September - April, mm) at four sites adjacent to the four herbicide treated plots, 1987 through 1995. * = data from herbicide control plots.

Year	Precipitation	Rock Valley	Yucca Flat	Frenchman Flat	Mercury Valley
1987	136	17 ± 10	–	1.7 ± 2.6	–
1988	203	34 ± 16	18 ± 8	13 ± 12	20 ± 12
1989	18	0	0	0	0
1990	31	0.06 ± .06	0	0	0.04 ± .04
1991	83	0.28 ± .22	.4 ± .6	0.02 ± .02	.32 ± .26
1992	200	13 ± 10	16 ± 21	0.02 ± .04	18 ± 18*
1993	257	68 ± 35	11 ± 6	0.17 ± .18	83 ± 35*
1994	64	0.17 ± .18	1.5 ± 1.5	0.11 ± .14	8.1 ± 4.9*
1995	2238	38 ± 15*	37 ± 21*	–	41 ± 26*

In these cases it was clearly germination conditions rather than seed production controlling the measured populations. In Rock Valley, Yucca Flat and Mercury Valley the 1992 populations must be attributed to seed surviving from 1988. In Frenchman Flat the seed bank declined significantly during the drought period, and did not recover during the study.

Effects of herbicide on Bromus— Densities and biomass of *Bromus madritensis rubens* were generally reduced 80 to 90% on sprayed plots in the year sprayed (Table 5). In the final years, when no control measures were applied, some residual effect was seen in Rock Valley and Yucca Flat, i.e. numbers and biomass were lower on previously sprayed plots. However, in Mercury Valley, where the herbicide was used only in two low-density years, the carryover effect was negligible on density (-28%, not significant), and absent on biomass. In Frenchman Flat densities following the 1989–90 drought never recovered, and though *Bromus* densities and biomass were totally eliminated by hand harvesting in 1992 and 1993, there was no residual effect in 1994. The Frenchman Flat plots were not censused in 1995, but numbers on the harvested plot were visually estimated as ~300 (i.e. 3/m^2). On the control plot *Bromus* was described as "much thicker", suggesting the plots had recovered to predrought densities, but were still much lower than in the other three Valleys (Table 3).

Effects on native species— Effects of the herbicide treatment on native species were quite complex, and varied with location. When native species were considered together, statistically significant differences between sprayed and control plots were just beginning to appear in the final years of the experiment (Table 6). In 1994 density and biomass of natives were significantly higher on the Yucca Flat sprayed plot. In 1995 average native densities were significantly higher on the Yucca Flat and Mercury Valley plots, biomass of natives was significantly higher on the Yucca Flat plot, and species per 0.025 m^2 quadrat were significantly higher in Rock Valley and Mercury Valley ($P<0.05$, t-test). However, over all years from commencement of spraying through 1995 average densities of native species were higher than controls in 14 of 15 instances, and equal in the fifteenth (significant at $P<0.01$, sign test). For biomass 10 of 13 plot averages were greater on the sprayed plots ($P<0.10$, sign test).

Effects on individual Species— Natives as a group were generally more numerous on sprayed plots, but what of the individual species? There were some that appeared in the quadrat data to be significantly increased as a result of the herbicide treatments.

Rock Valley— In Rock Valley there were two species which in 1995 were significantly ($P<0.05$, t-test) more numerous on the sprayed plot, *Phacelia vallis-mortae* (Table 7) and *Cryptantha pterocarya* (Table 8). Both species tend to grow in the fertile soil on mounds under shrubs. *Phacelia vallis-mortae* often twines among the branches of the covering shrub and its light violet flowers often appear at the top of the shrub canopy. On April 29, 1995 quick counts of open flowers were made on the sprayed plot (91) and control (52).

Besides the apparently positive population growth of *C. pterocarya*, its fruits were sometimes misshapen on the sprayed plots, which was tentatively considered a response to the herbicide.

Table 5. Densities and biomass of *Bromus madritensis rubens* populations on sprayed and control plots in four locations on the Nevada Test Site. * indicates plots were sprayed in early March with a grass-specific fluazifop herbicide, Ornamec®.

	Density, n/m²			Biomass, g/m²		
	sprayed	control	% reduction	sprayed	control	% reduction
			Rock Valley			
1991	88 ± 60	104 ± 59	–	1.4 ± 1.2	2.6 ± 2.4	–
1992*	44 ± 37	393 ± 122	-89%	4.0 ± 4.6	32 ± 24	-87%
1993*	672 ± 221	4538 ± 1673	-85%	8.5 ± 2.7	65 ± 21	-87%
1994*	13 ± 11	134 ± 47	-90%	0.07 ± 0.10	1.0 ± 0.5	-93%
1995	306 ± 95	1173 ± 338	-74%	11 ± 4	38 ± 15	-70%
			Yucca Flat			
1991	42 ± 34	8 ± 10		1.3 ± 1.0	0.1 ± 0.2	
1992*	8 ± 13	114 ± 89	-93%	1.3 ± 2.0	16 ± 15	-92%
1993*	94 ± 59	702 ± 468	-87%	3.5 ± 4.3	26 ± 20	-87%
1994*	29 ± 32	184 ± 138	-84%	0.7 ± 0.7	2.9 ± 2.5	-76%
1995	98 ± 73	742 ± 330	-87%	5.3 ± 4.0	37 ± 21	-86%
			Mercury Valley			
1991	16 ± 12	8 ± 9		0.9 ± 0.8	0.1 ± 0.2	
1992*	13 ± 9	76 ± 62	-83%	1.7 ± 1.5	18 ± 18	-91%
1993	3080 ± 3006	3104 ± 2638	(-1%)	77 ± 60	83 ± 35	(-7%)
1994*	128 ± 52	205 ± 72	-38%	2.0 ± 1.8	8.1 ± 4.9	-75%
1995	808 ± 202	1116 ± 318	(-28%)	41 ± 8	41 ± 26	(0)
			Frenchman Flat			
1991	0	0		0	0	
1992*	0	8 ± 8	-100%	0	0.9 ± 1.8	-100%
1993*	0	24 ± 44	-100%	0	0.1 ± 0.2	-100%
1994	3 ± 4	2 ± 2		0.0 ± 0.1	0.1 ± 0.2	

One species, the diminutive native grass *Vulpia octoflora*, responded negatively to the herbicide in Rock Valley (Table 9). This was presumably an effect of the herbicide.

Several other species appeared to be increasing on the sprayed plot in Rock Valley, but could not be statistically shown to have done so. On the sprayed plot the short-lived perennial *Eriogonum inflatum* was present in the shrub interspaces on the sprayed plot. The quadrat data, though not statistically significant, suggested an increase on the sprayed plot (Table 10). In 1994 a search of the whole plots found 57 live *E. inflatum* (plus one dead) on the sprayed plot and one live (plus 20 dead) on the control. In 1995, after censusing the quadrats, the *Eriogonum inflatum* with fruit stalks on the whole 100 m² area were counted. There were twelve on the sprayed plot, and none on the control.

There was a concentration of the rather showy aster *Rafinesquia neomexicana* under one shrub on the sprayed plot. On April 29, 1995 there were 13 plants on the 100 m² sprayed plot and only one on the control. In quadrats three were harvested from the control plot weighing 33, 16, and 27 mg. Two were harvested in sprayed quadrats, weighing 14 and 402 mg. Their average weight of 208 mg/plant on the sprayed plot was the highest for any species, the next highest being 71 mg/plant for 3 *Amsinckia tessellata*. In addition, on May 10, 1998

Table 6. Pooled native winter annual species' densities (n/m^2), biomass (g/m^2) and species richness (species per quadrat) on sprayed and control plots, 1991–1995. Pairs marked with an asterisk (*) are significantly different (P<.05) by t-test.

	Density		**Biomass**		**Species/0.025m^2 quadrat**	
	Sprayed	Control	Sprayed	Control	Sprayed	Control
			Rock Valley			
1991	30±24	82±43	0.7±0.5	3±2	–	–
1992	253±179	200±231	54±37	14±20	–	–
1993	532±206	355±252	8±7	2±1	4.1±0.6	2.2±.5
1994	5±5	3±4	–	0.01±0.01	0.3±0.2	0.9±0.2
1995	782±266	650±247	17±6	14±9	**5.1±0.8***	**3.7±0.7***
			Yucca Flat			
1991	6±9	8±9	0.4±0.5	0.9±0.9	–	–
1992	64±33	31±37	28±20	3±4	–	–
1993	668±196	532±153	18±8	10±3	4.6±0.8	6.0±1.1
1994	13±9	6±6	0.09±0.07	0.12±0.13	0.6±0.4	0.8±0.2
1995	**930±207***	**611±180***	**26±8***	**13±4***	5.0±0.8	4.4±1.0
			Mercury Valley			
1991	69±31	70±31	5±3	1.7±0.5	–	–
1992	212±76	149±73	26±22	21±14	–	–
1993	1796±598	1692±778	67±26	75±61	–	–
1994	**205±72***	**67±22***	4.4±2.2	2.3±1.5	2.6±0.6	1.8±0.4
1995	1116±318	696±174	69±42	49±16	6.8±1.3	4.6±1.0
			Frenchman Flat			
1991	6±6	2±4	0.9±0.4	0.1±0.1	–	–
1992	141±79	118±42	8±7	20±13	–	–
1993	898±279	804±239	57±99	8±4	3.2±0.8	3.4±0.7
1994	2±3	2±3	0.01±0.02	0.01±0.01	0.12±0.13	0.08±0.11

Table 7. Densities of *Phacelia vallis-mortae* on the Rock Valley herbicide plot and the adjacent baseline study plot, 1991 - 1995. * indicates years herbicide was applied in early March. **Bold** indicates pairs significantly different by t-test (P<0.05).

Year	Sprayed Plot	Control Plot	Baseline
1991	0	2±2	0
1992*	>0.01	2±4	>0.01
1993*	44±88	2±4	4±5.5
1994*	0	0	0
1995	**42±32**	**3±6**	–

Table 8. Densities (n/m^2) of *Cryptantha pterocarya* on the Rock Valley herbicide plot and the adjacent baseline study plot, 1991 - 1995. * indicates years herbicide was applied in early March. **Bold** indicates pairs significantly different by t-test (P<0.05).

Year	Sprayed Plot	Control Plot	Baseline
1991	0	0	>0.01
1992*	6±9	0	2±4
1993*	68±64	>0.01	12±14
1994*	>0.01	0	0
1995	**38±27**	**6±8**	–

Table 9. Densities (n/m^2) of *Vulpia octoflora* on the Rock Valley herbicide plot and the adjacent baseline study plot, 1991 - 1995. * indicates years herbicide was applied in early March. **Bold** indicates pairs significantly different by t-test (P<0.05).

Year	Sprayed Plot	Control Plot	Baseline
1991	14±11	34±12	30±13
1992*	21±18	53±41	16±11
1993*	178±96	277±215	74±53
1994*	0	1.6±3.2	0
1995	**29±22**	**293±178**	–

Table 10. Densities (n/m^2) of *Eriogonum inflatum* on the Rock Valley herbicide plot and the adjacent baseline study plot, 1991 - 1995. * indicates years herbicide was applied in early March.

Year	Sprayed Plot	Control Plot	Baseline
1991	0	0	>0.01
1992*	>0.01	0	>0.001
1993*	>0.01	0	>0.001
1994*	5±5	>0.01	–0.02
1995	30±43	2±3	–

developing fruit heads were counted for *Rafinesquia* on the two plots. There were 25 on the sprayed plot (15 under one shrub), and 6 on the control. We suspected *R. neomexicana* was increasing on the sprayed plot, but this was not apparent in the quadrat data (densities were 3.2±4.4 sprayed, 4.8±5.3 control).

Amsinckia tessellata, another species growing around the edges of shrubs, where *Bromus* thrives, was more numerous on the sprayed plot. It was censused in one quadrat (3 plants) on the sprayed plot, none on the control. A quick search of the 100 m^2 areas gave 27 on the sprayed plot, and one on the control.

Finally, another species found under shrubs, *Caulanthus cooperi*, was present in two quadrats (1 plant each, 3.2±4.4/m^2) on the sprayed plot in 1995. It had not appeared in quadrats throughout the experiment, though it was seen on 100 m^2 areas (sprayed, control, and baseline plots) in 1992. This species was present in the wet spring of 1973 at 1.62/m^2 on the IBP Validation site plot (Zone 20), and at lower densities in Beatley's plot 3 in 1968, 1969 and 1971. This rather cryptic, shade-adapted species is difficult to count outside the quadrats, hence the available data are merely suggestive.

Twenty of 26 native species found on the sprayed plot had higher average densities than on the control (P<0.01, sign test). Those with more than twice the control quadrat population included *Amsinckia tessellata* (3 vs 0), *Cryptantha circumscissa* (7 vs 2), *C. nevadensis* (11 vs 1), *C. pterocarya* (24 vs 4), *C. recurvata* (24 vs 2), *Pectocarya heterocarpa* (129 vs 56), and *Phacelia fremontii* (81 vs 18). Those with less than half the control population included *Caulanthus lasiophyllus* (2 vs 18), *Eriogonum trichopes* (3 vs 17), and *Vulpia octoflora* (18 vs 183, see Table 10). These ratios were not statistically significant, with the exception of that for *V. octoflora*.

Yucca Flat— The Yucca Flat plot was superficially similar to the Rock Valley plot, but the response of the winter annual community was considerably different. One species, *Chaenactis stevioides*, increased strongly enough on the sprayed plot to be statistically significant (Table 11). In 1995 *C. stevioides* made up more than half the total native population, in terms of both numbers and biomass. It made up 49% of the total annual population, including *Bromus madritensis rubens* and a low density of *Bromus tectorum*. It occurred in 24 of the 25 sprayed quadrats and 19 of 25 control quadrats.

Of the 25 species of native annuals on the two plots, 15 were less dense on the sprayed plot (not significant, sign test). Those with at least twice the control population in sprayed quadrats included *Camissonia kernensis* (4 vs 0), *Ipomopsis polycladon* (26 vs 8), *Lepidium lasiocarpum* (56 vs 19), and *Malacothrix glabrata* (7 vs 1). Those with less than half the control population included *Phacelia fremontii* (8 vs 55) and *Cryptantha nevadensis* (7 vs 22).

Malacothrix glabrata, a yellow aster, appeared visually to be much more prominent on the sprayed plot, but did not increase strongly in density (Table 12). Open flowers were counted during the censuses in both 1993 and 1995. In 1993 there were 330 open flowers on the sprayed plot, and 38 on the control. In 1995 there were 311 and 51, respectively. Average size of the plants in 4 censused quadrats on the sprayed plot was 52 ± 29 mg (2 se), and the one censused control plant weighed 16 mg (1995).

Because of the response of *Phacelia vallis-mortae* in Rock Valley it was purposely looked for on the Yucca Flat plot. On the sprayed plot 14 were found, 12 under one *Lycium andersonii* and one each under an *Ephedra nevadensis* and a *Grayia spinosa*. On

Table 11. Densities (n/m^2) of *Chaenactis stevioides* on the Yucca Flat herbicide plot and the adjacent baseline study plot, 1991 - 1995. * indicates years herbicide was applied in early March. **Bold** indicates pairs significantly different by t-test (P<0.01).

Year	Sprayed Plot	Control Plot	Baseline
1991	2±2	2±2	2±2
1992*	4±6	>0.01	2±4
1993*	**310±157**	**56±24**	290±135
1994*	3±6	0	2±4
1995	**499±139**	**82±38**	–

Table 12. Densities (n/m^2) of *Malacothrix glabrata* on the Yucca Flat herbicide plot and the adjacent baseline study plot, 1991 - 1995. * indicates years herbicide was applied in early March. There were no significant differences at P = 0.05.

Year	Sprayed Plot	Control Plot	Baseline
1991	–	–	>0.01
1992*	4±8	>0.01	>0.01
1993*	6±9	>0.01	6±7
1994*	2±3	0	>0.001
1995	11±12	2±3	–

the control plot four were found, three under a *Lycium* and one under an *Ephedra*.

Amsinckia tessellata behaved similarly. There were an estimated 50–100 on a single mound on the sprayed plot, and about 5 on the rest of the plot. On the control plot three scattered plants were found.

A note on the May 10, 1995 control plot data sheets read "Veg looks dryer here!" suggesting that the *Bromus* populations may have dried the soil there faster than on the adjacent sprayed plot.

Mercury Valley— Bromus was poorly controlled on the Mercury Valley plot, and it is difficult to attribute differences in annual populations to the treatment. Ironically, the one native species that did much better on the sprayed plot was the grass *Vulpia octoflora* (Table 13).

Of nineteen native species in 1995, 14 were denser on the sprayed plot and one was equal in density on both (P<0.05, sign test). No one species was significantly more dense by the t-test.

DISCUSSION

Interpretation of these results is complicated. Each of the four locations differed in the population dynamics of *Bromus madritensis rubens* and the effects of *Bromus* removal on the native species. Our interpretations are as follows:

1) In Frenchman Flat the *Bromus* populations failed to recover after the drought of 1989–1990. The densities were so low as not to significantly compete with native species. The hand removal of the few *Bromus* plants from this plot had no discernible effect on any species but *Bromus madritensis rubens* (Tables 3–6).

2) In Mercury Valley the turnover of soil by animals, and the near absence of shrubs greatly changed the ecology (there were scattered *Stanleya pinnata*, small suffrutescent shrubs). Most annual plants were therefore not shaded, and the dense concentrations of *Bromus* usually sprayed were not as large a portion of the population. In addition, the buried *Bromus* seed apparently weathered the drought well, and germinated profusely all over the plot in 1993 and 1995, when they were not sprayed. The result was poor control of the *Bromus* population, and hence no reason to expect effects on the native species.

The observation that in sprayed years *Vulpia octoflora* appeared to have greater populations on the sprayed Mercury plots (Table 13) is awkward. In Rock Valley it was reduced significantly on the sprayed plots, presumably due to the grass-specific herbicide (Table 9). I hypothesize the contradictory effects were a distribution phenomenon. On the Mercury plot *Vulpia* grew all over the plot, hence mostly in open areas, while in dry years the larger *Bromus* plants were primarily under shrubs. The herbicide was spot-sprayed on the denser *Bromus* clusters, missing most of the *Vulpia*, but removing its competitor. In Rock Valley the open areas were of desert pavement, largely without *Vulpia*. Therefore, in Mercury most Vulpia went unsprayed, whereas in Rock Valley they were sprayed because they were primarily under shrubs, mixed with *Bromus*. Since *Vulpia* accounted for a large portion of the native population in Mercury (Tables 6,13), it was largely responsible for the significant t-test in 1994 on that plot (Table 6).

3) Rock Valley had the most interesting response to the herbicide. As noted above, 20 of the 26 native species had higher density in 1995 on the sprayed plot. This was the expected response, and indicated a repression of the native populations by the high densities of *Bromus*. However, the response

Table 13. Densities (n/m^2) of *Vulpia octoflora* on the Mercury Valley herbicide plot and the adjacent control plot, 1991 - 1995. This plot was on a disturbed area with few woody perennials and soil turned over by animals. * indicates years herbicide was applied in early March. Shading indicates pairs significantly different by t-test ($P<0.05$).

Year	Sprayed Plot	Control Plot
1991	8±4	2±2
1992*	**55±34**	**4±6**
1993	984±508	356±559
1994*	**110±61**	**5±7**
1995	348±207	72±43

was not simply to increase the densities of native species. Certain species appeared to be favored, particularly those that grow preferentially on the "fertile islands" under shrubs. These were not the most common species when spraying began, and they were not expected to be the responding species. The census technique – using small, numerous quadrats – was aimed at the small, more evenly distributed species like *Vulpia octoflora,* the *Pectocarya* species, *Chorizanthe brevicornu,* and *Cryptantha* species. It was only in the later years, when the larger flowered species began to appear affected, that we began seriously trying to estimate their success.

The increase in *Eriogonum inflatum* in Rock Valley is harder to explain. The seedlings of *Eriogonum* were largely in open areas, where *Bromus* was present only in low densities and was not sprayed. *E. inflatum* is normally a biennial growing in open areas, and its increase suggested a process of reduced mortality of seedlings during the summer dry seasons following spraying. This might have occurred due to a slower drying of soil in the absence of *Bromus.* In this study soil moisture was not measured. However, the 1994 observations of 20 dead to 1 live *E. inflatum* on the control, versus one of 58 dead on the sprayed plot strongly suggested late spring drying led to differential mortality responsible for the increase on the sprayed plot. Note that in 1995 the Yucca Flat vegetation looked dryer on the control plot than on the sprayed plot at harvest (May 10). These observations suggest one method of competition by *Bromus* includes increasing the rate of soil drying in the spring, which might be expected to affect survival of annuals some distance from the *Bromus* concentrations. (Such drying might also affect shrub species whose establishment, growth, and reproduction occur primarily in the spring.)

In 1994 *Eriogonum inflatum* was rarely seen, but was also found at increased density ($C^2 = 19.9$, $P<0.001$) on a shrub-removal plot in Mercury Valley (Hunter 1995). This too suggested water use, in this case by shrubs, caused reduced densities of *E. inflatum*.

4) In Yucca Flat the response was apparently a switch of the dominant species from *Bromus madritensis rubens* to *Chaenactis stevioides,* as most species were found at lower density on the sprayed plots. However, a few other species, like *Malacothrix glabrata, Ipomopsis polycladon, Lepidium lasiocarpum* and *Amsinckia tessellata,* appeared to be increasing.

Statistics were affected by the high spatial and temporal variability, the differing characteristics of the many species, and presence of many different habitats and microhabitats. In the first experiment it worked out well to pick twenty similar microhabitats for harvest - it resulted in low variability in *Bromus* densities in the two microhabitats selected. The edge-effect problem was surely real, but could perhaps have been overcome by spraying the grass-specific herbicide on individual shrub clumps (@ $1\ m^2$ in area) and censusing permanent small quadrats within those clumps. That would have significantly reduced the spatial variability, although it would have limited applicability of the results to only those microhabitats selected for permanent quadrats. Since we found most effects were probably under shrubs, it might have been preferable to accept that limitation.

Table 14 demonstrates the change in wet-year native and *Bromus* populations since 1962 in Rock Valley. *Bromus madritensis rubens* has become the dominant winter annual species during that period, but pooled native densities did not clearly decline.

One rare species seen by Beatley in her Rock Valley Plot 3 in 1966 and 1973 was *Antirrhinum filipes,* a small snapdragon that twines among the branches of shrubs. It was not seen at any censused location on the NTS during the BECAMP program (1987–1994) (a specimen was collected near the Device Assembly Facility in Frenchman Flat in 1994, however (Woodward et al. 1995)). Its habit is similar to those that appeared to be most affected by *Bromus,* and its absence might tentatively be attributed to the increase in *Bromus.*

It is unlikely herbicides would make a good control treatment for *Bromus madritensis rubens* on large areas. Because most plants grow under shrubs they would be protected from most spray applications. A more promising avenue for control might be biological control through use of the smut organism, *Ustilago bullata* Berkeley, which infects a significant portion of the *B. m. rbuens* population already (15±3%, Hunter 1991).

In conclusion, it appeared from our experiments that *Bromus madritensis rubens* does indeed compete with some, but not all, native winter annual species, and that pooled native density is somewhat reduced by *Bromus*. The diversity of winter annuals is probably only temporarily reduced by introduced species like *Bromus*, and will ultimately depend on habitat diversity. Dominance by some of the 100+ native species can play roles similar to that of the introduced species. The complexities of the winter annual population dynamics make experimental demonstrations of competition difficult, and future work should be directed towards answering much narrower questions.

Table14. Densities of native winter annuals and *Bromus madritensis rubens* in various studies in Rock Valley, Nevada, in wet years (>100 mm total precipitation) between 1962 and 1995. Data are from Beatley (unpublished), 1962-1972; Ackerman (Turner's IBP Progress reports) 1973-1976; Hunter (unpublished 1983-85, 1995); Hunter (BECAMP status reports) 1987-1994. No data were collected 1977-1982 and 1986.

Year	Rain, mm	Native Density n/m²	*Bromus* density % of population
1966	140	70	4
1969	212	110	11
1973	220	118	0
1975	112	216	6
1976	126	327	22
1983	174	108	45
1985	118	111	58
1987	167	100	88
1988	203	86	96
1992	200	92	76
1993	259	154	93
1995	238	648	64

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The Role of Tortoises in the Thicket Biome, South Africa: Important Meso-Herbivores in a Mega-Herbivore Dominated Ecosystem?

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Abstract— **The Thicket biome, in the Eastern Cape, South Africa, supports four species of tortoises, but their role in this system is poorly understood. Leopard tortoises, *Geochelone pardalis,* and angulate tortoises, *Chersina angulata,* were radio tracked over a year. Dietary information was collected by direct observation and the analysis of feces, and the potential for seed dispersal was estimated from the occurrence of intact seeds in the feces of leopard tortoises. Although leopard tortoises had large home ranges, 70% of their activity was concentrated in activity nodes comprising only 1.4% of their home range, which had a higher frequency of geophytes, succulents and trees than non-node areas. Angulate tortoises had much smaller home ranges, but again 70% of their time was concentrated in nodes averaging 2.4% of the home range, which were dominated by trees. Leopard tortoises consumed 28 plant species, with 6 species comprising 75% of the diet, but did not appear to be true dietary specialists. Leopard tortoises dispersed seeds of only nine species of plants, the most important being the invasive cactus *Opuntia ficus-indica.* Tortoise biomass was only exceeded by elephants, and equalled that of the combined biomass of the smaller (non-megaherbivore) mammalian herbivores as well as that of black rhinoceros. Elephants and domestic goats have been blamed for the loss of some geophytes and succulents in the Thicket biome. In the light of the importance of these plants in the diet of leopard tortoises and the relatively high biomasses of tortoises, we hypothesize that tortoises may be playing a role in the observed loss of these geophytes and succulents, facilitated by habitat modification.**

The Thicket biome in South Africa (Low and Rebelo, 1996) supports a broad diversity and high density of indigenous herbivores, including up to four species of tortoises. This vegetation type is largely confined to the southeast coast, and is typically found in hot, semi-arid valleys. These thickets comprise a broad diversity of plant growth forms, including woody shrubs, lianas, forbs, geophytes, grasses and a variety of succulents, and in the intact state, form an impenetrable, thorny, evergreen thicket. The Thicket biome is recognised as being of high conservation status, particularly in the Eastern Cape Province, by virtue of the high diversity of woody shrubs, as well as the high diversity of endemic or near endemic geophytes and succulents (Lubke et al., 1986; Moolman and Cowling, 1994).

Indigenous mammalian herbivores range from elephants *Loxodonta africana* down to the diminutive blue duiker *Philantomba monticola,* and include black rhinoceros *Diceros bicornis,* Cape buffalo *Syncerus caffer,* kudu *Tragelaphus strepsiceros,* bushbuck *T. scriptus* and common duiker *Sylicapra grimmia.* Given the high diversity and density of these herbivores and the spiny, nutritious and evergreen nature of the thicket vegetation, it has been hypothesized that extensive co-evolution of the vegetation and herbivores has occurred (Cowling, 1983; Midgley, 1991).

However, with the introduction of domestic herbivores (chiefly goats *Capra hircus*), and removal of most of the indigenous herbivores, extensive degradation of these thickets has occurred. This degradation has been recognised as true desertification as it includes loss of species, increase in unpalatable and alien species, soil erosion and decreases in productivity, and is irreversible (Kerley et al., 1995). Part of the problem of dealing with this issue of degradation is that there is a relatively poor understanding of the natural processes and dynamics of these thickets and their herbivores, and how these are altered with the introduction of domestic herbivores. There has therefore been a recent increase in research effort into the role of herbivores in this system, as well as the evaluation of the sustainability of alternative forms of landuse (Kerley et al., 1995; Kerley & Boshoff, 1997).

A large proportion of the research effort has focused on the role of the charismatic megafauna, such as elephants, in this system (e.g. Stuart-Hill, 1992). To date, tortoises have been virtually ignored, despite the fact that this landscape supports a high diversity and abundance of tortoises, including the leopard tortoise *Geochelone pardalis*, angulate tortoise *Chersina angulata*, parrot-beaked tortoise *Homopus aureolatus*, and in the more arid sections, the tent tortoise *Psammobates tentorius*. In addition, it has been suggested that the leopard tortoises achieve larger body sizes in the thicket habitat than elsewhere (e.g. Branch, 1988). We therefore hypothesized that tortoises could be functioning as important herbivores in this ecosystem. We thus initiated a study of the home range and population densities of leopard and angulate tortoises, the two most abundant species, as well as investigating the diet and potential seed dispersal by the leopard tortoise. Here we report on these aspects of tortoise ecology and further develop a hypothesis on their role in the dynamics of the Thicket biome.

STUDY SITE

This study was conducted in the Addo Elephant National Park, 70 km northwest of Port Elizabeth on the southeast coast of South Africa. The actual study site was a 600 ha portion of a recently acquired portion (the farm Thembani) of the rapidly expanding Park, which had been used as a goat and cattle pastoral operation prior to its inclusion into the Park (Mason, 1997). The climate is warm with mean maximum and minimum temperatures being 25.5° and 11.2° C, respectively. Annual rainfall averages 396 mm p a (Mason, 1997).

METHODS

Transmitters were glued to the carapace of ten leopard tortoises and seven angulate tortoises and the animals tracked for 14 and 9 months, respectively. Animals were located at least four times weekly for six months (Dec 1994 – June 1995), and monthly thereafter (Weatherby, 1995; Mason, 1997). The Minimum Convex Polygon (Jenrich and Turner, 1969) estimates of home ranges, and the sizes and distribution of activity nuclei were determined using RANGES IV (Kenward, 1990).

Habitat associations were determined for both leopard and angulate tortoises, by comparing the environmental features of the activity nuclei with the remainder (non-nuclei) of the home ranges (Mason, 1997). Activity nuclei were calculated for the ranging data for both species at the level of 70% of activity, and located on the study site. The frequency of occurrence of bare ground and five plant growth forms (grass, geophyte, succulent, forb, tree) was determined for point intercepts at 10 cm intervals along 30 m line transects in nuclei and non-nuclei areas, and compared (Mason, 1997).

Tortoise density was estimated from the number of leopard and angulate tortoises marked during specific searches of the study site, as well as those encountered during radiotracking. These data, together with body mass measures for the animals and the size of the study area, were used to estimate tortoise density and biomass for the study site.

Diet of leopard tortoises was estimated from direct observations of feeding tortoises, as well as the analysis of fecal material. The fecal material was identified by comparing epidermal characteristics of dietary species to those of a known reference collection of plants (Gaylard and Kerley, 1995). The availability of dietary plants was estimated as the frequency of occurrence of these plants, measured as point intercepts of plants at ground level at 1 cm intervals along 30 m line transects (n = 19). Principle dietary items were identified as those with a frequency of greater than 5%, while preferred dietary items were those which occurred more frequently in the diet than in the habitat (Mason, 1997).

Leopard tortoise fecal samples were analysed for the occurrence of seeds which were identified with the aid of a reference collection of known seed species (Mason, 1997).

RESULTS

Leopard tortoises had large home ranges, averaging 106.4 ± 123.8 ha (mean ± SD, range = 17.9 – 376.6 ha), which did not differ between sexes, but did differ seasonally, being smaller in summer (mean = 73.5 ± 99.1 ha). As expected, the smaller angulate tortoises had much smaller home ranges,

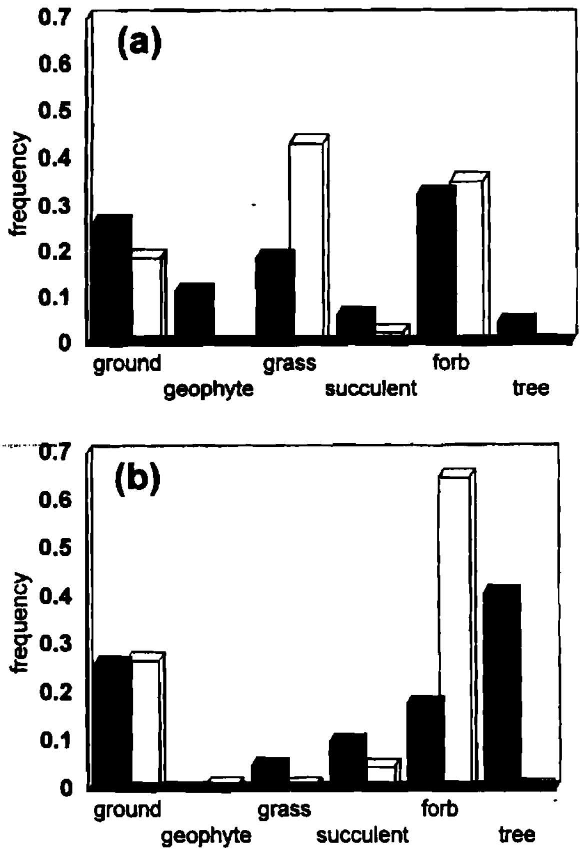

Fig. 1. Habitat features, expressed as the frequency of plant growth forms, of (a) leopard tortoise and (b) angulate tortoise activity nuclei (solid bars) in relation to the remainder of their home ranges (open bars).

averaging 2.0 ± 3.2 ha (range = 0.1 – 9.0 ha), which did not differ between sexes. Home range size was independent of body size for both species. Both species exhibited extensive overlap in their home ranges (Mason 1997).

Leopard tortoise population size was estimated as 113 adults in an area of 133 ha, indicating a density of 0.85 tortoise/ha and a biomass of 6.02 kg/ha. Angulate tortoise density was estimated at 1.61 tortoises/ha, with a biomass of 0.94 kg/ha (Mason, 1997).

Both leopard and angulate tortoises exhibited some selection for plant growth forms in their home ranges. Leopard tortoise activity nuclei tended to have a higher frequency of geophytes, succulents and trees (Fig 1a), which had lower frequency of grasses than non-nuclei areas within their home ranges. Angulate tortoises appeared to select for denser vegetation (Fig 1b), with a higher frequency of trees, succulents and grasses in their activity nuclei (Mason, 1997).

A total of 28 plant species were recorded in the diet of leopard tortoises (Table 1), although only six species made up 75% of their diet. Their diet was dominated by geophytes (47% of observations), and included a large proportion of succulents (20%) and grasses (19%). Woody shrubs and non-succulent forbs were less frequently eaten. Tortoises exhibited clear dietary preferences, consuming some plants more frequently than predicted by the occurrence of the plant species in the habitat (Table 1). The invasive alien cactus *Opuntia ficus-indica* was the most preferred plant in their diet. The geophyte *Albuca* sp. was the principal food item, comprising 30% of the diet (Mason, 1997).

Leopard tortoises feces contained relatively few seeds, averaging 25 seeds/fecal sample. Seeds of nine plant species were recorded in the tortoises' feces (Table 2). Although the invasive *O. ficus-indica* occurred in relatively few fecal samples, the abundance of these seeds indicated that this plant was the most frequently dispersed species (Mason, 1997).

Discussion

Home ranges— The home range sizes found here for leopard tortoises are comparable with those found for this species in savannah habitats (e.g. Hailey and Coulson, 1996). In contrast, angulate tortoises had much smaller home ranges in coastal areas of the Thicket biome (Els, 1989), possibly reflecting the more mesic characteristics of the coast. The fact that the vegetation of the Thicket biome is highly nutritious (Seydack and Bigalke, 1992) does not lead to smaller tortoise home ranges, suggesting that home range size for these two species is not a function of forage quality.

The seasonal variation in leopard tortoise home range size may reflect a seasonal migration of the population, with all except one individual moving onto higher hill slopes in winter. This may be an attempt to avoid the lower temperatures of the valley bottoms in winter (Mason, 1997). Tortoises exhibited reduced activity and did not appear to feed over winter (Mason, 1997), suggesting that low temperatures are important physiological constraints.

Habitat use— Leopard and angulate tortoises

Table 1. Dietary preferences of leopard tortoises expressed as the frequency of occurrence of plants in the diet in relation to availability in the general habitat.

Species	Consumption %	Availability %	Preference index
Poacaea			
Cynodon sp.	10.9	14.7	0.7
Digitaria eriantha	1.4	2.6	0.5
Eragrostis racemosa	1.4	0.5	2.9
Panicum deustem	1	0.3	3.9
Tragus berteronianus	3.9	0.9	4.5
Liliaceae-Hyacinthaceae			
Albuca sp.	30.4	5.3	5.8
Urginea altissima	9.5	1	9.9
Liliaceae - Asphodelaceae			
Bulbine latifolia	0.7	0.2	4.1
Bulbine sp.	4.6	0.4	11.4
Aloe ciliaris	0.4	<0.01	35
Amaryllidaceae			
Brunsvigea gregaria	0.4	0.9	0.4
Aizoaceae			
Galenia sp.	4.2	18.1	0.2
Crassulaceae			
Crassula expansa	8.4	3.5	2.4
Crassula sp.	0.7	0.02	35
Cotyledon sp.	0.4	<0.01	35
Fabaceae			
Acacia karroo	0.7	2.03	0.3
Indigofera sp.	0.7	0.1	10
Trifolium sp.	0.7	1.3	0.6
Schotia sp.	0.35	<0.01	35
Malvaceae			
Abutilon sonnerotianum	1.1	<0.01	105
Sterculiaceae			
Hermania althaeoides	1.1	2.1	0.5
Cactaceae			
Opuntia ficus-indica	9.5	<0.01	947
O. aurantiaca	0.4	0.03	11.7
Commelinaceae			
Commelina sp.	3.9	0.2	20.3
Oxalidaceae			
Oxalis sp.	1.4	0.6	2.3
Asteraceae			
Sonchus/Venedium sp.	1.1	0.6	1.8
Mesembryanthemaceae			
Drosanthemum hispidum	0.7	13.9	1.1
Sapindaceae			
Pappea capensis	0.4	<0.01	35

concentrated their activity in nodes which had a higher frequency of succulents and trees than the surrounding landscapes. In addition, leopard tortoises selected for areas with a high density of geophytes compared to the surrounding habitat. These habitat features may reflect dietary resources for

Table 2. Seeds recovered from the feces (n = 52) of leopard tortoises.

Species	Frequency of occurence	Number of seeds
Cynodon sp.	14 %	275
Digitaria eriantha	2 %	61
Eragrostis recemosa	2 %	5
Panicum deustem	2 %	34
Tragus berteronianus	4 %	47
Albuca sp.	12 %	26
Acacia karroo	6 %	5
Indigofera sp.	4 %	21
Opuntia ficus-indica	14 %	799
Unidentified sp.	4 %	2

leopard tortoises, particularly in view of the importance of geophytes and succulents in their diets. The focus on areas with a high frequency of trees, which is particularly apparent in the case of angulate tortoises, may reflect either physiological or predator refuges. It is unlikely that these trees represent dietary resources, as most tree foliage is beyond the reach of the tortoises, and woody plant species did not feature prominently in the diet of leopard tortoises. More information on tortoise physiology and predation risk is needed to evaluate this hypothesis.

Biomass— The biomass of tortoises observed here (totalling 7 kg/ha) is relatively high, particularly in comparison with large vertebrate herbivorous endotherms in this habitat. The recommended agricultural carrying capacity for domestic herbivores (chiefly browsing goats) is about 50 kg/ha (Stuart-Hill, 1992). For indigenous mammalian herbivores, Stuart-Hill (1992) estimated that the biomass to be 50 kg/ha, 85 % of which was made up of mega-herbivores (elephants and black rhinoceros). Thus tortoises represent approximately 14% of the biomass of mammalian herbivores in this thicket habitat, and are comparable to the combined biomasses of all non-megaherbivore species (7.2 kg/ha – Stuart-Hill, 1992). Leopard tortoise biomass also exceeds that of all the individual species (biomasses ranging 0.06 – 3.46 kg/ha – Stuart-Hill, 1992), besides elephants, but including black rhinoceros.

The relative impact of tortoises as herbivores needs to be expressed in terms of their metabolic biomass, which is relatively lower for ectotherms than endotherms. Alternatively, it should be recalled that the inefficient digestion of tortoises, relative to that of endotherms, will lead to a proportionally larger food requirement per metabolic biomass unit. These arguments therefore suggest that tortoises play a significant role as herbivores in the Thicket biome.

Diet of leopard tortoises— Leopard tortoises were observed consuming fewer plant species in the Thicket biome than in the semiarid Karoo (75 species - Milton, 1992) or Kalahari savanna (51 species – Rall and Fairall, 1993). This may reflect the availability of nutritious plant species in the Thicket biome, allowing the tortoises to fulfil their nutritional requirements with fewer plant species. Although leopard tortoises were highly selective in their consumption of plant species, and relied extensively on geophytes and succulents, they can not be classified as dietary specialists, as they consume a relatively wide variety of plant species and growth forms (Mason, 1997).

The reliance of leopard tortoises upon the consumption of geophytes (nearly 50% of their diet) is exceptional. These geophytes are relatively small plants (i.e. do not grow beyond tortoise feeding heights), are succulent and produced green foliage throughout the year (Mason, 1997). The quality and availability of these geophytes therefore appear to make them good forage items for the tortoises. It would be interesting to investigate the reliance of the other tortoises in this biome upon geophytes in order to test this hypothesis, as well as the importance of geophytes in the diets of tortoises in other habitats.

Seed dispersal— Tortoises are relatively unimportant in the process of zoochory in the Thicket Biome in terms of the number of seeds or the number of plant species, dispersing fewer seeds of fewer plant species than birds (Bruton, 1992) or mammals (Castley, 1992). Although tortoises disperse few seeds of relatively few plants, their impact on zoochory should not be discounted for two reasons. Firstly, as tortoises do not masticate seeds or subject them to severe digestion processes, seed survival may be relatively high during tortoise endozoochory. This is in contrast to the low survival of seeds consumed by bushpigs *Potamochoerus porcus* (Castley, 1992). Secondly, tortoises tend to use microhabitat-specific forms under shrubs and may defecate in these sheltered microsites (Mason, 1997). This suggests that tortoise zoochory may be highly targeted in terms of microsites, possibly leading to increased success of the establishment of plants which require such sites. Thus the significance of tortoise zoochory in the Thicket biome needs to be further explored in terms of the above hypotheses, particularly as Cowling (1983) speculated that the high floristic diversity of the Thicket biome could be attributed to the process of zoochory, with the seasonally variable dispersal of seeds to specific microsites being important.

Tortoises as important herbivores in the Thicket Biome— Herbivory has been identified as one of the major processes driving community structure and functioning in the Thicket Biome (Cowling, 1983), and the primary cause of the degradation of these systems (Stuart-Hill, 1992; Kerley et al., 1995). Poorly implemented pastoralism has therefore been shown to lead to the loss of phytomass, loss of palatable plant species, increase of unpalatable and invasive alien plant species, soil erosion and irreversible loss of productivity characteristic of desertification (Kerley et al., 1995). As a consequence there are concerns regarding the management and conservation of this biome. The Thicket biome is a major centre of endemism for succulents and geophytes and from a conservation perspective these are the most important components of the thickets (Moolman and Cowling, 1994). However, Moolman and Cowling (1994) have shown that goat (pastoralism) or elephant browsing leads to a loss of these succulents and geophytes. Many of the species apparently affected by elephant browsing are small and were not recorded in the winter diet of elephants (Paley and Kerley, 1998). This suggests that direct elephant herbivory may not be the cause of the observed loss of these species.

Relatively small herbivores have been shown to be important in ecosystem structuring in a number of instances, by virtue of their high densities and specialised feeding behaviour (e.g. Chew, 1974; Weltzin et al., 1997). Our findings here indicate that tortoises have a high biomass in relation to other herbivores, are selective feeders upon geophytes and succulents and concentrate their activities in the vicinity of succulents and geophytes. We therefore hypothesize that tortoises may play a role in the observed decline of geophytes and low-growing succulents. Tortoises appear to be somewhat ecotonal in their habitat preferences, avoiding the densest thicket habitat. For leopard tortoises at least, this may be a reflection of the difficulty that these large tortoises have in moving through dense thicket. Elephants and goats may therefore facilitate access for tortoises by opening up paths through the dense thicket. This hypothesis needs to be tested, as there is currently no information on the impacts of tortoise herbivory or on the density of tortoises in the presence or absence of elephants or goats. We therefore hypothesize that tortoises are important herbivores in a landscape apparently dominated by megaherbivores, and that this undervalued class of herbivore should receive more attention in order to understand the impact and role of herbivores in this ecosystem.

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The Functional Ecology of Creosotebush (*Larrea tridentata*) a Community Dominant in Desert Tortoise Habitat: A Review.

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Abstract— **The adaptations of creosotebush, *Larrea tridentata*, that contribute to its dominance in North American desert landscapes are reviewed. Canopy morphology adaptations include orientation of foliage that maximizes light interception in the early morning, variable stem angles (with respect to the soil surface) that affect stemflow and below canopy litter accumulations. Creosotebush requires both water and nitrogen for optimal growth and carbon gain. Root growth occurs later in the season than stem and leaf production. Root channelization of stemflow water enhances the resistance of *L. tridentata* to prolonged drought. Canopy morphology and use of sub-canopy soils by burrowing animals affect both the diversity and density of annual plants that are used as food by desert tortoises.**

Creosotebush, *Larrea tridentata*, an evergreen xerophytic shrub, is one of the most widespread perennial species of the North American deserts (Shreve 1942). It is a dominant plant both in terms of density and biomass on many landscapes in these deserts. *L. tridentata* remains metabolically active throughout the year and will grow and flower opportunistically whenever environmental conditions are suitable (Chew and Chew 1965, Oechel et al. 1972). As with most desert plants, growth of creosotebush is water dependent and varies with the season of availability of water. However, water is not the only factor limiting growth of creosotebush. Growth as measured by stem elongation and leaf production varies directly with both water and nitrogen availability (Romney et al. 1978, Fisher et al. 1988, Lajtha and Whitford 1989). There was no evidence that irrigation or nitrogen fertilization alone or in combination had any effect on root growth. Since the addition of both water and nitrogen increased above ground production, both additions appear to have reduced the relative allocation of photosynthate to roots. Nitrogen fertilization did not affect flower and fruit production but irrigation did (Fisher et al. 1988). Irrigation by small, frequent additions (6mm/week) resulted in larger growth increments than irrigation by single large additions (25 mm every fourth week). This confirmed the hypothesis of Ludwig and Flavill (1979) that small, frequent events were more effective than large, infrequent rain events. Physiological responses of *Larrea* appear to be similar in the Mojave and Chihuahuan Deserts suggesting that Sonoran Desert populations probably respond to water and nitrogen availability in a similar fashion.

In studies using irrigation and nitrogen fertilization to examine the growth characteristics of *Larrea*, Lajtha and Whitford (1989) found that both water and nitrogen additions resulted in significant increases in the number of live leaves on marked twigs. In the Chihuahuan Desert, creosotebush produced both spring and late fall cohorts of leaves. Leaves produced in spring had slightly higher maximum longevity than fall produced leaves. However no leaves on *L. tridentata* survived for more than 16 months (Lajtha and Whitford 1989). Leaf abscission is coincident with seasons or years of increased leaf growth and production. The explanation of this pattern was suggested to be caused by a redistribution of nutrients from old leaves to new leaves followed by shedding of the old, nutrient-poor leaves. However, leaf longevity was decreased in some of the leaf cohorts in plant that had received nitrogen fertilization. Patterns of physiological carbon gain were different from patterns of leaf production and stem elongation. Net photosynthetic assimilation

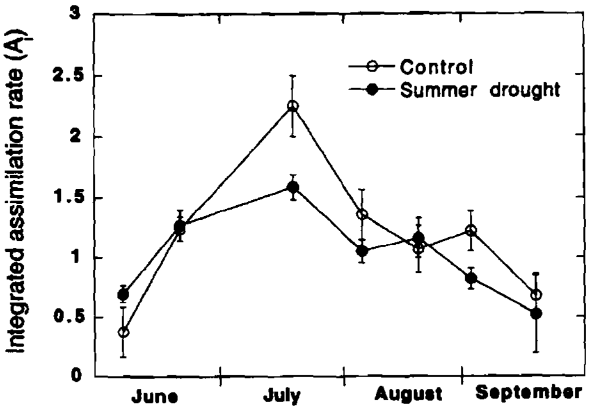

Fig. 1. Integrated rate of carbon assimilation in creosotebushes, *Larrea tridentata*, subjected to summer drought and creosotebushes allowed access to natural rainfall.

of carbon peaked in July in creosotebush plants receiving natural rainfall and those subjected to summer drought by "rain-out" shelters (Fig. 1) (deSoyza et al. 1996). This pattern of photosynthesis paralleled the patterns of stem elongation in *Larrea* subjected to summer drought. Water use efficiency defined as photosynthetic carbon gain per unit water transpired was positively related to leaf nitrogen (r = 0.49, P < 0.003) (Lajtha and Whitford 1989). Both leaf nitrogen and leaf age affected net photosynthesis, water use efficiency and nitrogen use efficiency in creosotebushes. Leaf nitrogen and leaf age explained between 44% and 75% of the variance in these parameters. *Larrea* resorbed between 48% and 72% of the leaf nitrogen from senescing leaves. Nitrogen resorption efficiency was greater in spring than in fall or winter.

The resilience of *Larrea tridentata* to summer drought is an important adaptation of this species and contributes to its dominance in the North American deserts. In a study using "rain-out" shelters to impose summer drought, Whitford et al. (1995) found that while drought severely limited stem elongation and leaf production in the summer, the plants subjected to drought put on rapid growth following the first rainfall after removal of the "rain-out" shelters (Fig. 2). That rapid growth resulted in stem and leaf production equal to that of the control and irrigated plants. Reproductive effort in *Larrea* as measured by flower production was affected by summer irrigation but not by summer drought (Fig. 2). This suggests that the availability of water during the preceding growing season has an effect on reproduction in creosotebush.

Peak growth of above ground parts and of roots of *Larrea* do not coincide temporally. Peak root growth in the Chihuahuan Desert plants occurred in September and early October (Fisher et al. 1988) while peak growth of above ground parts occurred in from late April through early June (Fig. 3). There were no differences in root growth of plants subjected to the various combinations of irrigation and nitrogen fertilization (Fisher et al. 1988).

Larrea has a C_3 physiology which limits active photosynthesis to the early morning hours during the summer. The C_3 photosynthetic physiology of *Larrea tridentata* results in cool season growth, and stem-leaf orientation that maximizes light interception in the early morning hours when cool temperatures and high relative humidity allow open stomata and efficient water use during photosynthesis. Leaf clusters are inclined between 33° and 71° from the horizontal. The inclinations of leaf clusters are steeper in shrubs in the drier and hot-

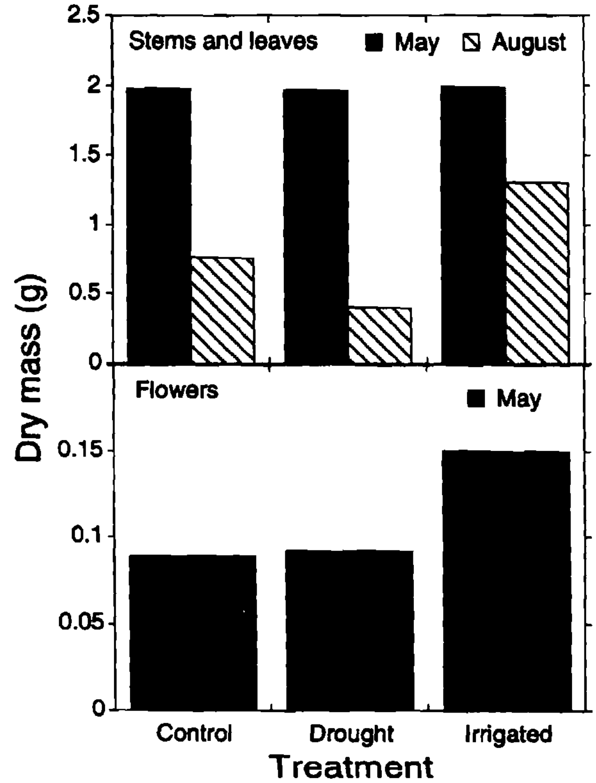

Fig. 2. Comparison of biomass production of stems and leaves and flowers of creosotebushes, *Larrea tridentata*, subjected to summer drought by "rain-out shelters", irrigation to double summer rainfall, and natural rainfall (control).

ter Mojave Desert than in the Chihuahuan Desert. Foliage clusters oriented toward the southeast exhibited less self-shading during the spring mornings than foliage clusters that were oriented northeast. This effect was not apparent at the summer solstice (Neufeld et al. 1988).

Creosotebushes have deep roots (> 3m) plus fine shallow roots emanating from the root crown. This rooting pattern allows the shrub to make use of soil water from small rain events and to access soil nutrients which are concentrated in the upper 10 cm of the soil profile. This rooting pattern when combined with the rainfall re-distribution pattern produced by the stem and canopy morphology results in deep soil water storage and drought resistance. Rainfall intercepted by the canopy of a shrub moves to the soil as throughfall or stemflow (Fig 4). Some of the water intercepted by a shrub canopy is retained on the leaf surfaces and evaporates thus contributing nothing to the soil water. The average throughfall fraction reported for *Larrea* was 64.7± 3.2% with a range of 5.9% to 26.9% (Whitford et al. 1997). Stemflow reported for *Larrea* was 16.8 ± 1.9%. Several variables affect stemflow and throughfall. Stem angle and stem length accounted for 41% of the variability in stemflow. Stemflow volumes were higher on stems with angles equal to or greater than 65° and there was little stemflow collected from branches with stem-angles equal to or less than 50°.

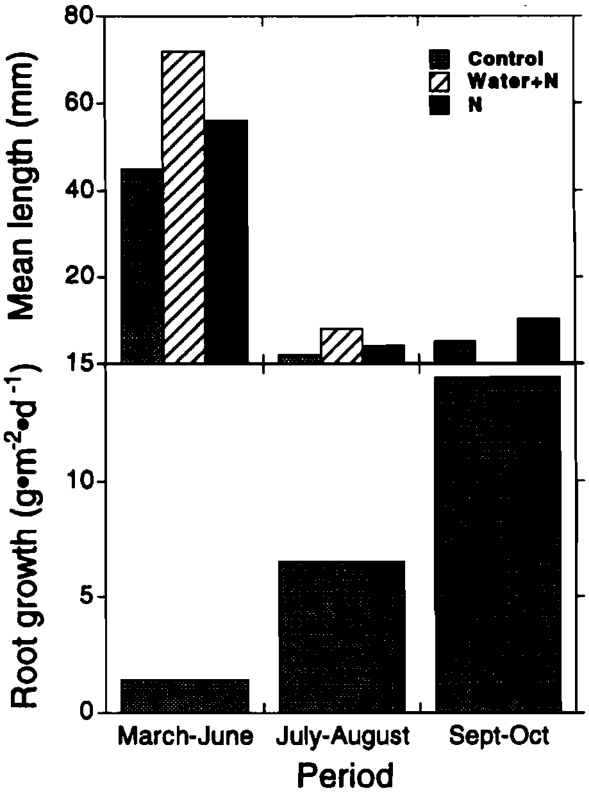

Fig. 3.Comparison of growth increments of stems and growth of roots in creosotebushes, *Larrea tridentata*, subjected to natural rainfall, irrigation by 6 mm of water per week plus nitrogen added at 10 gms N per square meter (water + N) and nitrogen fertilization at 10 gms. N per square meter. There were no significant effects of irrigation or fertilization therefore root growth is for all treatments combined.

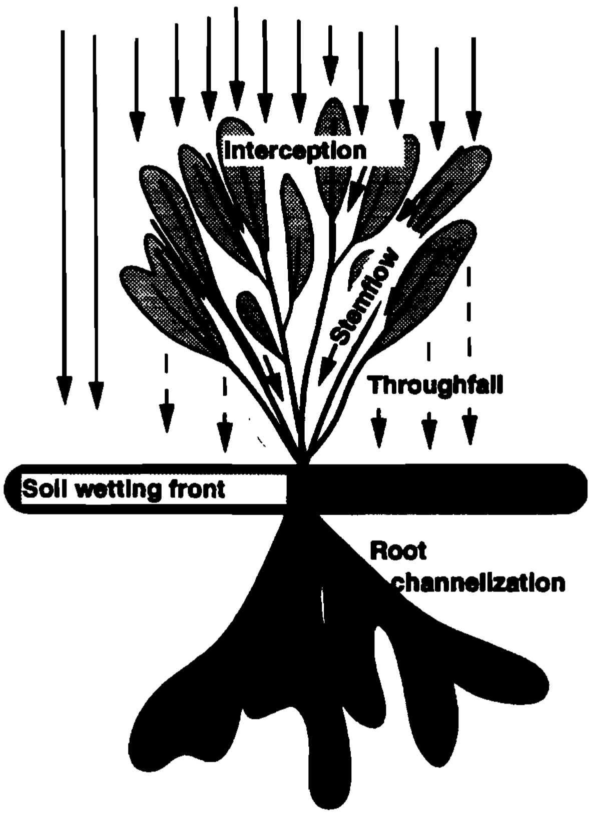

Fig. 4. Water redistribution by creosotebush, *Larrea tridentata*. Shaded soil indicates depth of water penetration along root channels and by gravitational water.

The inverted cone morphology of young plants and plants growing in extremely dry environments maximizes stem flow and channelization of stem flow water by roots to deep storage in the soil. In a study using fluorescent dye to trace the fate of stemflow water, Martinez-Meza and Whitford (1996) found that stemflow water was transferred to the greatest depth by root channelization in the creosotebush with the smallest canopy dimensions. Root channelization of stemflow water is an important process especially for young plants and plants in drier sites because that water is in a soil store that cannot be accessed by the root systems of annual plants or of herbaceous perennials growing under the canopy of the shrub. Root channelized water dyed soil at 25 to 35 cm while the throughfall water wetting front was at 6 to 10 cm (Martinez-Meza and Whitford 1996) (Fig. 4). This deep soil water can be used by creosotebush to produce foliage, flowers and fruits during droughts (Martinez-Meza and Whitford 1996, Whitford et al. 1995).

Both stemflow water and throughfall water is enriched in nutrients in comparison to bulk precipitation (Whitford et al. 1997), however stemflow water is enriched by an order of magnitude with respect to bulk precipitation. This pattern of nutrient enrichment of stemflow water from creosotebushes appears to be more than washing of dry-fall from the leaf surfaces. The stems of *Larrea* have a variable portion of the surface area covered with a black, crustose microbial layer. This microbial layer is dominated by fungi, *Coleophoma* spp. and also contains algae, bacteria, and cyanobacteria. High concentrations of nitrogen, phosphorus and calcium in stemflow water appears to be material washed from this microbial crust. Despite the high levels of nutrients in stemflow water, these nutrients contribute nothing to the "fertile island" that develops under creosotebush canopies. These nutrients are translocated to deep soils by root channelization and probably contribute to the capability of this species to resist drought and to recover quickly following drought.

The canopy morphology of creosotebush shrubs is a determinant of soil organic matter content and nitrogen content of the sub-canopy soils. Shrubs with inverted cone morphologies do not accumulate litter layers under the canopy while those with a spheroid morphology develop litter layers and elevated soil nitrogen under the canopy (deSoyza et al. 1997). Shrub canopy morphology affects the abundance and diversity of annual plants that grow under the shrubs (Table 1). Creosotebushes with spheroid morphologies have higher densities and diversities of annual plants under their canopies than do creosotebushes with inverted cone morphologies. Litter layers under shrub canopies not only contribute to the organic matter content of the surficial soils, litter layers also increase infiltration of throughfall and reduce evaporation of soil water. These factors are important for the survival and growth of annuals.

Table 1. Densities and average species richness of ephemeral plants under canopies of *Larrea tridentata* in the Mojave Desert near Las Vegas, NV.

Shrub type/ Location	**Density No. m^{-2}**	**Average Species Richness**
Intershrub space	22.0	2.0
Conical shrubs	83.0	4.2
Hemispherical Shrubs	128.0	5.9
Hemispherical with rodent burrow	210.0	6.7

There are important feedbacks between canopy morphology and animals that burrow under creosotebushes. In the Mojave, shrubs with kangaroo rat burrows exhibited higher stem growth increments and higher biomass, abundance and diversity of below canopy annuals (Table 1). Below canopy burrows of animals affect infiltration of throughfall water, soil water storage, and nitrogen mineralization rates. In a study of creostebush areas in the Mojave Desert, Soholt and Irwin (1976) reported decreased bulk density and higher infiltration rates in soils under creosotebushes with rodent burrows. The increased infiltration doubtless contributed to increased productivity of the shrub as well as to the productivity of the annuals. While desert tortoises may not eat creosotebush foliage, the functional ecology of this shrub is an important determinant of habitat suitability for tortoises.

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Preliminary Stratocladistic Analysis of the Genus *Gopherus*

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Abstract— **Stratophenetic and cladistic phylogenetic analyses have given different phylogenies for the tortoise genus *Gopherus*. A stratocladistic analysis of a previously published cladistic data set is here examined. A more resolved phylogeny of *Gopherus* was produced. The stratocladistic analysis also reduced the number of equally parsimonious trees from 549 to five. Two clades, one containing the extant *Gopherus polyphemus* and *G. flavomarginatus*, and another containing the extant *G. berlanderi* and *G. agassizii*, can be recognized. This phylogeny has systematic implications.**

This study is an examination of stratocladistic methods of phylogenetic analysis applied to a published data set for the gopher tortoise genus *Gopherus.*

The first detailed phylogeny of fossil and living *Gopherus* was Bramble (1971). Bramble's results are here presented as a dendrogram (Fig.1) with no presumptive ancestors, to facilitate comparison to later phylogenies. He recognized two clades in the traditionally constituted *Gopherus:* a clade containing the modern *Gopherus polyphemus* and *Gopherus flavomarginatus*, to which he restricted the name *Gopherus*, and a clade containing the modern *Gopherus agassizii* and *G. berlanderi* for which he proposed the genus *Scaptochelys* (Bramble, 1971, 1982). Subsequently, Bour and Dubois (1984) noted that *Scaptochelys* was a junior synonymy of *Xerobates* (Brown, 1906). A paraphyletic stem group referred to as *Proscaptochelys* was also recognized by Bramble (1971).

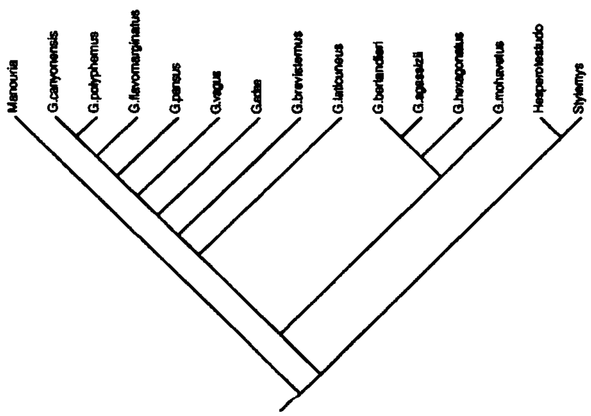

Fig. 1. *Gopherus* phylogeny of Bramble, 1971. The phylogeny is here expressed as a dendrogram to facilitate comparison to later cladograms.

A cladistic analysis, using maximum parsimony methods and morphological characters, has subsequently been made of the species of *Gopherus*, as well as of the other genera of tortoises (Crumly, 1994). The resulting phylogeny (Fig.2) differs from that of Bramble. *Gopherus, sensu stricto,* remains a holophyletic group, but *Xerobates* appears paraphyletic, if one includes the fossil taxa referred to the genus by Bramble, and not demonstrably holophyletic, if one only considers the living species. On this basis, Crumly recommended (1987) that *Xerobates* be abandoned, and all of the gopher tortoises be included in *Gopherus.*

Maximum parsimony cladistic analyses using mitochondrial DNA characters of living species only have also recently been presented (Lamb, et al., 1989; Lamb and Lydeard, 1994). These phylogenies are congruent with Bramble's and differ from Crumly's in recognizing distinct *Gopherus* s.s. and *Xerobates* clades.

I will re-examine Crumly's (1994) morphological character matrix using stratocladistic analysis. Conventional cladistic analysis attempts to achieve morphologic parsimony by avoiding "ad hoc" explanations and minimizing homoplasies. Resulting cladograms make specific prediction of the order of appearance of taxa. These cladograms may not coincide with the order apparent in the fossil record thereby lacking stratigraphic parsimony. Stratocladistics considers both morphologic and stratigraphic parsimony and favors phylogenetic hypotheses that reconcile the observed and expected order of temporal occurrence (Fisher, 1991, 1992).

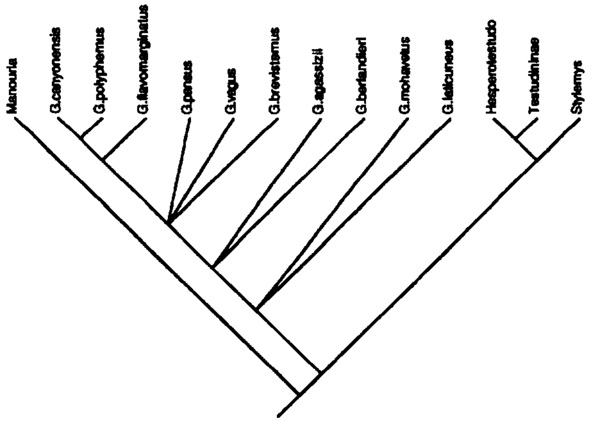

Fig. 2. Adams consensus tree of Crumly, 1994.

MATERIALS AND METHODS

The morphological characters correspond to Crumly's (1994) characters 1 through 42. Full description of these characters, including polarity assignment, is given by Crumly (1984, 1994). The original data set was kindly provided to the author for this analysis. The stratigraphic character is based on North American Land Mammal Ages. Although North American Land Mammal Ages are not of equal duration, there is no requirement that time intervals be of a particular relative or absolute depth, only be of a particular order of occurrence (Fisher, 1992). Stratigraphic occurrence of all North American taxa is based on Bramble (1971) and Crumly (1994). Stratigraphic coding includes: 0, Wasatchian and Bridgerian; 1, Uintan; 2, Chadronian and Orellian; 3, Whitneyan; 4, Arikareean and Hemingfordian; 5, Barstovian; 6, Clarendonian and Hempilian; 7, Blancan; 8, Irvingtonian; and, 9, Rancho le Brean and Recent. Stratigraphic range of the non-North American Testudinidae is approximated based on a first occurrence not later than the Oligocene (Auffenberg, 1974) and roughly continuous thereafter, here coded as 2 and higher.

Taxa included are the same as in Crumly (1994). *Gopherus edae, G. hexagtonatus,* and *G. praecedens* were omitted, as they are inadequately characterized. *Hadrianus* is here viewed as a junior synonymy of *Manouria.*

This paper employs the conservative approach to stratocladistics of using stratigraphic parsimony to select the morphologically and stratigraphically shortest tree (s) from among numerous trees of equal length determined by morphology alone (Suter, 1993). All analysis was accomplished using PAUP 3.1.1 (Swofford, 1993) and MacClade 3.0 (Maddison and Maddison, 1992). Branch and bound search of the data was made with all taxa and morphological characters alone and the resulting shortest trees were saved to a file. The stratigraphic information was then added to the character matrix with the character designated as "stratigraphic" in MacClade. All trees were then examined with the subsequent shortest trees saved to a file. Strict and Adams consensus trees were determined for these remaining trees.

RESULTS

As expected, branch and bound search resulted in 549 equally parsimonious trees with a tree-length of 60, as had previously been reported in Crumbly (1994). Examination of these trees stratocladistically resulted in tree-lengths varying from 90 to 78, with five equally parsimonious trees found with a length of 78. Consistency index from these trees was 0.82. The Adams consensus tree (Fig.3) was more resolved than that of Crumly (1994).

DISCUSSION

This conservative approach to stratocladistic analysis should not be expected to locate the most parsimonious morphological trees, only to aid in determining the subset of those morphological trees to be employed in resolving the phylogeny. Other approaches are possible. One suggested approach is to search for and save all morphological trees equal to or shorter than the shortest tree in

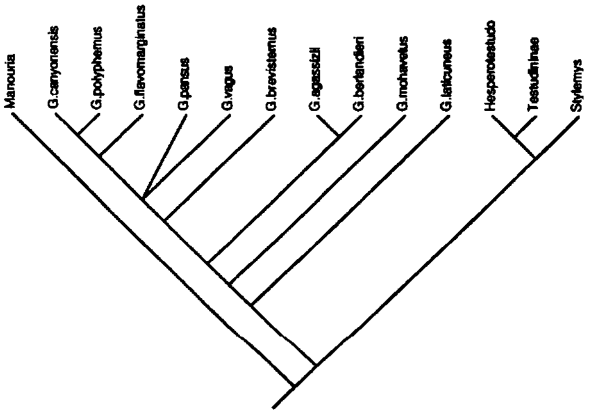

Fig. 3. Adams consensus tree from stratocladistic analysis (this paper).

the stratocladistic analyses (in this case, 78). These trees could then be examined to see if any less than most parsimonious morphological tree would give a more parsimonious stratocladistic tree (Fisher, 1992). Such an analysis would be difficult with this data set. The number of trees of length 78 or less exceeds the memory of any computer available to the author and the examination of those thousands of trees would be laborious, to say the least. It is also standard practice in stratocladistics to collapse branches with a length of zero and thereby erect a hypothesis of being an ancestor (Carroll, 1988) for those taxa. Both the importance of the recognition of ancestors and the likelihood of them being recovered is being increasingly recognized in phylogenetic analysis (Carroll, 1988; Fisher, 1992; Paul, 1992; Wagner and Erwin, 1995). Unfortunately, cladist data sets, such as the one used here, concentrate on the "informative" autapomorphies. The assignment of taxa as ancestors with these data sets would not be prudent.

Both the Adams consensus tree and the strict consensus tree produced a more resolved tree than they did in the cladistic analysis. This is not surprising, with far fewer trees to obtain consensus from. Stratocladistics also narrowed the number of most parsimonious trees from 549 to 5, a much more manageable number for individual examination, especially when one remembers that only one of those trees may be right.

One shared derived character potentially unites G. *agassizii* and *G. berlanderi*, the reduced or absent hip spines (Crumly, 1994). The uniting of *G. agassizii* with *G. berlanderi* with statocladistic analysis is not suprising. It is far more parsimonious to postulate one largely unknown lineage of Gopher Tortoises than two.

It should be noted that the more resolved consensus tree produced by stratocladistics agrees with the earlier trees of Bramble (1971), and Lamb and Lydeard (1994) in recognizing two clades, one containing the extant *Gopherus polyphemus* and *G. flavomarginatus*, and another containing the extant *G. berlanderi* and *G. agassizii*.

This paper is, as titled, preliminary. The true phylogeny of the gopher tortoises is far from resolved with certainty. The characters and polarities used here remain to be verified. Characters suggested by others (Hutchison, 1996) should be incorporated. Nevertheless, this phylogeny does have some systematic significance. Crumly (1987) recommended that *Xerobates* should be abandoned as its holophyly could not be demonstrated. It should be noted that even with Crumly's (1994) analysis, *Xerobates* could still be considered a metataxon (Donoghue, 1985; Gauthier, 1988). This analysis suggests that *Xerobates* may be useful to retain as a descriptor of the clade, here postulated, containing G. *agassizii* and G. *berlanderi*. I favor the suggestion of Charles H. Lowe (1990) that *Xerobates* be considered a subgenus.

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The Arizona Interagency Desert Tortoise Team: Progress Report

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The Arizona Interagency Desert Tortoise Team (AIDTT) was first convened in April 1985, at which time it consisted of representatives from U.S. Fish and Wildlife Service (USFWS), Arizona Game and Fish Department (AGFD), U.S. Bureau of Reclamation, U.S. Bureau of Land Management, and the U.S. Forest Service (Tonto and Coronado National Forests). The Arizona State Land Commission, U.S. Bureau of Indian Affairs, U.S. National Park Service (Saguaro National Park, Organ Pipe National Monument, and Lake Mead National Recreation Area), Yuma Proving Grounds (U.S. Department of the Army), Luke Air Force Base, and Marine Corps Air Station — Yuma were added later. The original purposes of the Team were to 1) formulate a research program, the results of which would guide development of long-term strategies for tortoise management and conservation in Arizona, and 2) prepare draft interim management policies that agencies in Arizona would hopefully adopt while more comprehensive, long-term strategies were developed through research. The Team became an especially important forum for discussing and coordinating desert tortoise research priorities and management issues, such as setting the Arizona State bag limit on tortoises to zero, grazing issues on public lands, and standardization of research methodologies and handling protocols.

Efforts began in the late 80s to develop an AIDTT Management Plan in fulfillment of the second purpose of the AIDTT. Agency review drafts were prepared in 1989 and 1990. A draft Memorandum of Understanding (MOU) was also prepared at that time to formalize the organization and objectives of the Team. A number of actions resulted in a funneling of resources and efforts to the Mojave population, beginning in August 1989 with the emergency listing of the Mojave population, followed by a final rule listing that population as threatened in April 1990, and a June 1991 petition finding by the USFWS that the Sonoran population of the desert tortoise did not warrant listing. As a result of these changing priorities, progress was slow on development of an AIDTT MOU and management plan.

The AIDTT renewed work on the MOU in the early 1990s and it was signed in 1995 by 11 State and Federal agencies. Among the objectives of the AIDTT as set forth in the MOU was to implement the AIDTT Management Plan, once that plan was completed. With much input from all of the Team members, the Plan was finalized and printed in March 1997 (AIDTT 1996). The Plan addresses only the Sonoran population of the desert tortoise. Management and research of tortoises located north and west of the Colorado River is guided by the Mojave population recovery plan (USFWS 1994).

The AIDTT Management Plan is divided into three major sections, including 1) an introduction that is similar to the introduction of a recovery plan; 2) a discussion of priority research and monitoring needs, and 3) recommended management options. In regard to monitoring needs, the Plan notes that current population trend data for Sonoran population desert tortoises, collected at 18 plots beginning in 1987, are inadequate to detect anything less than a catastrophic population decline, and any such finding would be limited to the study plots. Standard survey and population monitoring protocols are needed for the Sonoran desert tortoise. In comparison to Mojave population tortoises, Sonoran tortoises are more difficult to census because they are generally more patchily distributed and are difficult to detect in the rocky, well-vegetated terrain that typify the habitat of this population. As a result, plot studies developed in the Mojave Desert (Berry 1984), are less effective for Sonoran populations. We suspect reduced detectability, a highly variable detection function due to variable terrain and visibility, and increased patchiness may also make line-distance sampling, as currently proposed by Anderson and Burnham (1996), of questionable usefulness in determining size of Sonoran desert tortoise populations.

Research priorities described in the Plan include various topics in population dynamics, habitat management, and disease. In regard to population dynamics, the Plan calls for long-term demographic studies that might allow construction of a life table and development of a population viability analysis (PVA). Of particular concern is that Sonoran desert tortoises populations typically occur in relatively small, isolated mountain ranges.

Few of these populations are likely in the range of 20,000 to 60,000 animals, the population size found by the Mojave Population Recovery Team as necessary to provide reasonable assurance of persistence for 500 years (USFWS 1994). Although their finding was based in part on declining populations in the Mojave Desert, and this is generally not the case in Sonoran populations, small, montane island populations of Sonoran tortoises may not be able to persist in the long-term without occasional interchange with other populations. Valleys between mountain ranges in Arizona are increasingly impassable to tortoises due to urban or agricultural development, or construction of barriers such as canals and major highways. A PVA would be helpful in determining the importance of occasional interchange and habitat fragmentation on population viability.

Habitat research priorities focus on quantifying effects of habitat change, particulary changes caused by wildfire and livestock grazing, on Sonoran desert tortoises. Much of the richest tortoise habitat in the Sonoran Desert is increasingly vulnerable to fire damage due to a prevalence of nonnative plants that carry fire, particularly brome grasses (*Bromus rubens, Bromus tectorum*) and other winter/spring annuals (Schmid and Rogers 1988; Medica et al. 1995; Minnich 1995), but also the introduced perennial bufflegrass (*Pennisetum ciliare*), which is of growing concern in southern Arizona and a serious problem in Sonora (Bowden 1993).

Livestock grazing, believed to be incompatible with recovery of the Mojave population (USFWS 1994), is probably less important in the Sonoran Desert because tortoises occur primarily on slopes where cattle grazing is light; and tortoise sheltersites are often amidst boulders or in caliche caves that are well-protected from trampling by livestock. Nonetheless, livestock grazing is known to cause many long-term changes in desert plant communities and soils (see Appendix D of USFWS 1994). These effects need to be studied in the Sonoran Desert in relation to possible effects on tortoise populations.

Recent work by Dickinson et al. (1995) in west-central Arizona and other studies suggest that upper respiratory tract disease is not epidemic in the Sonoran Desert; however, cutaneous dyskeratosis has been documented in virtually every tortoise population studied in Arizona. The Plan acknowledges that the effects of these diseases on Sonoran desert tortoise populations needs to be better understood.

Management options in the Plan consist of alternative management prescriptions from which participating agencies can select to address specific management problems. These options are in no way meant to be mandatory, but are designed to serve as tools for assisting agencies in developing management strategies for Sonoran tortoises. Key to this process is identification by land managers of "Sonoran Desert Management Areas" (SDMAs). Similar to Desert Wildlife Management Areas for the Mojave population (USFWS 1994), SDMAs should be designed and managed in ways that promote long-term viability of tortoise populations. The AIDTT has developed some preliminary recommendations for SDMAs and is in the process of preparing a status report that will facilitate further development of SDMA recommendations.

Management options for Sonoran desert tortoise habitat are segregated into forage management and surface management alternatives. Forage management alternatives focus primarily on managing livestock and burros in a way that leaves adequate spring and late summer forage for tortoise growth and reproduction. Surface management alternatives are designed to reduce direct loss of tortoises and their habitat due to surface-disturbing activities. Suggested alternative measures include limiting surface disturbance due to mining, development of utility corridors, and other construction activities; prohibiting competitive off-highway vehicle events in tortoise habitat; limiting vehicular access to designated routes; following guidelines for fire suppression developed by Duck et al. (1994), which are included as an appendix to the Plan; and other similar measures. The Plan also recommends acquisition from willing sellers of inholdings within SDMAs, and compensation for residual impacts in accordance with the compensation formula developed by the Desert Tortoise Compensation Team (1991). Guidelines for handling desert tortoises encountered on development projects are also included. A recently finalized mitigation protocol has been developed as a supplement to the Plan.

Although the AIDTT Management Plan is a product of the Team and not the agencies, it is hoped that it will be used by land managers to develop appropriate management for long-term viability of Sonoran desert tortoise populations. Applicable management options could be implemented through habitat management plans, land use plan amendments, integrated resource management plans on military installations; or other similar planning processes. The AIDTT is also seeking other cooperators, particularly tribes in southern Arizona, in the conservation of Sonoran desert tortoise populations. The AIDTT will remain active to work with land managers in the implementation of the plan and will continue to serve as a forum for discussions of tortoise research, conservation, and management.

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Federal Biological Opinion Analysis for the Proposed Eagle Mountain Landfill Project

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During a lawsuit challenging the sufficiency of the original EIR/EIS for the Eagle Mountain project, Judge McConnell of the San Diego Superior Court made the following ruling on July 26, 1994:

> There is not substantial evidence to support the conclusion that the mitigation measures will be effective in reducing the risks to the desert tortoise...[t]he EIR discusses the threats and describes proposed mitigation measures including monitoring, relocation, construction of culverts under the road and rails, berms over the tracks, and barriers, among other measures. The EIR concluded "...given the proposed tortoise mitigation, tortoise impacts appear mitigable to nonsignificance." (6 A.R. 2652.) There is nothing in the record to support this conclusion.

The Service consulted with the Bureau under Section 7 of the Federal Endangered Species Act and determined, in its Biological Opinion (1-6-92-F-39) (USDI Fish and Wildlife Service 1992), that the Project would not jeopardize the continued existence of desert tortoise if specified Terms and Conditions (i.e., mitigation measures) were implemented. This "no jeopardy" opinion was confirmed in 1993, following reinitiation of consultation due to the anticipated establishment of critical habitat for the desert tortoise (USDI Fish and Wildlife Service 1993).

Circle Mountain Biological Consultants (CMBC) chose to address the Judge's concerns by conducting a thorough analysis of Biological Opinions issued for the desert tortoise. CMBC reviewed 234 Biological Opinions that authorized 263 projects in California and Nevada where tortoises could have been affected. CMBC reviewed 126 of the 133 (95%) Biological Opinions issued for tortoises in California, excluding those opinions that regulated off-highway vehicle events and grazing. One-hundred-and-eight (108) of the 182 (59%) opinions issued in Nevada were reviewed. The remaining files were not available at the central field office in Reno, Nevada. Since a vast majority of the habitat of the desert tortoise is located on Federal lands, this analysis covers the bulk of projects for which tortoise mitigation has been required by the Service.

In each opinion, anticipated harassment limits (i.e., the number of tortoises that may be handled) and anticipated mortality limits (i.e., the number of tortoises that may be accidentally killed) are specified. If either of these limits is met, the project proponent is instructed to cease construction or operation of the project and reinitiate consultation between the Federal Lead Agency and the Service to determine why the limits were met, and determine additional measures to avoid exceeding revised limits. Failure by the proponent to report meeting these limits, and failure to reinitiate formal consultation with the Service when limits are met, are violations of the Act, and proponents and contractors are subject to civil and criminal penalties for such violations.

Also in each opinion, Terms and Conditions and other measures required by the Service are given to avoid excessive harassment and mortality of tortoises. A consultant's report may indicate that 10 tortoises occur on a given site. For such a site, the Service may say that 10 tortoises can be handled and one accidentally killed. The Service reasons that the Terms and Conditions will avoid mortality for all but one of the 10 tortoises; if one tortoise is accidentally killed, the Terms and Conditions are said to effectively protect tortoises. Therefore, the authorized mortality limit is the acceptable number of tortoises that may be accidentally killed, in spite of the Terms and Conditions, without jeopardizing the species (pers. comm. Ray Bransfield and Kirk Waln, Service wildlife biologists, 11 Oct 1995).

In California, there have been approximately 150 Federal Biological Opinions issued for the desert tortoise by the Ventura and Carlsbad offices of the Service; more than 180 have been issued out of the Reno and Las Vegas offices of the Service in Nevada. Each of these opinions includes: (a) a jeopardy or non-jeopardy opinion; (b) measures proposed by the Federal Lead Agency to minimize impacts; (c) an incidental take statement, which lists the number of tortoises that may be accidentally killed and the number that may be handled; and (d) the Terms and Conditions that are to be implemented to ensure that the take limits are not exceeded.

The objectives of this study were to obtain all Biological Opinions addressing desert tortoises; to determine for each opinion the number of tortoises that may be handled and accidentally killed; to determine the similarities and differences between the measures given in those Biological Opinions with the measures given in the Biological Opinion issued for Eagle Mountain; and to determine the actual numbers of tortoises handled and accidentally killed during construction, maintenance, and operation of those projects. Then, given this information, determine if tortoises would be adequately protected by the mitigation measures proposed for Eagle Mountain.

The objectives were met, in part, as follows:

- A total of 126 Federal Biological Opinions for projects affecting tortoises in California was obtained from the Ventura and Carlsbad, California offices of the Service. An additional 108 opinions were obtained from the Reno, Nevada office of the Service.
- Opinions issued for the desert tortoise relative to livestock grazing and motorized racing events were considered to be sufficiently different from the proposed Eagle Mountain Project that they were excluded from the analysis.
- The following information was tabulated for each Biological Opinion: (a) project name, location, Federal identification number, date issued, and office issuing the opinion; (b) project type and number of acres expected to be impacted; (c) project proponent, Federal Lead Agency, and, where possible, the name of the consulting firm implementing the Terms and Conditions; (d) the anticipated harassment and mortality take limits; (e) the actual harassment and mortality take limits as reported by the Federal Lead Agency, project proponent, biological monitor, or other knowledgeable individuals; and (f) the mitigation measures given in each opinion that are (i) similar and (ii) different from those given in Eagle Mountain's Biological Opinion.
- Approximately 145 individuals, including biological monitors and other individuals, were contacted to determine the actual number of tortoises

handled and accidentally killed during implementation of the Terms and Conditions.

- CMBC met with representatives of the primary Federal Lead Agencies (i.e., Bureau of Land Management in California and Nevada, and Edwards Air Force Base in California, etc.), and either discussed the Biological Opinions with staff or evaluated case files, which track project statuses.

Authorized versus actual harassment limits.— In California, 126 Biological Opinions have authorized 123 projects, 101 of which have occurred.

- Eighty-eight (88) of those 101 opinions authorized the handling (harassment) of 1,362 tortoises.
- The remaining 13 opinions allowed for unlimited harassment.
- Thus far, 919 tortoises have been reportedly moved from harm's way as authorized by those 101 opinions.

In Nevada, 108 opinions have authorized 140 different projects, 70 of which have occurred.

- Sixty-six (66) of those 70 opinions authorized the handling (harassment) of 1,742 tortoises.
- The remaining four opinions allowed for unlimited harassment.
- Thus far, 536 tortoises have been reportedly moved from harm's way as authorized by those 70 opinions.

Therefore, during construction, operation, and maintenance of about 171 different projects in California and Nevada:

- a total of 1,455 individual tortoises have been moved from harm's way. Individual tortoises were often handled multiple times. Many other tortoises were kept from harm's way by other mitigation measures, such as tortoise-proof fencing.

Harassment limits have been:

- met in California (101 opinions) one time and exceeded six times.
- met in Nevada (70 opinions) two times and exceeded six times.

Most of the tortoises have been handled during long, linear projects, such as pipelines and transmission lines, and a majority of these tortoises were handled during only three projects. Such projects differ from the landfill and rail operation proposed at Eagle Mountain in that new areas were impacted on a continuous basis as construction proceeded, and fencing of construction areas was impractical.

- Of the 565 tortoises handled during pipeline projects, 559 of them (98.9%) were handled during construction of the Mojave-Kern Pipeline, which spanned the entire north-south and east-west axes of the tortoise's range, through California, Nevada, and Arizona.
- Of the 227 tortoises handled during installation and maintenance of transmission lines, 174 (77%) have been handled during installation of the Meade, Nevada to Adelanto, California transmission line.
- Of the 53 remaining tortoises (i.e., 227 minus 174 handled on the Meade-Adelanto project), 41 (77%) were handled along the access road and project site at the LUZ Solar Generating Plant near Harper Lake, San Bernardino County, California.

Cumulatively, 774 of the 919 tortoises handled (84%) were handled during these three projects.

Authorized versus actual mortality limits. — Unlike some harassment limits that allow an unlimited number of tortoises to be handled, there are no unlimited mortality limits; every opinion has a stated number of tortoises that may be accidentally killed. If the mortality limit is reached, all project activities that may result in another death must stop, the Federal Lead Agency contacted, and consultation reinitiated with the Service.

In California, the 101 opinions implemented:

- Authorized the incidental mortality of 394 tortoises.
- Of 394 mortalities authorized, 53 tortoises (13%) have been accidentally killed.
- The mortality limit has been met one time (American Girl Mine in Imperial County, where only one tortoise death was authorized).
- The mortality limit has been exceeded one time (Kern portion of the Mojave-Kern Pipeline where 29 tortoises were accidentally killed, exceeding the 25 tortoise mortality limit by four tortoises).
- Thirty-eight (38) of the 53 tortoises reported dead (72%) were accidentally killed on the Mojave-Kern Pipeline.
- Four linear projects have been responsible for 91% (i.e., 48 of 53) of reported tortoise mortality:
    - Mojave-Kern Pipeline (38 tortoises)
    - LUZ Solar Electric Generating Plant (four tortoises, three found along the access road, which is not fenced)
    - Meade-Adelanto Transmission Line (three tortoises)
    - Fort Irwin's Current Mission (four tortoises found along tank trails)
- Tortoise mortality has been reported on only

8 of the 101 projects that have occurred. These included:

- two mining projects
- one highway project
- two electrical transmission projects
- one pipeline
- two miscellaneous military projects

In Nevada, the 70 opinions implemented:

- Authorized the incidental mortality of 702 tortoises. The relatively large mortality limit is due mostly to one project, the Kerr-McGee Apex Project, where 416 tortoise deaths were authorized.
- Of 702 mortalities authorized, six tortoises (0.8%) have been accidentally killed.
- The mortality limit has been exceeded one time (Mission Hills Flood Control Structure in Henderson, Nevada where one construction-related and two maintenance-related mortalities were authorized; two tortoises, an adult and a juvenile, were actually killed during construction).
- The mortality limit has not been met for any of the other 69 opinions.
- Unlike California, most of the mortality cannot be attributed to one or several projects. The six tortoises were accidentally killed on five different projects:
  - three tortoises during transmission line and fiber optic cable installation
  - one tortoise during expansion of a landfill
  - two tortoises during construction of the Mission Hills facility.

Cumulatively, in both California and Nevada, during the 171 opinions that have thus far been implemented:

- the Service authorized the incidental mortality of 1,096 tortoises.
- Fifty-nine (59) of the authorized 1,096 tortoise mortalities (5.4%) reportedly occurred.

The Service has indicated that the authorized mortality limit is the acceptable number of tortoises that may be accidentally killed, in spite of the Terms and Conditions, without jeopardizing the species; tortoises would be effectively protected if the authorized mortality limit was met for each project. We see with the above analysis that only 5.4% of the authorized mortality limit was reportedly met; an additional 1,037 reported mortalities could be allowed and tortoises still effectively protected.

The above analysis also indicates that 1,455 tortoises were moved from harm's way during the 171 projects that occurred. Although not all of the tortoises would have died if not moved, it is reasonable to assume that some of these tortoises would have been killed if not rescued. In the absence of the Terms and Conditions, these 1,455 tortoises would have been exposed to construction and maintenance activities without the benefit of protection.

Given this information, CMBC concluded that implementation of the Terms and Conditions for projects that have thus far occurred has effectively protected tortoises; the number of tortoises actually killed relative to the numbers that were authorized is substantially lower than would be expected in the absence of protective measures.

To further address the Judge's concerns, it is important to determine the similarity of the Terms and Conditions thus far successfully implemented to reduce tortoise mortality with the Terms and Conditions that would be implemented for the Eagle Mountain Project.

Similarity of previously implemented Terms and Conditions with those of Eagle Mountain's Biological Opinion. — Terms and Conditions given in Eagle Mountain's opinion are separated into 21 different categories. Nine of these are termed "core conditions," as they are typical requirements found in other Biological Opinions (Table 1). Eight of the remaining 12 categories have occasionally been required in other Biological Opinions, and four are unique to Eagle Mountain (Table 2).

Core conditions.— Each of these conditions would be required for the Eagle Mountain Project. They are lettered "a" through "i": (a) buy land to compensate impacts; (b) revoke permit if conditions are not implemented; (c) appoint a field contact representative; (d) conduct tortoise awareness programs; (e) check beneath vehicles to avoid

Table 1. Percent core conditions found in 101 California and 70 Nevada opinions that have been implemented.

Description	California	Nevada
a. Buy land	44%	0%
b. Revoke permit	22%	1%
c. Appoint field contact	77%	87%
d. Awareness program	99%	99%
e. Check beneath vehicles	64%	25%
f. Define work zone	91%	93%
g. On-site monitor	98%	99%
h. Tortoise-proof fences	59%	75%
i. Project end report	72%	8%

Table 2. Number of opinions for which "other conditions" are required.

Description	California	Nevada
j. Install ballasts	0	0
k. Rail line culverts	2	2
l. Roadway culverts	6	5
m. Cover refuse	1	3
n. Monitor ravens	11	0
o. Remove road-kills	0	0
p. Monitor train trips	0	0
q. Monitor populations	7	1
r. Fence landfill	2	2
s. Chemical raven deterrent	0	0
t. Eliminate raven nests	18	0
u. Conservation trust fund	0	2

crushing tortoises; (f) designate the work area and restrict project activities to that zone; (g) have a biological monitor on-site throughout construction phases of the project; (h) use tortoise-proof fences to restrict tortoises from the work area; and (i) report efficacy of the measures to the regulatory agencies at the end of construction or periodically during project operation.

Having categorized the measures, CMBC then evaluated each of the 234 opinions issued in California and Nevada, and summarized the commonness of the core conditions in those opinions. Since CMBC was interested in the efficacy of the Terms and Conditions that have been implemented, only those 171 opinions that have been implemented are included in Table 1.

The three most common Terms and Conditions cited in all Biological Opinions, including the one issued for Eagle Mountain, are *tortoise awareness program*, *define work zone*, and *on-site monitor*. Five of these nine Terms and Conditions (d, e, f, g, and h) are field-related measures that are intended to avoid tortoise mortality during construction, operation, and maintenance. Based on CMBC's experience monitoring construction in occupied tortoise habitat and discussions with Ray Bransfield and Kirk Waln of the Service's Ventura office, we believe that the four measures that provide the most protection to tortoises include *tortoise awareness program*, *define work zone*, *on-site monitor*, and *tortoise-proof fences*.

Tortoise education programs given to construction personnel in the field result in an increased awareness of tortoises on the job site. In CMBC's experience, many tortoises are reported to our monitors by construction personnel who far out number the one or two monitors typically assigned to a project. In one case, a professional geologist working for three years near Ludlow, California reported that he had never seen a tortoise on the project site (LaRue, personal observation). He and others were given a tortoise awareness program on a Monday morning and he saw his first tortoise on the project site on Friday of that same week.

Defining work zones and restricting construction activities to those zones minimize impacts to tortoises and their habitat. Physical demarcation of the construction zone reminds workers that they are in tortoise habitat and allows the biological monitor to enforce restriction of construction activities to that zone. The impact area is closely surveyed, tortoise burrows excavated, and tortoises removed from harm's way. Restricting construction to that cleared area protects tortoises and burrows found outside the impact zone. *On-site monitors* move tortoises out of harm's way, enforce compliance with the Service's Terms and Conditions, heighten the awareness of workers, etc. *Tortoise fences* exclude tortoises from harm's way. Most reported mortalities have occurred on pipelines and transmission lines, which cannot be effectively fenced. Boarman's studies (1995) have clearly indicated that tortoise mortality is significantly lower along Highway 58 because of tortoise-proof fences.

In the previous section, CMBC reported that only 59 tortoises have been reportedly killed during 171 projects where the above Terms and Conditions were required. We concluded that these numbers indicate that tortoises have been effectively protected during Service-authorized projects. In this section, CMBC reports that core conditions d, f, and g were required for most of the 171 projects where tortoises were protected. Based on professional experience and discussion with the Service, we conclude that these three measures and tortoise-proof fencing are the most effective measures in protecting tortoises during construction, operation, and maintenance activities of projects in tortoise habitat. CMBC cites this information as evidence that tortoises have been protected by the same Terms and Conditions that would be required for the Eagle Mountain Project.

Other Conditions.— These measures are also found in the Eagle Mountain opinion, but are not typically found in other Biological Opinions. These other measures are lettered "j" through "u": (j) install ballasts along the rail line; (k) install culverts under rail line; (l) install culverts under roadway; (m) cover refuse at landfill; (n) monitor raven populations; (o) remove road-kills to reduce potential raven forage; (p) monitor rail line to remove tortoises from tracks; (q) monitor tortoise populations; (r) fence landfill to exclude predators; (s) control ravens with chemical deterrent; (t) eliminate ravens observed nesting on facilities; and (u) collect fees to be used in a conservation trust fund.

Table 2 lists the number of opinions in which the same or similar measures are required. The table includes all projects with the required measure, including those that have not yet occurred.

Measures k and l require the installation of culverts along the access road and rail line. Culverts are intended, often in combination with fencing, to reduce impacts from roads and railroads to the desert tortoise. Negative impacts to tortoises from roads and highways have been well documented (Nicholson 1978, LaRue 1992, Boarman 1995, Hoff et al. in prep., etc.). However, the question of whether culverts can be effective in preventing fragmentation of tortoise populations divided by barriers such as highways and railroads remains unclear.

Reported culvert use by tortoises along fenced highways has been equivocal (Boarman 1995): "The most conservative interpretation of the data available suggests that tortoises may occasionally use culverts to cross a highway or similar barrier. ...There are currently no data to support the contention that tortoises will regularly use culverts." However, since Boarman's report, two tortoises have crossed under Highway 58 on four occasions between July and September, 1995 (Boarman, pers. comm., 15 September 1995). Studies of culvert use by tortoises in experimental settings (Fusari 1982, Ruby et. al. 1994) show that tortoises appear to learn to use culverts over time, especially tortoises resident in areas adjacent to culverts. More data are needed to determine tortoise use of culverts (Fusari 1982, Boarman, pers. comm., 15 September 1995).

Tortoise-proof fencing would be erected around the landfill and along the access road and, if needed, along the rail line. Boarman recommends that culverts be used in combination with fences to prevent road kills and avoid population fragmentation (Boarman 1995). The effectiveness of tortoise-proof fences in preventing road-kill mortality has been fairly well studied. Boarman (1995) found significantly fewer tortoise carcasses along a fenced road than along an unfenced road, indicating a 93% reduction in mortality due to protection afforded by the fence. Additionally, 88% fewer vertebrate carcasses (other than tortoise) were found along fenced versus unfenced roads.

Other important recommendations for use of fences and culverts include using automatic gates or "tortoise-guards," similar to cattle guards at gates (Boarman 1995), and avoiding chicken wire or similar materials in fencing, to prevent stress, potential injury, and energy impacts to tortoises (Fusari 1982), and, in so doing, avoid injury and mortality of other animals, including snakes, lizards, and hares (Engelke 1992).

Installation of ballasts to reduce fragmentation of tortoise habitat (measure j in Table 2), removal of road-kills to avoid feeding tortoise predators (measure o), removing tortoises from the rail line ahead of each train trip (measure p), and chemical deterrence of ravens (measure s) are all intuitive measures that have been recommended for Eagle Mountain, but have not been recommended for other projects authorized by the Service. Since they have not been implemented, there is no record available to determine how effective they may be in protecting tortoises and avoiding habitat fragmentation.

California offices of the Service require more mitigation measures addressing potential impacts associated with Common Ravens than do the two offices in Nevada (i.e., consider measures n and t). However, none of these measures has been implemented for a period longer than five years, since 1990 when the tortoise was Federally listed. Although these measures are intuitively appropriate, and may serve to eliminate the sponsorship of ravens by new development, there is little opportunity to determine their efficacy in avoiding increases of ravens in the desert. Non-project-related conditions that benefit ravens, such as increased road-kills and nesting opportunities, result in inflated raven populations even when development projects are designed to avoid that increase.

For Eagle Mountain, monitoring raven populations would be required to test the efficacy of the measures. Elimination of ravens, chemical deterrence, and other measures are required as contingencies to ensure that raven populations do not increase. And, into the foreseeable future, the regulatory agencies and others will be enlisted to continue to address the potential impact and develop and implement new measures as they are identified and required to avoid raven sponsorship.

Measure u, the conservation trust fund, is a key measure. It is likely the most substantial mitigation ever required for a project in desert tortoise habitat. Only two other projects reviewed have similar requirements, but neither of them approaches the scale of this project. Assuming full capacity of 20,000 tons of refuse each day, this fund could generate up to $6,000,000 per year for the purchase and conservation of desert tortoise habitat in Riverside County.

Given the preceding analysis and discussion, CMBC concluded that implementation of the Terms and Conditions for projects that have thus far occurred has significantly reduced the number of tortoises actually killed relative to the numbers that were authorized. Had all mortality limits been met, tortoises would not have been jeopardized in the Service's opinion, which CMBC equates with effective protection. In California, of 394 tortoise mortalities authorized, 53 tortoises (13%) have been accidentally killed, and in Nevada, of 702 authorized, six tortoises (0.8%) have been accidentally killed. Tortoise mortality has been reported on only eight of 101 projects occurring in California and on only five of 70 projects occurring in Nevada. Most known tortoise mortalities have occurred during construction of long, linear projects, such as pipelines and transmission lines.

CMBC has concluded that *tortoise awareness programs*, *defining work zones*, *on-site monitors*, and *tortoise-proof fences* have afforded the most protection to tortoises during construction, operation, and maintenance activities on previously approved projects. These measures have been required for 99%, 92%, 98%, and 67%, respectively, of the projects occurring in California and Nevada where only 5.4% of authorized tortoise mortality has reportedly occurred. Given the similarity of the Biological Opinion issued for Eagle Mountain with the previous opinions issued, CMBC concludes that the mitigation measures required for the Eagle Mountain project would effectively protect tortoises. Monitoring studies would be implemented and advisory committees established to ensure that protection was afforded and measures modified as necessary to deal with unforeseen impacts to tortoises and other biological resources.

Other Terms and Conditions included in the opinion for Eagle Mountain are unique or rarely required for other projects. Some of these (e.g., culverts) require more research and monitoring to determine their efficacy; others (e.g., fencing roads) appear to effectively reduce mortality of tortoises and other vertebrates. The establishment of a conservation trust fund is considered one of the most critical of these other conditions. The amount of this fund, which could exceed $6,000,000/year, is unparalleled by any other project, and should facilitate conservation of key tortoise habitat in other locations in Riverside County.

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Reproduction in Sonoran Desert Tortoises: A Progress Report

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Desert tortoises (*Gopherus agassizii*) in the Mojave and Sonoran deserts differ genetically, morphologically, and ecologically (Germano, 1993; Lamb et al., 1989; Luckenbach, 1982), so we might also expect differences in life history traits. Reproductive biology of wild desert tortoises is known primarily from the Mojave Desert (Hampton, 1981; Henen, 1997; Roberson et al., 1989; Rostal et al., 1994; Turner et al., 1984, 1986). Little information exists on reproduction of desert tortoises in the Sonoran Desert (Murray et al., 1996; Wirt and Holm, 1997), with no data on temporal or spatial variation. This paper presents reproductive output data from two Sonoran Desert tortoise populations in Arizona, one of which has now been studied for four years.

Our primary site was near Sugarloaf Mountain on the Tonto National Forest, 48 km northeast of Mesa, Maricopa County, Arizona. Elevations at Sugarloaf range from 671–900 m with steep, rocky slopes divided by many arroyos. Boulders up to 4-m diameter occur on many slopes. Our secondary site was in the Granite Hills, near the northeast end of the Picacho Mountains, approximately 30 km southeast of Florence, Pinal County, Arizona. Elevations at the Granite Hills range from 600-702 m, and topography is similar to Sugarloaf. Vegetation at both sites is classified in the paloverde-mixed cacti series in the Arizona Upland Subdivision of the Sonoran Desert (Turner and Brown, 1982).

At Sugarloaf, we monitored up to 13 female tortoises (184–288 mm straight midline carapace length — MCL) using radiotelemetry beginning on 14 April 1996 (Table 1). We attached AVM Instruments Inc. (Livermore, CA) or Telonics Inc. (Phoenix, AZ) transmitters using 5-minute gel epoxy to the anterior carapace. We monitored telemetered tortoises weekly. Except during hibernation, we weighed each tortoise with spring scales each week. We initiated radiography on 15 May 1997 using an HF-80 (MinXray Inc., Northbrook, IL) portable X-

Table 1. Egg production of desert tortoises at Sugarloaf Mountain, Arizona, 1996-97. MCL is midline carapace length. X-radiography was not used and clutch sizes not determined in 1996.

			1996			1997			
Tort.#	Initial MCL (mm)	Date telemetered	Eggs last palpated	Eggs laid by	mass (g)	Eggs last detected	Eggs laid by	mass (g)	Clutch size
3	269	13 Apr 96	20 Jun	28 Jun	-450	17 Jun	24 Jun	-190	2
25	248	13 Apr 96	3 Jul	11 Jul	-215				
1	243	3 Jul 96	*	3 Jul	*				
46	249	11 Jul 96							
51	235	8 Aug 96							
55	208	9 Aug 96							
57	254	9 Aug 96				1 Jul	8 Jul	-275	4
58	239	9 Aug 96							
61	184	23 Aug 96							
29	253	20 Sep 96				1 Jul	8 Jul	-275	5
63	221	13 Mar 97							
65	239	20 Mar 97				1 Jul	8 Jul	-250	4
68	288	10 Jun 97							

*Tortoise remained at burrow of initial capture from 3 Jul to 23 Aug 96; eggshell fragments found in burrow on 20 Sep 96

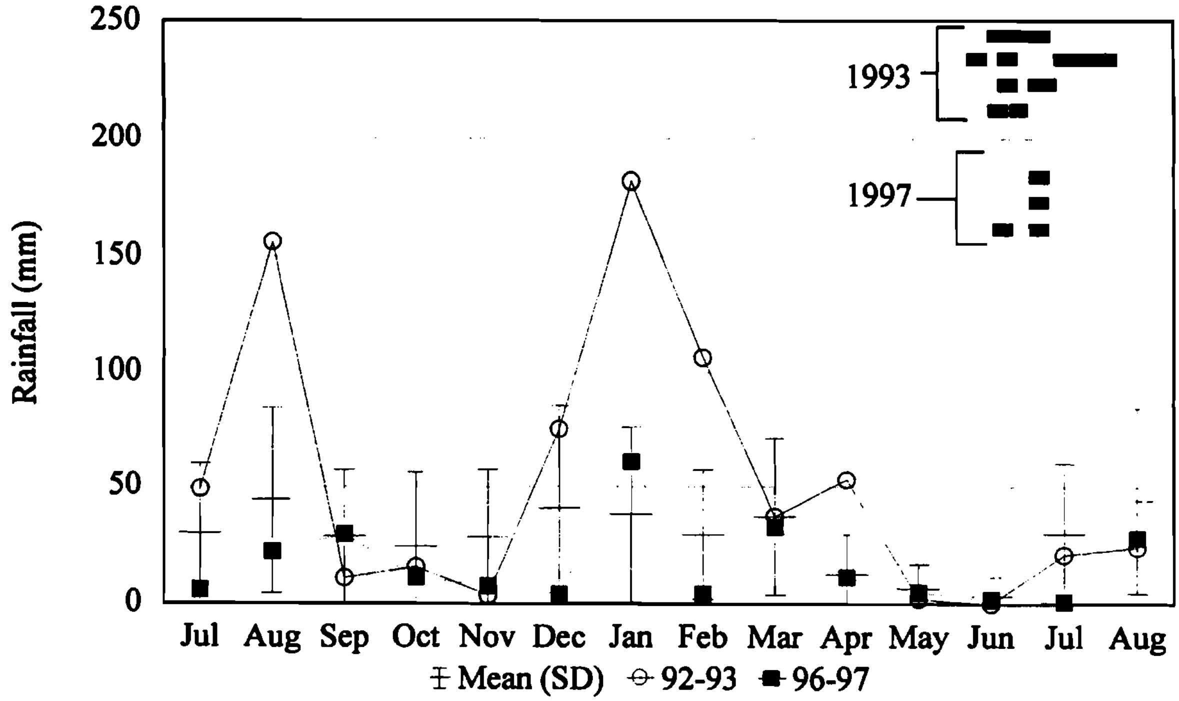

Fig. 1. Periods of oviposition (horizontal bars) of individual tortoises at Surgarloaf Mountain, Arizona, in relation to rainfall in 1993 (from Murray et al., 1996) and 1997. Long-term mean rainfall (±1 SD) from Stewart Mountain (from National Oceanic & Atmospheric Administration), approximately 13 km south of Sugarloaf, is plotted for comparison.

ray machine powered by a gasoline generator. We radiographed tortoises weekly unless we could detect eggs by palpation after we had confirmed clutch size on a previous radiograph. Weekly radiography continued until 12 August 1997. We also radiographed tortoises on 16 September and 21 October 1997. We recorded rainfall each week from a raingauge on site. We conducted weekly radiography at the Granite Hills from 4 June to 14 August 1997. Tortoises at the Granite Hills were individually marked but not telemetered, so we searched for as many females as possible, focusing on individuals previously radiographed.

We found and attached transmitters to most tortoises at Sugarloaf after the reproductive season was already under way in 1996 (based on data from 1993 (Fig. 1); Table 1). However, at least three of the four tortoises we found by early July laid eggs (Table 1). We detected eggs by palpation in tortoises #3 and #25, who oviposited by the end of June and beginning of July, respectively. We initially found tortoise #1 on 3 July and did not detect eggs by palpation; however, she remained at the same burrow until at least 23 August, and eggshell fragments were found in this burrow on 20 September. In 1997, four out of 12 tortoises (33%) with transmitters during the observed reproductive season laid eggs (Table 1). Eggs were first detected by radiography on 28 May, and oviposition occurred between 17 June and 8 July; we found no tortoises with eggs in September or October. Oviposition during both years occurred just before the onset of the summer monsoon (Fig. 1). Clutch sizes ranged from two to five eggs (*O(x,¯)*=3.8 ± 1.26 (1 SD)) in 1997, and no tortoises laid more than one clutch.

We radiographed 16 tortoises at the Granite Hills on at least one occasion, and eggs were detected in four individuals. Eggs first appeared on radiographs on 4 June and were last observed on 19 June (two individuals), 10 July, and 7 August; none of these individuals were recaptured after laying, so oviposition dates could not be confirmed. Clutch sizes ranged from one to five eggs (*O(x,¯)*=3.3 ± 2.06). Several tortoises were only captured either early or late in the reproductive season, so we probably failed to detect some clutches. Mean clutch frequencies at Sugarloaf in 1997 differed from those in 1993. In 1993, eight of 10 telemetered tortoises laid eggs at this study site (Murray et al., 1996). The difference in clutch frequency between 1993 and 1997 may be related to rainfall patterns preceding oviposition, during egg production. Summer monsoon rainfall in 1992 and winter rainfall in 1992–93 were both higher than the average at Stewart Mountain, about 13 km south of Sugarloaf (Fig. 1; rainfall data from National Oceanic & Atmospheric Administration). These wet conditions provided abundant summer and spring forage prior to the 1993 reproductive season, when most females laid eggs. Summer rainfall in 1996 and the following winter were both below the average at Stewart Mountain (Fig. 1). Tortoises had little fresh forage during the year prior to the 1997 reproductive season, and few tortoises laid eggs.

Wirt and Holm (1997) conducted radiography at two sites in the Sonoran Desert in 1994. They radiographed six adult female tortoises at the Maricopa Mountains (about 27 km northeast of Gila Bend, Maricopa County) and found eggs in two (33%); these tortoises had clutch sizes of four and six eggs. They also radiographed eight females at Espanto Mountain, 12 km east of the Maricopa site. All eight tortoises laid eggs, and clutch sizes ranged from two to nine eggs ($O(x,^{-})$ =5.6 ± 2.23). Wirt and Holm attributed the difference in clutch frequency between the two populations to recent environmental differences between the two sites. The Maricopa Mountains had apparently suffered a major drought during the decade prior to the study, while conditions had apparently been less severe at Espanto Mountain (Wirt and Holm, 1997).

Tortoises at Goffs, California, in the Mojave Desert, laid one to three clutches/year from 1983 to 1985, and only one monitored tortoise during this time failed to lay eggs (Turner et al., 1986). Turner et al. found a significant relationship between mean clutch frequency and spring annual plant production, which is directly related to winter rainfall. Henen (1997), also working at Goffs, found that total egg production did not differ between a year following normal winter rainfall and a year following a significantly drier winter, but fewer tortoises produced eggs in the dry year. He also concluded that summer forage can affect egg production, because energy obtained from this forage could be allocated to eggs the following spring. We are continuing to collect reproductive output data from Sugarloaf in 1998. These additional data will help determine how seasonal rainfall affects reproduction in the Sonoran Desert.

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ABSTRACTS FROM THE 1997 DESERT TORTOISE COUNCIL SYMPOSIUM

Ecosystem Wide Scientific Database

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Department of Defense (DOD) assets in the Mojave Desert are large, mission essential, unique and represent holdings of all four major services. As large as the installations are in the region, they are not autonomous ecological units. Just as their missions are only a part of the entire defense mosaic of the nation, their lands are a part of the larger, more complex Mojave Desert ecosystem. Large scale land management planning is not a new phenomena for the Mojave Desert. Department of Interior (DOI) has engaged in planning for the public lands under their jurisdiction for decades. The DOD installations in the region have generally become active in land use planning for natural and cultural resources over the last decade. Individual installations have concentrated on inventorying their own resources and developing internal strategies for integration of stewardship mandates. In spite of these efforts, much needs to be learned about both the habitat and the inhabitants of the entire ecosystem. Currently, planning is underway for regional segments of the entire eco-geo-physio-bio-socio-unit. These plans have been undertaken primarily by the major DOI land holders in cooperation with agencies responsible for conservation of threatened, endangered and sensitive species. Involvement has been actively encouraged from public and private interest groups, elected officials and the military. For the most part, military involvement has been in the role of observer rather than participant. Two simultaneous phenomena have changed this approach. First, lessons have been learned, and are being applied, from military installations located in centers of increasing urbanization. Second, DOI planning in the Mojave Desert includes the lands under the jurisdiction of the DOD. These realities have led to an understanding that the long term success of the military readiness mission is tied to the health of the ecoregion, and the greater the success of the planning effort, the longer the ecoregion will remain healthy. It can also be seen that the success of the planning effort depends on both the reliability of the scientific data upon which it is founded and the degree to which it is available and useful to the manager. The Mojave Desert Ecosystem Initiative represents DOD's attempt to ensure the successful accomplishment of both these criteria.

A Six-Year Rewiew of Accomplishments of the Health and Disease Research Program for Desert Tortoises (*Gopherus agassizii*): A Consensus Statement

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A conference to critically review six years of desert tortoise research on health profiles, health reference ranges, and diseases (primarily upper respiratory tract disease [URTD]) was held at Soda Springs, California from October 31 to November 3, 1996. Twenty scientists conducting the research attended, as did 16 wildlife biologists and managers representing government agencies. Three internationally recognized experts on health profiles and reference ranges and mycoplasma (Drs. John Lumsden, Joe Tully, and Joel Baseman) were invited to chair sessions and conduct a critical review. The participating research scientists are contributing to development of a consensus statement. The findings can be placed in four categories: areas of certainty, areas of uncertainty, suggested areas for research, and recommendations and guidelines for conservation and management of tortoises.

Areas of certainty.— In terms of field techniques, sterile procedures are essential, not only because of mycoplasma, but also because of the existence of other diseases. The health profile forms and accompanying 35 mm slides provide essential quantitative and qualitative data about clinical signs of disease, which can be coupled with data from laboratory tests. The salvage and necropsy of selected ill, dying, and recently dead tortoises are critical components to research on diseases and causes of mortality.

Routine laboratory tests provide ancillary and supportive information for determining the health status and overall well-being of desert tortoises. Marked physiological alterations in routine laboratory test results are associated with season, rainfall, sex, and reproductive cycle in adult animals. Such test results are not diagnostic for tortoises with mycoplasmosis, however. Specific tests for mycoplasma include cultures, ELISA and PCR tests. *Mycoplasma agassizii* is infectious, causes URTD, and is a horizontally transmissible disease. Clinical signs vary in onset, severity, and duration. In adults, the disease is chronic and may be clinically silent. In the case of the gopher tortoise (*Gopherus polyphemus*), tortoises become "sicker quicker" on repeated exposures to mycoplasma. *Mycoplasma agassizii* should be considered a threat to the well being and recovery of all wild populations of desert tortoises.

Areas of uncertainty.— The following are some areas of uncertainty requiring more definitive research throughout the geographic range of desert tortoises in the U.S.: the effect of URTD on the survival rates of individual animals; the relationship among infection rates, transmission rates, population size, and clinical expression of disease; effects on population dynamics and viability; the role of burrow/fomite/vector in transmission; the protective immunity of tortoises; vertical transmission of disease; and the presence and pathogenic nature of other mycoplasma strains.

Recommendations and guidelines for future research.— The above areas of uncertainty need to be pursued. In addition, for URTD, epidemiological research on wild populations is a critical issue, as is determining systemic effects of URTD, and effects on reproduction and behavior in individual animals. Research needs to be conducted to determine if URTD can be transmitted via burrows and fomites.

Recommendations for conservation and management of tortoises.— Routine hematologic and biochemical laboratory testing should be part of the protocol for both initial and subsequent evaluations of ill tortoises. Salvage of ill, dying, and recently dead tortoises should be expanded to ensure that critical data are collected on tortoises with signs of URTD (to identify the pathogens and for epidemiology), as well as to continue the existing research program on causes of mortality and the role of environmental toxicants. Guidelines and protocols for a wide variety of activities need to be up-dated, finalized and implemented, using the latest information, e.g.: for screening and handling tortoises that are part of field and laboratory research projects; for determining the disposition of clinically ill tortoises and seropositive clinically healthy tortoises; for determining translocation projects; and for management of captive tortoises.

Assessing Gender in Free-ranging Desert Tortoises (*Gopherus agassizii*) Using External Morphology

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When using external morphology to determine the gender of tortoises, researchers have long relied on the work of Woodbury and Hardy (1948; Ecological Monographs, 18:145-200). However, these results pertain primarily to large tortoises, and there has always been a need for a quantitative method to determine gender of smaller tortoises.

We applied multivariate statistical techniques to 22 measurements of the external morphology of 105 tortoises to determine whether these measurements could be used to identify male and female tortoises. We determined gender independently of external morphology (serum testosterone levels, x-rays, behavior) for 35 females and 13 males. Of the remaining individuals, those with carapace length (CL) greater than 200 mm (5 females, 33 males) were assigned to a gender category based on morphology that was similar to individuals of known gender. Nineteen individuals (CL < 200 mm) of unknown gender were not assigned to gender *a priori*.

Three discriminant analyses were performed: only animals of known gender, all larger animals (CL > 192), and all smaller animals (CL < 220). Analysis of the data set containing only animals of known gender correctly classified all but two males (CL = 179, 206) using 11 characters. In the trivial case of discriminating larger animals, all classified correctly. Although it is generally considered easy to classify larger animals based on external morphology, the model required 9 characters to correctly classify all of these individuals. When only smaller animals were considered, all individuals of known gender classified correctly using 5 characters, and when the 19 small individuals of unknown gender were classified with this discriminant function, all animals fell cleanly into two groups.

Only three characters were important for separating males and females in all analyzes. In each, a deep plastron concavity (always the largest coefficient) and wide front foot (always a large coefficient) were associated with males. Gular length projection was only associated with males for the data sets containing all animals and large animals. For the smaller tortoises, a long gular was associated with females.

Despite the apparent success of these models, when the discriminant scores were plotted against carapace length (a proxy for age), it became clear that males with a CL of 100-190 were probably classified correctly, but all animals smaller than this were classified as females. While it is possible that all of these animals were female, it is more likely that animals with a CL less than 100 included males that had not started to acquire secondary sexual characters. Therefore, it appears possible to use multivariate statistics to determine the gender of tortoises with carapace lengths as short as about 100 mm.

Effects of Recreational Noise on Wildlife: An Update

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Any sound made by humans in wildlife habitat may be *noise* (unwanted sound) from an animal's perspective. Bowles (1995) reviewed the literature on noise effects, emphasizing recreational noise; there has been increasing interest since the review was written. Here is an update.

The effects of recreational noise are difficult to assess because a number of adaptive responses may be involved, making the overt behavioral or physiological changes in response to noise highly variable. These responses include the acoustic startle, the orienting response, other species-typical and individual strategies for coping with novelty, species-typical defensive behaviors, and responses conditioned by previous exposures to humans. Although some types of recreational noise are never associated with human intrusions, most are, making conditioned (>learned=) responses particularly likely. Animals may therefore be affected by recreational noise because the noise itself affects them or because they associate the noise with human intruders. To date, most experiments have not differentiated the two potential causes, although the level of exposure tolerated and the probability of habituation are likely to vary greatly between the two.

Laboratory studies of captive animals exposed to continuous or nearly continuous noise at high levels (averaging > ~80 dB SPL and < 120 dB SPL) for long periods (many days or weeks) can experience significant behavioral and physiological effects. These include audiogenic (sound-induced) seizures, increases in activity, enlarged adrenals, irritability, reproductive failures, and hearing loss. Very high and very low levels of noise are associated with effects on growth as well, but several authors have commented on an apparent increase in growth rate at moderate levels (~60-80 dB SPL). These effects are correlated with the cumulative level of exposure rather than individual incidents. Behavioral experiments have demonstrated that noise at high levels is mildly aversive in and of itself, apparently because the physiological events stimulated by noise are aversive (*e.g.*, muscular flinch, vasoconstriction, bradycardia). However, noise is not aversive enough to be an effective conditioning stimulus over the long-term. This explains the failure of most acoustic harassment devices to deter wildlife from favored areas.

Wild animals exposed to intense noise with sudden onset can panic and injure themselves or their young. However, these injuries are virtually impossible to study experimentally - so-called >blind panic=, in which animals behave as though they are unaware of their environment, is difficult to induce without active pursuit. Animals control their movements to minimize risk. Loss rates have varied greatly in the few documented cases of injury or loss; mammals and raptors appear to have little susceptibility to these losses, whereas the most significant losses have been observed among waterfowl. Panic responses habituate quickly and completely (<5 exposures). Animals in remote areas are most likely to panic because they are naïve to human disturbances.

More moderate responses habituate slowly. For example, migratory waterfowl often make brief flights in response to aircraft overflights. If individuals are susceptible to damage as a result of these moderate responses, noise may continue to have an impact over long periods. For example, gulls nesting in colonies can take advantage of brief defensive flights to cannibalize one another's eggs (Burger 1981). Unfortunately, little information is available on the actual extent of such losses. Migrants and animals living in areas with high concentrations of predators are most vulnerable. Longer-term changes in activity and habitat use have been observed in response to noise at low or moderate levels. Human speech is an excellent example of such noise - human speech arouses particularly strong physiological responses, even at low signal-to-noise ratios, apparently because animals associate speech with handling or intrusion. Animals use sound to obtain information at long range about the presence of danger. Speech is an example of noise that *signals* danger (human presence), and responses to it are best interpreted as a reaction to human *intrusion* rather than the noise *per se*. Primitive reflexes such as the startle response enhance these responses when noise has a high onset rate (responses are strongest to sounds with onsets of 5-20 ms at levels > ~80 dB). Unfortunately, very little effort has been invested to measure the specific acoustic characteristics of recreational noise that arouse the greatest responses.

The responses to human-made noise that have been observed include increased movement after the exposure, avoiding or evacuating areas when noise is present (*e.g.*, in parks on weekends), changes in eating or drinking patterns (*e.g.*, drinking early in the morning), and arousal of species-typical defensive behaviors (*e.g.*, flight, aggression). Although these responses could potentially lead to effects on health or reproduction, it is clear that animals adapt their behavior to minimize the effect of noise disturbances. Displacement from favored habitat by persistent human encroachment, signaled by noise, is still the only well-documented negative effect. Future studies of effects such as changes in energy expenditure, food and water consumption, and care of young, should demonstrate the outcome of a change (*e.g.*, decreased body-weight as a result of changes in feeding patterns) rather than short-term changes in behavior.

There are great gaps in this literature. Many important groups of animals have received little or no attention to date, including large carnivorous mammals, reptiles, and amphibians. In addition, research on specific problem sources (*e.g.*, ORV's, ATV's, snowmobiles) has tended to draw attention away from basic research that is badly needed. In particular, most research on recreational noise has emphasized effects that are the result of noise as a *signal* for some other disturbance. Few efforts have considered the effects of noise *per se*. One of the most important and least-studied is masking, which occurs when human-made noise obscures an important natural sound for a significant proportion of the time. Although the literature on this topic area (now called >acoustic ecology=) is growing, there are still no definitive studies showing that human-produced noise causes significant masking of important sounds for any species, even though the potential for this effect is very obvious. Future studies should be designed to detect subtle effects, as animals often alter their listening and calling patterns to adapt to interfering noise, whether natural or human-made.

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Effects of Simulated Sonic Booms and Low-Altitude Aircraft Noise on the Behavior and Heart Rate of the Desert Tortoise, (*Gopherus agassizii*)

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Several species of tortoises, including the threatened desert tortoise (*Gopherus agassizii)*, have acoustic social signals, and are known to react to meaningful sounds in their environment. Concerns have been expressed that high-intensity sonic booms and subsonic aircraft noise could materially alter their behavior. Unfortunately, very little is known about the responses of reptiles to noise. Therefore, Hubbs-Sea World Research Institute (HSWRI) investigators studied the effects of worst-case simulated jet noise and sonic booms on desert tortoise hearing, behavior, and physiology in the

laboratory from 1993-1995 under funding from the U.S. Air Force, with support from the Environmental Management Office at Edwards Air Force Base, California. The goals of the present portion of the study were to measure behavioral and cardiac responses to noise exposures in a laboratory setting during exposure to both simulated sonic booms and subsonic low-altitude aircraft noise.

Species-typical defensive responses of testudinates to the approach of danger include startling, running, diving underwater, wedging the shell into a crevice, urinating and defecating on an attacker, producing threatening sounds, freezing, and withdrawing into the shell. Based on the evidence prior to the start of this study, the plausible potentially-damaging responses were (1) urination by a water-deprived tortoise, (2) long-term changes in normal activity patterns, and (3) inappropriate behavioral responses (*e.g.*, emerging from the burrow in the heat of summer).

The rearing conditions of the tortoises and experimental acoustic exposures have been described in a previous abstract. In this series of experiments with 12 of the 14 tortoises, individuals were exposed to worst-case subsonic aircraft noise and simulated carpet booms in a chamber equipped with a time-lapse video monitoring system. Tortoises were allowed to acclimate to the chamber for several hours before exposure (overnight) and were monitored until the end of the day of exposure. They received three series of 20 exposures lasting 40 min separated by at least 2 hr. Half the tortoises exposed using this protocol were equipped with heart-rate monitoring electrodes implanted in the shell to determine heart rate responses.

Results of both series of experiments showed that, while the tortoises exhibited startle responses (*e.g.*, muscular flinching, increases in heart rate, abrupt movements) after being touched, they did not have an acoustic startle response - no muscular flinch was observed and no abrupt increase or decrease in heart rate could be measured.

Exposures to simulated jet overflights produced a typical reptilian defensive response - freezing. Freezing to initial exposures was abrupt, with head and appendages often left extended. After several exposures, tortoises looked overhead as though attempting to identify the location of the sound source, followed by a decrease in activity. The behavioral change was abrupt during initial exposures. During or after the exposures, tortoises frequently became quiescent (totally immobile) for periods of up to 113 minutes. Tortoises investigating their habitat stopped walking and eating tortoises stopped eating. Averaged heart rate measurements showed a 7-8% decrease during the same period, corresponding to the drop in activity. Recovery occurred within 2-4 hours of the exposure. Over a 24 hr period, these changes did not result in significant decreases in heart rate.

Tortoises were also exposed to simulated sonic booms. Two sets of experiments were performed using (1) two series of ten sonic booms at levels from 0.25 to 4 psf, and (2) intermittent exposures to 4 single sonic booms ranging from 1 to 6 psf. Tortoises did not freeze after initial exposures. Head withdrawal was not observed. Typically, they looked around briefly (orienting), and then resumed their previous activity. Both increases and decreases in activity followed the exposures, but lag times varied greatly and the changes could not be linked causally to the simulated sonic booms. There was no relationship between heart rate or increases in activity and the level of the sonic boom. Orienting responses on the sonic booms declined with successive exposures, suggestive of habituation.

The tortoises urinated and defecated frequently on days when they ate well and rarely when they did not eat. Defecation and urination were not expected during noise exposures after it was determined that the tortoises did not have an acoustic startle, but it was possible that changes in activity could have stimulated changes in voiding rates. However, the rate of urinations and defecations *relative to food consumption* was not detectably different during exposure experiments. Because the tortoises ate less in the experimental chambers overall and possibly also because they were slightly less active, voiding rates were actually slightly lower under exposure conditions. Because the tortoises were never food- or water-deprived, these results should be extrapolated with caution to natural conditions.

In summary, the tortoises were responsive to sounds in their environment, including aircraft noise. They exhibited freezing and a small decrease in activity in response to protracted subsonic noise exposures and orienting responses to sonic booms. Decreases in activity as a result of protracted exposure to subsonic aircraft noise resulted in a 7-8% decrease in heart rate. These decreases included halting of eating for periods > 1 hr. Repeating exposures on separate days provided evidence of habituation, but the rate was slow.

Effects of chronic exposure (frequent, repeated exposures) to aircraft noise cannot be evaluated based on these experiments because measurements of habituation over protracted periods were not conducted nor were the tortoises held under natural conditions. However, tortoises had begun to habituate within the scope of the experiments, suggesting that they are capable of doing so over time. Changes in activity with repeated exposure to sonic booms should be investigated under natural conditions, allowing measurements of habituation rate and also responses under conditions that were not simulated in the laboratory (water deprivation, hunger, torpor).

Effects of Simulated Sonic Booms and Low-Altitude Aircraft Noise on the Hearing of the Desert Tortoise (*Gopherus agassizii*)

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Testudinates (turtles and tortoises) have been characterized as deaf because man species exhibit little overt response to transient sounds in their environment. However, they possess auditory organs, and the few species that have been examined can hear, even if they lack great sensitivity. Several species of tortoises, including the threatened desert tortoise (*Gopherus agassizii)*, have acoustic social signals and are known to react to meaningful sounds in their environment. Therefore concerns have been expressed that high-intensity sonic booms or jet aircraft noise could damage desert tortoise hearing or mask social and other important natural signals.

Hubbs-Sea World Research Institute (HSWRI) investigators studied the effects of simulated jet noise and sonic booms on desert tortoise hearing in the laboratory from 1993-1995 under funding from the U.S. Air Force, with support from the Environmental Management Office at Edwards Air Force Base, California. The worst-case sonic boom expected from the aircraft of greatest concern, the F-22, was modeled in the Hubbs-Sea World Research Institute's Impulse Noise Test Facility (INTF). Desert tortoises were exposed to simulated sonic booms in the INTF with energy equivalent to both focused and more typical carpet booms. Focused booms were simulated with exposures to (1) 10.5-psf simulated booms with a rise time of 0.4 ms and a total duration of 130 ms and (2) 10 exposures to 6-psf booms with a rise time of 0.4 ms and a duration of 120 ms. Carpet booms were simulated with exposures to two 6-psf booms. Worst-case subsonic (low-altitude) noise was simulated with 20 subsonic exposures over a period of 40 minutes, with levels ranging from 94.6 to 114.2 dB CSEL. Peak SPL of these overflights reached 126.1 dB. These exposures were delivered in an IAC Sound Isolation Chamber using a U.S. Air Force Aircraft Noise Sound Simulation System.

The goals of the study were two-fold: to measure the auditory and vibration sensitivity of desert tortoises, and (2) to measure temporary changes in auditory sensitivity after exposure to worst-case aircraft noise and sonic booms (temporary threshold shift or TTS).

Fourteen desert tortoises were captured at the site of a planned development in Barstow, California in late February of 1995 and were transported to individual holding pens at HSWRI. The tortoises were held at 28-32EC and 18-30% humidity under a summer day-night cycle (16 hr daylight, 8 hr darkness). Weights ranged from 1.2 to 3.6 kg at capture (carapace lengths 19.68-31.38 cm). One individual had mild symptoms of URTD at capture, which were treated; in addition, tortoises were treated for intestinal parasites and anemia as needed. Tortoises were fed and watered ad libitum.

Auditory and vibration thresholds were measured using stimulus-evoked potentials (auditory brainstem responses [ABR], vibration-evoked whole-brain potentials) in the IAC chamber. Tortoises were lightly sedated with valium during the procedure. The range of hearing was tested using tone pips with frequencies from 50 to 4000 Hz; sensitivity to noise exposure was tested using broadband clicks with energy throughout the range of tortoise hearing. At the temperatures used in this study, the most sensitive individuals had best frequencies at 250 Hz of slightly over 20 dB SPL, while the least sensitive had thresholds in excess of 50 dB SPL. The most sensitive individuals thus heard as well as lizards and some birds. Thresholds averaged 34 dB SPL at best frequency for the 12 individuals tested, about 10 dB more sensitive than our expectation based on laboratory studies of small turtles. Hearing sensitivity declined by 60 dB above 2 kHz and below 125 Hz. Vibration sensitivity was maximal below 500 Hz.

No significant temporary threshold shift (TTS) was detected even in the most sensitive individuals after worst-case exposure to subsonic aircraft noise. The hearing of 5 tortoises was tested before and after exposure to simulated sonic booms. No significant (detectable) TTS was produced by exposures to simulated carpet booms (2 exposures to the 6 psf boom with an interval of 3 s) or the 10.5 psf boom. Tortoises exposed to cumulative energy equivalent to that of a 25 psf sonic boom by presenting them with 10 simulated 6 psf sonic booms did experience TTS. It is recognized that this method was likely to underestimate losses due to non-linear effects resulting from peak level exposure and overestimate losses due to the number of exposures; this was the closest approximation that could be achieved in the INTF. TTS ranging from 5-15 dB was measured in the tortoises tested by this method (5 individuals); recovery times were usually < 1 hr (the duration of the post experimental observations), but one individual recovered > 1 hr and < 48 hr.

In summary, some tortoises proved to have relatively sensitive hearing at summer temperatures. The average best sensitivity of the tortoises was better than expected based on previous studies of turtles, which were tested at standard laboratory temperatures. Small changes in temperature produced large changes in auditory sensitivity during our study, suggesting that the results of these experiments cannot be extrapolated to very high and very low temperature conditions. Tortoises experienced small (< 15 dB) temporary threshold shifts in response to worst-case exposures. These shifts recovered within 1 hr in all but 1 case and always recovered completely within 48 hrs.

The significance of TTS cannot be assessed based on laboratory evidence alone. Further studies must determine the source levels of sounds that are important to desert tortoises in their environment and the degree of masking they can tolerate. The shifts that were observed during this study would be considered small for birds and mammals. Unfortunately, so little is known about the function of hearing or hearing loss in reptiles that any guesses we could make about tolerable TTS would be purely speculative. Note, however, that tortoises are likely to share with birds and amphibians the capacity to regenerate lost hair cells.

Population Density and Ecology of Desert Tortoise in Mountainous Habitats

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Utah State University as cooperator with Marine Corps Logistics Base Barstow will be attempting to determine if the Mojave population of desert tortoise occur on steep mountain sides throughout their range as has been reported in the Newberry Mountains. The important question is: are there different subpopulations on mountain slopes and in the bajadas, or, do individuals move between the two habitats. This issue could raise serious questions about previous population estimates. Because this study will require transmittering many animals at several locations, the National Training Center, Ft. Irwin has provided additional funding to develop protocol for using transmittered animals as part of the newly proposed line transect monitoring to determine long-term population trends. We will be presenting our research proposals and seeking input from the audience on these projects.

Relationships Between Habitat Factors and the Dominance of Alien Annual Plants at the Desert Tortoise Research Natural Area. I. Soil Measurements

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I evaluated the effects of three habitat factors on soil nitrogen, phosphorous, compaction, and depth during April of two years of contrasting rainfall at the Desert Tortoise Research Natural Area (DTNA), Kern County California. The habitat factors were: (1) fenced protection (from off-highway vehicles and sheep grazing); (2) topographic position (uplands and washlets); and (3) microhabitat (intershrub, beneath the north creosote bush canopy, and south canopy). Each sample was collected within separate 25 x 50 cm sampling areas. I established five replicate blocks within a 150 ha area bisected by the fence on the northeast boundary of the DTNA. Each block consisted of a pair of 2.25 ha plots, one inside and one outside the fence, that were matched for slope, aspect, elevation, proportion of washlet to upland topography, and soil type. Sampling within each plot was replicated four times and stratified by topographic position and microhabitat (5 blocks x 2 plots x 2 topographic positions x 3 microhabitats x 4 replicates = 240 samples/year). Soil compaction was measured at the center of each sampling area at 2 cm increments from 2 to 16 cm beneath the surface using a recording soil penetrometer. Soil depth was recorded as the depth at which further penetration of the penetrometer ceased (approximately 70 kg/cm^2). Two cylindrical soil cores (8 cm diameter x 7 cm depth) were collected from within each sampling area and analyzing for total Kjeldahl nitrogen and Olson-extractable phosphorous. I collected the samples in mid-April 1994 and 1995, following winter rainfall that respectively totaled 50% and 200% of the 50-year average. Second year samples were taken adjacent to first year samples. I determined statistical differences by repeated measures analysis of variance using the type III sums of squares from the block-by-factor interaction as the error term ($p \leq 0.05$). Year was used as the repeated measure for the response variables nitrogen and phosphorous whereas depth was used as the repeated measure for soil compaction. Above-ground live biomass of annual plants were also measured and reported elsewhere in these conference proceedings.

Year did not affect soil nitrogen or phosphorous concentrations and the values that I report below are averages of samples taken during the two years. Nitrogen was significantly higher in uplands (910 ppm) compared to washlets (795 ppm), though the difference may not have been biologically significant. Phosphorous did not vary with topographic position. Phosphorous was higher under creosote bushes (27 ppm) than intershrub spaces (11 ppm), but did not differ beneath the north and south canopies. In contrast, nitrogen concentration was significantly different between all three microhabitats, creosote bush-north (1201 ppm), creosote bush-south (1028 ppm) and intershrub (328 ppm). Both nitrogen and phosphorous were unaffected by protection.

Soil compaction was approximately 50% higher in uplands compared to washlets, and intershrub spaces than beneath creosote bushes. Compaction was similar beneath the north and south sides of creosote bushes, and compaction increased with depth. Soil compaction was significantly higher outside (9 kg/cm^2) compared to inside (7 kg/cm^2) the DTNA only at the 2 cm depth. Soil depth was significantly higher in washlets (24 cm) compared to uplands (21 cm), and under creosote bushes (24 cm) than intershrub spaces (20 cm). Soil depth was unaffected by protection.

Soil nitrogen, phosphorous, and depth were highest and compaction was lowest beneath creosote bushes compared to intershrub microhabitats. Protection only affected soil compaction at the 2 cm depth, and sampling year had no affect on any measured soil characteristic. Differences in the dominance of alien annual plants that are associated with topographic position or microhabitat may be due to variations in soil compaction, depth, or nutrient status, but differences due to the level of protection from human disturbance likely are not associated with them at the DTNA. Differences in annual plant structure between years appear to be due more to the amount of available water than to variations in soil characteristics.

Relationships Between Habitat Factors and the Dominance of Alien Annual Plants at the Desert Tortoise Research Natural Area. II. Annual Plant Biomass Measurements

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I evaluated the effects of three habitat factors on the biomass of alien annual plants during the spring of two years of contrasting rainfall at the Desert Tortoise Research Natural Area (DTNA), Kern County, California. The habitat factors were: (1) fenced protection (from off-highway vehicles and sheep grazing); (2) topographic position (uplands and adjacent washlets); and (3) microhabitat (intershrub, beneath the north creosote bush canopy, and south canopy). I established five replicate blocks within a 150 ha area bisected by the fence on the northeast boundary of the DTNA. Each block consisted of a pair of 2.25 ha plots, one inside and one outside the fence, that were matched for slope, aspect, elevation, proportion of washlet to upland topography, and soil type. Sampling within each plot was replicated four times and stratified by topographic position and microhabitat (5 blocks x 2 plots x 2 topographic positions x 3 microhabitats x 4 replicates = 240 samples). I collected the samples in mid-April 1994 and 1995, following winter rainfall that respectively totaled 50% and 200% of the 50-year average. Second year samples were taken adjacent to first year samples. For each sample all live annual plants rooted within a 25 x 50 cm frame were severed at ground level, dried to a constant mass, and weighed to determine above-ground live biomass. Statistical differences were determined by repeated measures analysis of variance using the type III sums of squares from the block-by-factor interaction as the error term ($p \leq 0.05$) and year as the repeated measure. Soil nutrient status, compaction, and depth were also measured and reported elsewhere in these conference proceedings.

The most common alien annual plants were the grasses *Bromus madritensis rubens* and *Schismus spp*, and the forb *Erodium cicutarium*. The alien annual grasses *Bromus trinii* and *Bromus tectorum* were collected in very small amounts and were not analyzed individually, but they were included in the analysis of total alien species biomass. The biomass of the native annual grasses, *Vulpia octoflora* and *Vulpia microstachys* were combined for analysis as were the various native forb species.

Biomasses of alien annual grasses, especially *Schismus spp*, were significantly higher outside compared to inside the DTNA. Protection did not affect the biomass of native annual grasses, native forbs, or *Erodium cicutarium*. Washlet compared to upland topographic positions contained higher biomass of *Bromus madritensis rubens*, native forbs, and all species combined. Biomass of all species were highest in the creosote bush-north microhabitat, except for *Erodium cicutarium* and *Schismus spp.* which were highest in intershrub spaces during the dry year, and the creosote bush-south microhabitat during the wet year.

Topographic position-by-microhabitat and year-by-microhabitat interactions suggest that the availability of water to plants was the overriding factor affecting the composition of this annual plant community. Mineral nutrient content of the soil seemed to be of secondary importance. During the above-average rainfall year, when water was theoretically less limiting to plant growth, the biomass of all annual plants were significantly higher in microhabitats with the greatest concentration of soil nitrogen and phosphorous, under creosote bushes. This pattern was less apparent during the dry year.

The proportional biomass of the three predominant alien species were each significantly higher during the below-average rainfall year, whereas the proportional biomass of native forbs was higher during the above-average year. Proportional biomass of native annual grasses showed no difference, possibly due to their exceedingly small proportions during each year. The combined proportional biomass of alien annuals was approximately 95% during the dry year and 30% during the wet year. Germination requirements may be less stringent for alien than for native annuals, allowing the aliens to germinate during years of low rainfall when natives remain dormant as seeds. This germination strategy should benefit populations of alien annual plants if they could survive long enough to set seed, but would be detrimental if they died before reproducing.

Comparing Hectare Plots and Line Transects to Estimate Abundance of Desert Tortoises

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Distance sampling (line transects) is a statistically robust method of estimating animal abundance. However, transect density estimates for desert tortoises may be sensitive to year-to-year differences in activity. In 1996, we estimated tortoise abundance by distance sampling and with 1-ha removal plots in Ivanpah and Piute valleys, to compare the accuracy, precision, and cost of each technique, and to test the sensitivity of each technique to seasonal changes in tortoise activity. We established 18 2.6-km long transects, 9 in Ivanpah Valley and 9 in Piute Valley. Six, 1-ha plots were established on each transect. Transects and plots were surveyed in April-May and were repeated in June. Four biologists sampled 2 transects (5.2 km) or 6 plots each day. More tortoises were observed on transects than on 1-ha plots, but plots yielded higher density estimates. Numbers of tortoises observed (density), April-May and June samples combined, were: Piute 1-ha plots, 10 ($18/km^2$), Piute transects 22 ($9/km^2$); Ivanpah 1-ha plots 17 ($32/km^2$), Ivanpah transects 39 ($22/km^2$). The low density estimates from transects may reflect low activity by tortoises in a year when almost no green food was available. Our attempt to determine a seasonal effect on density estimation failed, apparently because there was little difference in environmental conditions between our early (April-May) and late (June) samples. There were no differences in numbers of tortoises observed for either transects or 1-ha plots. Determination of a seasonal effect requires another year of sampling.

Status of the Northern & Eastern Colorado Desert Coordinated Management Plan

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One of three large ecosystem plans in progress which address the management of the desert tortoise in the California Desert, the Northern & Eastern Colorado Desert Coordinated Management Plan (Plan) focuses on the Northern Colorado Desert, Eastern Colorado Desert and a small portion of the Joshua Tree Recovery Units. The planning area is 5.5 million acres in size. The major cooperating agencies are the Bureau of Land Management, Joshua Tree National Park, US Marine Corps Air Station, Yuma (for the Chocolate Mountains Aerial Gunnery Range), US Fish & Wildlife Service, US Geological Survey (including the Biological Resources Division) and the California Department of Fish & Game (which has provided the lead biologist for the project). The project is moving from collection, digitizing, and quality review of data into species-habitat modeling and plan formulation. Development of the approximately 75 spatial data coverages involved is about 95% completed, allowing a complex set of species-habitat and use effects analyses to be performed. Another prerequisite to running these models, field verification of the plant communities coverage and collection of additional habitat information, is also completed. This field work is based on a stratified random sampling of 850 points. Finally, all desert tortoise census records for the Bureau of Land Management, Joshua Tree National Park and Chocolate Mountains Gunnery Range were translated into digital format.

Two additional analyses have recently been completed which provide considerable planning focus for the desert tortoise: *Current Desert Tortoise Management Situation in the Northern & Eastern Colorado Desert Planning Area*, and *Analysis of Current Desert Tortoise Management Situation in Relation to Desert Tortoise Recovery Plan in Northern & Eastern Colorado Desert Planning Area.* The former documents the aggregate of desert tortoise habitat management and protection by all agencies and private land owners; while the latter, written by biologists from the cooperating agencies, expresses the management and protection adequacy and shortfall of current management.

The Bureau of Land Management, lead agency for the project, hopes to issue a draft Plan and EIS by the end of 1997. For access to more information about the Plan via a Home Page, go to: http://www.ca.blm.gov/ne. Project lead Dick Crowe may also be contacted for more information at above address or by calling (909) 697-5216.

Home Range, Burrow Use, and Activity Patterns of the Desert Tortoise in the Southern Mojave Desert: A Comparison Between a Military Installation and a National Park

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We conducted a radiotelemetry study of a desert tortoise population at Sand Hill training range of the Marine Corps Air Ground Combat Center (MCAGCC) in 1995 and 1996 and compared the results with a study population in a similar but pristine landscape in the Pinto Basin of Joshua Tree National Park (JTNP). Sand Hill, located in the southwestern corner of the installation in the southcentral Mojave Desert, has only been lightly impacted by military training activities, and contains the largest contiguous expanse of high quality desert tortoise habitat on MCAGCC. Three

Desert Wildlife Management Areas, designated by the U.S. Fish and Wildlife Service for tortoise recovery, are located near the installation, but the Sand Hill population is relatively isolated by urbanization, mountains, and Marine Corps heavy-use training ranges. Pinto Basin is located 64 km directly southeast of Sand Hill.

We compared the spatial ecology of desert tortoises in military training and pristine landscapes using the following parameters: 1) sex-specific home range, 2) interyear variation in home range, 3) number of burrows used, and 4) surface activity patterns.

We fitted a total of 36 adult tortoises with radiotelemetry transmitters at two square 9.0 km^2 study plots in Sand Hill training range. The sex ratio was approximately 1:1. Twenty-nine tortoises were available in each of the two years for data analysis. The simultaneously monitored study plot at JTNP consisted of 10 tortoises with an equal number of both sexes in a square 2.6 km^2 plot. Productivity of annual vegetation was very high in the first year of the study, because winter precipitation was 2 1/4 times higher than the 44-year mean. The second year of the study was a drought year, where winter rainfall was only 25 percent of the baseline long-term mean.

We calculated home range with the minimum convex polygon method, although two other algorithms were also investigated. Male and female tortoises possessed similar home range sizes at the Sand Hill training range during the productive year. This was in sharp contrast to the results in Pinto Basin and published studies in the Mojave Desert, where males exhibited a much larger home range than females. Both male and female tortoises dramatically reduced their home range sizes and the number of burrows they used during the drought year at both study sites. During this drought, Sand Hill male tortoises possessed a significantly larger home range than females, and their home range was similar to Pinto Basin males. Female tortoises possessed similar home range sizes at both Sand Hill and Pinto Basin during both productive and drought years. Pinto Basin tortoises of both sexes used more burrows than Sand Hill tortoises in the productive year, but in the drought year tortoises used the same number of burrows at both sites. Surface activity of desert tortoises found during radio-tracking were similar at both Sand Hill and Pinto Basin, averaging 29 percent in the productive year and dropping to 17 percent in the drought year.

Effects of Jet Aircraft Flight Noise on Heart Rate and Metabolic Rate of the Desert Tortoise (*Gopherus agassizii*)

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Little information is available on the physiological response of reptiles to anthropogenic sound. Of the physiological responses to such perturbations, increases in the rate of energy consumption (metabolic rate) could be quite detrimental for the Desert Tortoise (*Gopherus agassizii*). Desert tortoises survive harsh desert environments by optimizing energy reserves, water and by controlling activity periods. Chronic increases in energy expenditure, while not immediately fatal, could impact growth, time to maturity, reproductive output, and in extreme cases may result in death of the animal. In this study Hubbs-Sea World Research Institute scientists sought to measure changes in metabolic rate brought on by sound generated during jet aircraft overflights. This work was supported under funding from the U.S. Air Force, with support from the Environmental Management Office at Edwards Air Force Base, California.

While the goal of this study was to measure metabolic rate changes, such measurements can be difficult if not impossible when also trying to subject the tortoises to a wide range of acoustical stimulus. Because for many terrestrial species heart rate can be utilized to indirectly determine changes in metabolic rate, the first experiments were designed to quantify this relationship. Metabolic rate and heart rate were measured simultaneously on Desert Tortoises under 3 experimental conditions: 1) resting, 2) voluntary exercise on a treadmill, and 3) exercise on a treadmill with an indwelling catheter for measuring blood lactate concentration. Temperature was controlled at 30°C, and body temperature of the tortoises was also measured before and after each trial. Tortoises were fitted with small mask and trained to walk voluntarily on a treadmill. During rest and exercise mass-specific oxygen consumption was measured. VO_2 at rest ranged from 0.9137 to 1.996 ml/min/kg (mean = 1.472, s.d.= 0.410). Resting heart rate ranged from 6.15 to 18.03 BPM (mean = 11.82, s.d. = 3.91). Exercising heart rate ranged from 10 BPM to 42 BPM, though heart rate was most common at approximately 30 BPM. There was no increase in blood lactate levels during or post exercise for any of the tortoises. There was a strong positive relationship between heart rate and metabolic rate for the exercising tortoises.

As described in other abstracts in this proceedings, tortoises were then exposed to the noise of aircraft overflights as well as sonic booms. Heart rates (and thus metabolic rates) were consistently lower (7.6%) for tortoises after jet overflights. However, heart rate showed no statistical difference before and after sonic boom exposure. These results are consistent with behavioral data suggesting the tortoises freeze in response to perturbation. The data also indicate that there is no increase in energy consumption by tortoises but rather they reduce energy consumption by reducing activity after overflights. Further there does not appear to be any metabolic response to sonic booms.

Desert Tortoise Hatchling T-Maze Spatial Performance in Locating and Remembering Artificial Burrow Sites

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Desert tortoise neonates have been observed attempting to disperse from their nests in search of burrows and pallets soon after hatching. The need to find these sites appears to be highly motivating to the neonates. It is unknown, however, whether this behavior is simply reflexive for survival reasons or if the animals have the cognitive awareness to search out and remember the location of burrows and pallets. This study examined whether desert tortoise hatchlings are able to learn their environment by requiring twenty-four captive bred neonate desert tortoises to learn and remember the position of a simulated burrow located at the end of one arm on a standard T-maze.

The subjects were divided by age into two groups (one month (1M) and two months (2M)) and then randomly assigned into either a right (R) or left (L) arm group. During training trials only the burrow on the assigned arm was accessible to the subject. A training trial began with the subject being placed at the start of the maze runway and ended when the subject made an arm choice. If the subject correctly chose the assigned arm it was rewarded with entrance to the burrow. If the subject chose the unassigned arm, the trial was considered finished and the animal was returned to the start area. Each subject was run for three trials per day for four sets of six days.

Results indicated that the neonates were able to learn the direction of their assigned arm. The total number of correct arm choices (CAC) across subjects increased from 46% (= 8.29) in Set 1 to 66% (= 11.88) in Set 4, with a significant increase for all groups, except the 2ML group. The subjects entered the burrows for 87% of all CAC. There did not appear to be any significant difference in CAC between the two age groups in any one set, though, the 2M groups had significantly more total CAC. While the 2M groups started with a higher percentage of CAC, in Set 4 the 2M groups experienced a decline in CAC resulting in better performance by the 1M groups. There also appeared to be an interaction between arm direction and age with the 2MR group making the largest number of CAC. While these findings are not conclusive that desert tortoise hatchlings consciously seek out burrows and pallets, they do suggest that the neonates are capable of developing cognitive maps of their environment early in their development.

Use of Spatial Reference Cues by *Gopherus agassizii*

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Observations of the desert tortoise in their natural habitat suggest that they possess the ability to learn to use spatial cues to locate important natural resources. Little research has been done, however, to determine which navigational cues are being utilized. Using controlled conditions, this study investigated the possible use of three spatial reference cues: odor, light, and landmarks. Fifteen captive bred desert tortoises, aged 4 months to 3 years, were required to navigate a maze using one of the three cues to designate a food reward. After each subject was trained using each cue separately, they were presented with the three cues simultaneously to determine if there was a preference for one cue.

Results indicate that the tortoises were able to learn to use the light and landmark reference cues to navigate the maze, however, the odor cue did not appear to be used by the tortoises to locate the food reward. The tortoises also did not appear to have a cue preference and when presented with all three cues simultaneously they did not approach one cue significantly over another. The finding that desert tortoises are capable of learning a specific cue to navigate a maze suggests that these cues might also be used by the animals to navigate in their natural environment. These conclusions could have important implications in the relocation efforts of the desert tortoise. Knowing what cues are relied on for orientation means locations can be chosen that will best meet this species'situational requirements.

The Reliability of Tortoise Density Estimates: Multi-year Tests Using Corroborative Methods

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Data from six consecutive years at Joshua Tree National Park were used to point out problems with sampling tortoises in general. All work was conducted at a single 2.59 km^2 plot using several corroborative methods. Transect surveys were conducted weekly in spring by teams of observers. Ten radio-transmittered animals were followed for three years and a study of burrow longevity was conducted. Population density was determined for each year separately and for all years combined. The best population estimate was 67 adult tortoises based on empirical Bayesian methods. Home ranges of males were significantly larger than those of females. Yearly variation was pronounced especially in contrasting the four rain years with the two dry years. In dry years, home ranges decreased, captures decreased, and effort required to find each tortoise nearly doubled. Home ranges in general were circumscribed (= 43.5 ha for males and 9.7 ha for females). Tortoises not seen for several years most often reappeared within 300 m of their previous location. Each parameter is presented in light of the need for a better sampling method. The most important consideration in designing improved sampling schemes for tortoises is to account for strong inter-year variation and the difficulty of finding the animals in dry years. These data suggest that plot-based studies are unlikely to provide large-area population assessment of desert tortoises, and that sampling should not be conducted in very dry years.

Recreation Causes Extinction of Human-Sensitive Organisms

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Increasingly, undisturbed wilderness areas in many parts of the world are limited to government-owned lands. Much of the international conservation effort has focused on issues related to the establishment and management of such government-owned and funded parks and wilderness areas (Shafer 1990; Wright 1992; Garber 1994; Garber and Burger 1995). Based on our research it is possible to assess risks of species decline in wildlife reserves when predicting human using known life history data (Burger and Garber 1995). We have also determined when such extinctions can be predicted, prevented, or reversed. Proper management is necessary otherwise protected areas will prove insufficient and inadequate to ensure the survival of species the parks were designed and managed to protect. Many believe species protection policies in parks and nature reserves will depend on long-term population monitoring programs (Davy and Jefferies 1981; Mehrhoff 1989; Soule and Kohm 1989; Holsinger and Gottlieb 1991). Such programs often prove costly and rarely lead to sufficient policy improvements. In fact, although biologists report the decline of amphibian and reptile populations worldwide (Wake 1991, Pechmann and Wilbur 1994), supporting long-term census data are uncommon (Dunson et al. 1992; Blaustein 1994). Hypotheses that attempt to explain their widespread decline cite habitat destruction, forest fragmentation (Garber 1987, Beebee 1991), climate disturbance (Pounds and Crump 1994), increased penetration of ultraviolet radiation through the atmosphere (Blaustein et al. 1994a), natural population fluctuations (Pechmann et al. 1991), ozone depletion (Blaustein et al. 1994a), predation (Temple 1987, Congdon et al. 1993), and collecting and other human impacts (Pechmann and Wilbur 1994). Because amphibian eggs are not shelled, their sensitivity to acid rain (Harte and Hoffman 1989, Sadinski and Dunson 1992) and aluminum (Beattie and Tyler-Jones 1992) may differ from reptiles. In this paper we examine the relationship between human recreation and population declines of North American wood turtles, and conclude that human recreation often leads to people removing many human sensitive species such as turtles faster than the populations can tolerate, and therefore local extinctions are inevitable, without proper protection, education, and reintroductions. These local extinctions could well lead to more widespread extinctions of entire species from the wild. We report on our efforts to reintroduce wood turtles where it was determined that recreation was the cause of local extinctions, and we present data showing that wood turtles in a population experiencing a population bottleneck exhibited age-dependent sex selection (which we term the sexy grandmother hypothesis).

As reported by biologists, eastern North American turtle populations are declining, particularly species in the genera *Clemmys, Terrapene, Sternotherus, Kinosternon, Emydoidea,* and *Malaclemys* (Garber 1987, 1988a,b,c,d, 1989a, b, c, 1990a, b; Garber and Burger 1995). Of the studies that examined long-term population dynamics or factors that cause changes in turtle population levels, few were designed to test causes for the decline of turtles. The North American wood turtle is thought to be in decline throughout its range (Restore: the North Woods, et al. 1994; Garber and Burger 1995; Garber and Burger 1997). The senior author was the first to examine the factors that may be causing a decline. He studied the population dynamics of two allopatric wood turtle populations, monitoring their populations when numbers were growing, stable, and declining, and he analyzed the population demographics by sex and age class and investigated possible reasons for the decline.

The senior author conducted a mark and recapture study on two wood turtle populations on a 1,000-ha section of a protected watershed in south-central Connecticut (New Haven County). The two turtle populations were physically separated about 100 years ago when a 1.5 km long human-made pond was constructed. Both wood turtle populations are now reproductively isolated from one another: there was no overlap of turtle home ranges during the entire study (wood turtles mate and find mates in streams and rivers, not in huge reservoirs). During the first 9 years of our study (1974-1982) the entire watershed was closed to recreation. These rules were enforced by regularly patrolling South Central Connecticut Regional Water Authority security officers. In 1983 the watershed was opened to recreation, and this policy continues to present. Both wood turtle populations were stable during the first 9 years of the study, then the trends of both populations changed and each went into decline throughout the rest of the study. In 1982 the total number of wood turtles was 106 turtles, at the moment the area was opened to recreation. 99% of the turtles disappeared during the next 10 years.

The effects of human recreation on wood turtle populations when management of the forest changed from wilderness to a recreational forest (terminology after Ireland 1982) were tested. The results enable us to model the effects of human recreation on wildlife reserves, and the extent to which human recreation will lead to the extinction of specific populations. The study animals, wood turtles, were convenient study organisms for long-term species decline demographics because they are easily marked, adults are easily found, observed, and handled 12 months of the year, they live a long time, can be recaptured for decades, and remain within a relatively small area throughout their life lifetimes, and they can be studied in many different habitats ranging from wilderness to urban forest and therefore are suitable for minimum viable population analyses. In addition, dead-turtle shells survive long after a turtle has died, sometimes providing clues regarding the cause of death. The original distribution of wood turtles before widespread logging, farming, and development extended from Minnesota and Iowa east to the Atlantic coast, from Virginia north to Quebec, New Brunswick, and Nova Scotia (Garber and Burger 1995).

Since male wood turtles were found to mate with significantly older females, this mating strategy is referred to as the sexy grandmother hypothesis. Data are presented from two wild populations of wood turtles exhibiting compensatory mechanisms that help reduce the number or the effects of deleterious recessive genes resulting from inbreeding-associated homozygosity. During the population bottlenecks we found evidence for the sexy grandmother hypothesis, that small and declining populations of North American wood turtles avoid inbreeding with a mate selection mechanism involving disparate ages that acts as a bottleneck survival strategy. Young male wood turtles mated with considerably older females, and thus preserved higher levels of genetic diversity and heterozygosity. Such animals often have higher fitness than those with lower levels. Because small isolated populations rapidly lose genetic variation, heterozygosity, numbers of alleles per locus, and undergo reduced polymorphism, several authors have suggested that these populations eventually experience detrimental effects of inbreeding (Mayr 1954; Lewis and Roberts 1956; Williams 1966; Carson 1971; Denniston 1977; Packer 1979). Inbreeding is advantageous when mortality losses from outbreeding exceed the effects of inbreeding depression (Bengtsson 1978). With a reduced mutational load, the loss in fitness due to inbreeding depression can be reduced to where it becomes advantageous for offspring to mate with their parents, as often occurs among fallow deer (Smith 1979). Inbreeding depression is not sufficient for understanding the evolution of mating systems, especially for plants (Holsinger 1988). Populations that recover from bottlenecks within one or two generations may play an important role in evolutionary change (Lewin 1987; Carson 1990). There is some evidence that population bottlenecks are sometimes accompanied by increased genetic variance (Carson and Wisotzkey 1989). Clegg and Allard (1972), Rick et al. (1977), and Clegg and Brown (1983) reported that following a bottleneck populations of inbreeding plants had much higher levels of genetic diversity than predicted. Certain species may have evolved life history strategies or mechanisms that moderate the detrimental effects of a bottleneck by conserving genetic heterozygosity and allelic diversity. This mechani-dependent mate selection and longevity in wood turtles facilitates and increase in exogamy and a decrease in endogamy. Such a strategy may enhance the chances that populations will survive through changing climatic conditions or varying regimens of human disturbance, competition, predation, disease, or parasitism. A species' resistance to bottlenecks may be increased if it has a social system that protects its small populations from the genetic hazards of a bottleneck by preserving heterozygosity.

We are documenting species decline, however, we must document our reintroductory efforts so others can learn from our successes, and build on the best and most effective methods available. Our program was ideal because we knew about all the turtles that lived there before recreation began, we documented the population numbers, habits, movements, age structure, and decline for decades. With the populations no longer viable, efforts to reintroduce wood turtles to the protected habitats have begun. We report on issues we found were necessary to solve, including sources of turtles, captive breeding, gene pools, turtle ages, where and when to release animals, tests performed by veterinarians before release, human education, permits, politics, and diplomacy.

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The West Mojave Coordinated Management Plan

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The Bureau of Land Management, in cooperation with 27 participating federal, state and local agencies, cities and counties ("participating agencies"), is preparing a multi-species bioregional plan which addresses the management of the desert tortoise and 88 other special status plants and animals within the 9.4 million acre West Mojave Planning Area. The participating agencies intend to prepare a plan that sets forth a streamlined program for compliance with the California and federal endangered species acts.

The Plan is being drafted by the West Mojave Interagency Planning Team with the assistance of a steering committee composed of representatives of the participating agencies and other interested organizations. Collection and mapping of data are being completed, and the formulation of the management strategies which will comprise the substance of the plan will begin shortly.

The Planning Team recently released the Current Management Situation in the West Mojave Planning Area, a report describing the conservation management which the participating agencies are already providing for the desert tortoise and other special status species. This document, together with all collected and mapped data, will be analyzed by a team of biologists representing the U.S. Fish and Wildlife Service and the California Department of Fish and Game. The team will evaluate the effectiveness of existing programs and identify opportunities for their enhancement. The findings of the evaluation team, together with the recommendations of the steering committee, will be used by the planning team to develop alternatives for consideration in a draft plan and environmental impact statement and report. The draft plan and EIS/R will be released for a 90-day public review by the end of 1997.

Additional information may be obtained from the plan's Internet home page, which may be accessed at htp://www.ca.blm.gov/mojave/

homepage.htm. Project manager William Haigh may also be contacted for more information at the above address or by calling (619) 255-8823.

Long-term Monitoring of Density Changes for Desert Tortoise Populations in Recovery Units

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The Desert Tortoise (Mojave Population Recovery Plan (1994) designated six Recovery Units, which may be individually delisted, across the Mojave Desert. One criterion for delisting is that tortoise densities must show a stable or increasing trend for one tortoise generation. Traditional permanent monitoring plots have been found inadequate to determine regional trends in tortoise densities; there, the Technical Advisory Committee to the Desert Tortoise Management Oversight Group (MOGTAC), assisted by academic biologists and the Biological Resources Division of the U. S. Geological Survey, evaluated alternative monitoring techniques. The MOGTAC selected distance sampling as the most appropriate method and has preliminarily identified 43 total strata across the six Units (range = 3-11 strata/Unit) to increase the precision of density estimates within each Unit.

The monitoring effort will require two teams of two workers walking up to 240 km of transects per stratum. In addition a team of two will be required to monitor as many as 20 radio-telemetered tortoises in each stratum to determine tortoise detectability. We estimate that monitoring a single stratum will cost $60-$80K; total cost to monitor all strata in a single year would range from $2.5 - $3.5 m. A full-scale baseline study, in which all strata in all Recovery Units are surveyed, is recommended for the first five years, Thereafter strata could be monitored on a rotating basis. The success of this monitoring strategy will require a tremendous commitment of resources from the responsible land and wildlife management agencies.

Factors Affecting Reproduction of Desert Tortoises and Resultant Implications for Management

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An ongoing reproductive study of 23 to 31 desert tortoises per year has been conducted in the eastern Mojave Desert since 1991. Results given in this paper are primarily for the period 1991 through 1995. Radiotransmittered tortoises were radiographed every 12-15 days during the nesting season every year and nesting was monitored during three years, 1991-1993. Precipitation levels were well above-average in three years and below average in 1994; 1991 was an average year. (For interpretation, 1994 is hereafter referred to as the "poor" year, while the remaining years are referred to as "good" years.)

In years unaffected by drought, two clutches were typically laid (84.1% of 69 clutches); one clutch was laid 8.7% of the time and 3 clutches were laid 2.9% of the time. Nearly every female of reproductive size reproduced each year, from 1991 through 1995 (92 - 100%). The appearance of eggs on radiographs (shortly after ovulation) occurred as early as April 10, but typically occurred between 15 and 19 April. The earliest detected oviposition was 11 May (n = 62 clutches), although it may have occurred slightly earlier. For tortoises laying ≥2 clutches, oviposition of the first clutch was completed by 14 June, although most first clutches were laid by 1 June (observed n = 51 clutches). Observed second clutches were laid beginning 2 June (n = 60) and nesting was typically completed by 29 June in 2 of 3 years and by 8 July in the remaining year (n = 55); the latest oviposition date observed was 17 July.

The mean size of Clutch 1 was 4.0 eggs; Clutch 2 was 3.7 eggs. The first clutch was only significantly larger than the second in one year, 1993 (t_{23} = 2.311, P = 0.03), although the trend in three of the remaining four years was for smaller second clutches. The mean total annual production (TAP) for all years and tortoises was 6.6 (S.E. = 0.241, n = 116, range = 0 - 12). For the non-drought years alone, it was 7.1 (S.E. = 0.239, n = 93, range = 0-11) and for 1994 it was 4.9 (S.E. = 0.633, n = 23, range = 0 - 10).

The smallest tortoise that reproduced was 180 mm in carapace length; the median carapace length for tortoises reproducing for the first time during the study was 188 mm (range: 180 - 215 mm; n = 5), although six tortoises with a median score of 184.5 mm (range: 180 - 203 mm) had yet to reproduce. Drought and post-drought effects (see below) may have delayed the onset of reproduction in two of these tortoises.

Up to 188.4 mm in carapace length, the mean TAP was 4 eggs (simple regression of TAP on carapace length, averaged over all years). At 188.4 mm TAP was 5 eggs and an addition of 1 egg occurred for every 14.4 mm increment in carapace length. This relationship was linear between the carapace lengths available for examination: 180 and 247 mm.

The number of eggs produced by a tortoise is influenced by the body size of the adult female. However, this relationship is less than straightforward and strongly influenced by size class, year, and whether the first or second clutch is considered. TAP was significantly correlated with carapace length only in the good years (P = 0.003 - 0.019); in the poor year, reproduction was inconsistent relative to tortoise size (P = 0.31). The size of the first clutch was not significantly correlated with tortoise size ($F_{1,30}$ = 1.967, P = 0.17), although the largest clutches (6 - 7 eggs) were produced either by tortoises exceeding 223 mm in carapace length (4 of 9 tortoises) or old, but small, tortoises (3 of the remaining 5 tortoises). By contrast, the second clutch was strongly influenced by body size ($F_{1,30}$ = 20.985, P < 0.0001), except in the poor year ($F_{1,21}$ = 2.604, P = 0.12). The correlation between clutch frequency and tortoise size was weak, except in the drought year, 1994. Only tortoises >208 mm in carapace length produced two clutches in 1994. In general, then, small adult females have a lower reproductive output than do larger females. Not only do they have fewer second clutches in a poor year, but their second clutches are smaller than those of larger females. Growth rates for small females are higher than for larger females and reproduction is more costly for the first clutch because of the higher relative mass loss (i.e., compared to body mass). Following production of the first clutch, there are relatively fewer reserves to partition to reproduction in light of maintenance and growth demands.

Body condition indices (CI; mass:volume) were calculated repeatedly throughout the year and four CI's were used to assist in analyzing reproductive output: (1) early to mid-April, prior to ovulation of the first clutch; (2) early to mid-May, prior to ovulation of the second clutch; (3) early to mid-July following nesting; and (4) late October/early November prior to brumation. Body condition was poorly correlated with reproductive output, except during drought years and post-drought years. During the drought year only, the size of Clutch 2 was correlated with body condition in both early and mid-spring (P = 0.01 - 0.03, respectively). Furthermore, in 1994, in the size group for which some females laid second clutches (i.e., >208 mm in carapace length), those females that laid a second clutch had a significantly higher early spring body condition than those that did not lay a second clutch ($F_{1,13}$ = 6.099, P = 0.03). Both groups ended the nesting season with the same CI. Notably, small females (<208 mm in carapace length) also ended the nesting season with a CI similar to larger tortoises and mean early-spring CI was low (6.96 X 10^{-5}) compared to larger tortoises that produced two clutches (7.21 X 10^{-5}), further supporting the hypothesis that smaller females had insufficient resources to produce two clutches and maintain CI. Had small tortoises produced a second clutch, they would have experienced a loss of 105 g (the average mass of a second clutch of 3 eggs), resulting in a post-nesting CI of only 5.965 X 10^{-5}, well below that for larger tortoises, 6.54 X 10^{-5}, and perhaps compromising survival.

Residual effects from drought were also apparent. Only in 1995, a post-drought year, was the size of Clutch 2 significantly correlated with CI during the previous fall ($F_{1,21}$ = 5.043, P = 0.04, R^2 = 0.19). Follicle development occurs during the previous year and vitellogenesis is completed by brumation. If CI were sufficiently low during vitellogenesis, as it might be in a drought year, then fewer follicles might develop, resulting in a lower TAP the following spring.

A second post-drought effect influenced body condition rather than reproductive output. In general, TAP was not correlated with post-nesting CI, but in 1995, tortoises that produced more eggs ended spring in significantly lower body condition ($F_{1,22}$ = 7.306, P = 0.01, R^2 = 0.25). Absolute CI in early spring was low, a residual effect from the drought of 1994; however the abundant forage in Spring, 1995, allowed tortoises to gain mass rapidly. Those tortoises that responded to their relative mass gains (rather than their absolute mass), or otherwise responded to the abundant forage levels by reproducing maximally, sacrificed body condition. By contrast, the reproductive strategy in 1994 was to reproduce well only if CI was sufficient. In 1996, a year of even more severe drought, there was complete reproductive failure, associated with CI in early spring that was lower than that measured at any point in the previous four years. As both drought years were preceded by years of abundant forage, during which vitellogenesis is assumed to have proceeded normally, it is suggested that reproduction was truncated by the mechanism of follicular atresia prior to ovulation.

It is typically assumed that drought causes direct, within-year effects, but residual effects from drought, especially in a year of abundant forage, are often overlooked. Given the nature of those effects on the state- and federally-listed desert tortoise, it is suggested that land managers and persons handling tortoises incorporate those effects into their management prescriptions and protocols.

Effects of Outdoor Recreation on Wildlife

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Outdoor recreation is increasingly becoming the principle use of public lands in America (Christensen 1997). Although many people believe that recreational activities have minimal effects on wildlife and are of little consequence, data suggests otherwise (references in Knight and Gutzwiller 1995). For example, a recent survey of factors responsible for the decline of federally listed threatened and endangered species finds that outdoor recreation is the second leading cause (Losos et al. 1995).

Recreational Impacts and Wildlife Responses— Outdoor recreation has the potential to affect wildlife at the level of the: individual, population, and community. There are four ways by which recreational activities can impact wildlife: 1) harvesting, 2) habitat modification, 3) pollution, and 4) disturbance (Knight and Cole 1991). Of these ways, disturbance is perhaps the most important, considering that it is usually unintentional and largely unmanaged.

Immediate response—The most extreme response of wildlife to disturbance is death. Although this is the intended result of consumptive activities, nonconsumptive activities also result in the death of animals. The other type of immediate response is a change in behavior. Most of our understanding of disturbance is confined to the immediate behavioral response of individuals to recreationists.

Long-term effects on individuals— Many of the responses of animals to disturbance are short-lived, although they can become long-lasting changes. One behavioral change is abandonment of disturbed areas in favor of undisturbed sites. Displacement into new environments can lead to a number of further behavioral changes, such as altered feeding ecology. Disturbance can also reduce the vigor of individuals and ultimately result in death (Gabrielsen and Smith 1995). Elevated heart rates, energy expended in disturbance flights, and reduction of energy acquisition may all result in increased sickness, disease and potentially death of individuals. While these response have been suggested, evidence is largely circumstantial.

There are numerous studies, albeit mainly for birds, which have documented decreased productivity in response to recreational disturbance. For example, songbird nest predation is elevated alongside of recreational trails (Miller et al. In press).

Long-term effects on populations— While consumptive recreation activities (hunting) can impact the abundance, distribution and demographics of populations, we know very little about how other forms of recreation affect populations. We can only speculate that increased mortality, reduced productivity and displacement of individuals (all documented, at least anecdotally) will result in decreased populations. Difficulties in establishing cause-and-effect make documentation of this response problematic.

Long-term effects on communities— Our knowledge on the impacts of recreationists on community structure is still rudimentary (see Gutzwiller 1995). It is hypothesized that recreational disturbance could cause alterations in species diversity, depending on the severity of the disturbance, the spatial and temporal scale of the disturbance, and the level of the biological hierarchy for which diversity is being described. Several studies (Skagen et al. 1991, Knight et al. 1991) have demonstrated how disturbance of a key species in a wildlife community can disrupt the dynamics of the entire community resulting in altered species composition and populations.

Factors That Influence Responses— There are five characteristics of recreational disturbance which can affect wildlife responses. These include: 1) type of activity, 2) timing, 3) location, 4) frequency, and 5) predictability. In addition, there are characteristics of wildlife which predispose them to different types of responses to disturbance.

Characteristics of disturbance which affect wildlife— Different types of recreation activities may elicit different responses. For example, motorized activity often causes quite different responses from wildlife than do activities that are either quieter or slower (e.g., hiking). Particular recreational activities should not be viewed in isolation. There may be synergisms or interactions when more than one activity is occurring simultaneously.

Disturbance at any time of the year can affect an animal's inclusive fitness. Disturbance during the breeding season may affect its productivity while disturbance outside of the breeding season may affect its ability to forage and, therefore, its survival. In addition, there are temporal aspects that affect wildlife responses to disturbance. These types of responses are largely influenced by the life-history traits of the species (e.g., nocturnal versus diurnal).

The spatial context in which disturbance occurs can influence the response shown by wildlife. For example, some species, like bighorn sheep, show a stronger response when approached from above rather than below.

The frequency of disturbance can influence wildlife responses. Birds whose nests are visited frequently have lower reproductive success than those visited occasionally. Along with frequency, the duration and interval between disturbances can also shape wildlife responses to recreational activities.

Finally, the predictability of disturbance affects wildlife responses. When disturbance is predictable and benign, it causes little response. When it is unpredictable wildlife show a more intense response.

Characteristics of wildlife which affect their response to disturbance— A variety of factors associated with wildlife may alter their response to recreational activities. The size and composition of wildlife groups can influence how wildlife respond. For example, animals feeding in groups responded to approaching threats at a greater distance than solitary individuals. Age and sex of individuals may also influence wildlife responses to recreationists. For example, groups that contain females with their young will often frighten more easily than groups with adult males.

Wildlife responses to disturbance is also correlated with species' body size. Smaller species have both reduced flushing responses and shorter flushing distances than larger species. This relationship has been attributed to both energetic considerations (surface area to body volume ratios) and persecution histories (larger animals more heavily persecuted than smaller animals).

The nutritional state of an animal also affects its response to recreationists. Poorly nourished individuals are less likely to flush, and flush at shorter distances, than individuals in good nutritional condition. This suggests that disturbance that disrupts feeding wildlife should be of greater concern than other types of disturbances.

Origin of Wildlife Responses to Recreationists— The genesis of wildlife responses to recreational disturbance is considered to have both a learned and a genetic component (Knight and Temple 1995a). The learned component has been attributed to the number and outcome of interactions between wildlife and people over the individual's lifetime. There are three categories of learned responses to disturbance: 1) attraction, 2) habituation, and 3) avoidance. Habituation is defined as a waning of a response to a repeated stimulus which is not associated with either a positive or negative reward. A positive reward would result in attraction, a negative stimulus would result in avoidance (Eibl-Eibesfeldt 1970).

In addition to learning, animals have a genetic component affecting their responses to disturbance. Animals are genetically predisposed to certain behaviors which are, in turn, influenced by environmental factors (Hailman 1969). This genetic component predisposes wildlife to be either less or more tolerant to a variety of human activities.

Management Approaches for Wildlife and Recreation— Four general approaches which may be used in attempting to manage for coexistence of recreationists and wildlife include: 1) spatial, 2) temporal, 3) behavioral, and 4) visual categories (Knight and Temple 1995b). Spatial restrictions are perhaps the most common technique and result in "buffer zones" where human activities are restricted. The time frame during which disturbance occurs is of critical importance in affecting wildlife responses to recreationists. Therefore, temporal restrictions during critical times of a species' annual cycle may be employed. Although spatial and temporal restrictions on human activities are the most often used techniques, alteration of human behavior is also a viable management approach (Vaske et al. 1995). Because such things as noise, speed, and type of recreational activity elicit difference responses from wildlife, aspect of these categories could be modified. Researchers have noted that wildlife are often less affected when visually shielded from human activities. The role of visual buffers is an important concept as it can result in reduced spatial restrictions separating critical wildlife-use areas from disturbances. Components of visual screening that can influence wildlife responses to disturbance include the juxtaposition of the animals, the location of the vegetation, and the location of the disturbance.

Conclusions— The pressures of recreational activities on wildlife in wildlands will not soon diminish. Responsible wildland management necessitates that we fully understand the numerous dimensions of recreation and wildlife. Although progress in this field to date has been slow, we are beginning to develop a conceptual model of the interrelationships between the two and can anticipate rapid conceptual advances in the years to come. One factor that will facilitate this understanding is for land-management organizations to view land-use perturbations as experiments and monitor results before and following these disturbances (MacNab 1983).

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Concluding Remarks: Effects of Outdoor Recreation on Wildlife

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"The worse thing that can happen to a piece of land, short of coming into the hands of an unscrupulous developer, is to be left to open to the unmanaged public."— Wallace Stegner, American Places

That line by Wallace Stegner serves as the motivation for my concluding thoughts. The purpose of our public lands have changed considerably from the days when they were simply to be used for logging, mining, and livestock grazing. Today, more than ever before, they are being used for outdoor recreation. We are living during a remarkable shift in emphasis in what we consider to be the highest and best use of our public lands. In the American West and elsewhere, that use will be outdoor recreation.

There is a potentially dangerous trap, however, in this trend. Whereas many people have viewed commodity uses of the land as destructive, they have believed that outdoor recreation was benign, that it did not alter biological communities. Increasing evidence, however, suggests that this belief is incorrect and that outdoor recreation, like any use of land, can be quite damaging.

Are these changes in emphasis on how we use our public lands o.k.? Will more recreation and less grazing, logging, and mining promise us a new and better West? Or will this new West, based on the economies and communities of outdoor recreation, be like the old? The answer to these questions is: it depends.

Ecosystem management argues for the protection of biological diversity as well as the production of commodities and amenities on our public lands. With the increasing use of these lands for outdoor recreation, what are the implications to public-land managers?

Because outdoor recreation has the capability of altering native biodiversity, just as does logging and livestock grazing if carried to excess, it is incumbent for land managers to steward these lands so our natural heritage is protected. Something we have always asked from them regarding grazing, mining, and logging, we must now also ask of them regarding outdoor recreation. The difference, of course, is that outdoor recreationists are a much larger component of our population than are the commodity users. In addition, federal land-management budgets are shrinking rather than increasing during a time when there is considerably more need for stewardship.

Land stewardship will require that limits be placed on outdoor recreation activities and that much more careful consideration be given when locating recreational sites, such as hiking trails, camping and picnic areas, climbing cliffs, and areas for motorized users. Land managers will need everyone's cooperation.

There is evidence that many outdoor recreationists will be amenable to these demands. A recent survey of birdwatchers found that their primary motivation was to contribute to wildlife conservation (McFarlane 1994). This study highlighted two important points. First, people care about wildlife; indeed, it is often the primary purpose why they visit our public lands. Second, people's goals can change over time as they gain greater insights and appreciation of nature.

Land stewards, therefore, can use the "power of the resource" to educate people about their impacts on wildlife and to gain greater compliance for restrictions. As people learn that outdoor recreation, unmanaged, can alter our natural heritage, managers will experience greater success in building a level of coexistence between wildlife and recreationists.

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Can Burrows and Scats be Used as Robust Estimators for the Distribution and Density Patterns of Desert Tortoise Populations on Landscape Scales?

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The estimation of the distribution and density patterns of desert tortoise populations on landscape scales has been a formidable task for four important reasons: 1) the magnitude of the spatial scales involved, 2) the typical low densities found in tortoise populations, 3) the patchy or clumped nature of tortoise populations on both local and landscape scales, and 4) the fossorial behavior of tortoises and low levels of surface activity. Tortoises spend over 95 percent of their time in burrows on an annual basis. However, surrogates of tortoise presence, burrows and scats, are not only readily visible on the surface under all environmental conditions, but they are present at much higher densities than actual tortoises.

The use of surrogate measures to assess or monitor wildlife populations, including desert tortoises, has often been criticized on both perceived and real issues of relevancy, accuracy, or precision. However, statistically valid empirical field data based on unbiased robust sampling designs are lacking to support or reject the hypothesis that tortoise sign densities can be use as a suitable estimate of actual tortoise densities. EDA (exploratory data analysis) using our database has shown that there is a strong association among tortoises, burrows, and scats along sampled transects.

The motivation for this research was to develop an economic sampling protocol to estimate with moderate accuracy and precision the distribution and density patterns of desert tortoises on landscape scales. Four modules comprise the sampling protocol: 1) the use of remote sensing and GIS to define the sampling universe, 2) the sampling design to locate subplots and transects in the landscape, 3) Line Transect Distance Sampling Modeling (LTDSM) to estimate the densities of actual tortoises, carcasses, burrows, and scats at multiple-nested spatial scales, 4) interpolation and smoothing algorithms to construct spatially explicit GPS referenced density surfaces of the estimated sampled elements. Landscape subplots were 9 km^2 in size and four square transects, each 4 km in length, were randomly located in these subplots. Tortoise density for the entire landscape unit was estimated from LTDSM data from live tortoises. The local variation and pattern in the distribution and density of tortoises within the landscape unit was estimated from the multi-scale estimates of burrow and scat densities. The estimated density surface of desert tortoises in the landscape was constructed by interpolation/smoothing functions. A variety of algorithms have been evaluated, including thin-plate splines, cubic splines, and kriging.

Additionally, 29 adult tortoises of approximately equal sexes were fitted with radiotelemetry transmitters in two of the 9 km^2 subplots at Sand Hill. The data from this portion of the study were used to estimate: home ranges, relative occurrences of tortoises in burrows compared to surface activity, number of burrows used by each tortoise, and spatial variation in these parameters.

The pilot study for this protocol was conducted in the southern Mojave Desert at Sand Hill Training Range, Marine Corps Air Ground Combat Center (MCAGCC); and Pinto Basin, Joshua Tree National Park.

Growth of Desert Tortoises at Yucca Mountain

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We compared growth of three groups of tortoises at Yucca Mountain, Nevada, that differed in the size and duration of disturbances to which they were subjected (High-impact, Low-impact, Control). We tested for differences among groups by comparing yearly growth increments and fitted parameters derived from logistic-by-length growth curves developed using interval equations.

Controlling for tortoise size using analysis of covariance, yearly growth increments differed among treatment groups, years, and sex. Pooled over years, tortoises in the low-impact treatment group grew an average of 4.4 mm year^{-1}, whereas high-impact and control tortoises grew an average of 3.5 and 2.6 mm year^{-1}, respectively. Although there were differences in growth of tortoises among treatment groups, the magnitude of differences over time did not change, indicating that the disparities in growth were most likely not due to factors associated with activities at Yucca Mountain. More likely explanations are habitat variability and local microclimatic differences. Pooled across treatment groups, tortoises grew most in 1995 (6.3 mm), least in 1994 (1.3 mm), and an intermediate amount in 1993 (3.2 mm). Yearly differences in average growth reflect the variability in rainfall during the study and the resulting differences in plant productivity. On average, males had larger yearly growth increments than females, yet these differences were less pronounced for smaller individuals. In all years, smaller tortoises generally grew more in absolute length than larger ones, and this difference was greater during years with higher productivity. Males and females tended to grow at the same rate until they began to diverge at approximately 140 mm carapace length.

Growth models confirmed results of analyses on yearly growth increments. Overall, males were predicted to reach approximately 277 mm in length and females approximately 258 mm. Tortoises in the high- and low-impact treatment groups were predicted to reach larger sizes than tortoises differences were most apparent for females. Control males were predicted to reach asymptotic sizes approximately 3 mm less than males in the high- or low-impact treatment groups. In contrast, control females were predicted to reach asymptotic sizes approximately 15 mm less than females in the other treatment groups.

Recreation Management And Endangered Species Conservation In a Coastal Beach And Dune Ecosystem

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Massachusetts' coastline includes over 220 miles of barrier beaches, many of which are exemplary coastal beach and dune habitats. Conservation of these natural communities depends on effective management of human recreation. Over the past decade, conservation efforts have emphasized preserving the rarest faunal components and maintaining natural processes of sand erosion and accretion. The Piping Plover (*Charadrius melodus*), a migratory shorebird endemic to North America, has received considerable conservation attention and has been an umbrella species for other inhabitants of the beach and dune ecosystem. Recovery efforts for Piping Plovers in Massachusetts have yielded positive results and provide an example of how management can balance restoration of natural communities with human recreation.

The Atlantic Coast population of Piping Plovers nests from the Carolinas north to Newfoundland and winters from the Carolinas south to Florida, the Caribbean, and the Gulf Coast. It is federally listed as "threatened" and was estimated at about 1,350 pairs in 1996. Typical breeding habitat is a narrow zone of sandy beaches, dunes, and intertidal areas that provide nesting, feeding, and brood-rearing habitat. Piping Plovers return to Massachusetts and establish breeding territories from late March through May. Nests are simple scrapes in the sand. Although peak hatching occurs in June, unfledged chicks may be present on beaches from late May through early August. Chicks are precocial and may move hundreds of meters up and down the beach each day feeding on invertebrates. Chicks attain flight at 25-35 days of age.

Piping Plovers in Massachusetts increased from 140 to 454 breeding pairs between 1990 and 1996. Population increases ranged between 3 and 36% per year. We attribute this rapid increase primarily to high reproductive rates that averaged 1.75 chicks fledged/pair from 1989 to 1995 (range = 1.4 - 2.0). Modeling has estimated that an average annual productivity of 1.24 chicks fledged/pair is needed to maintain a stationary population in Massachusetts (Melvin and Gibbs 1996). From 1989 to 1995, the rest of the Atlantic Coast population averaged only 1.18 chicks fledged/pair and increased by only 6%. Percent of the Atlantic Coast population breeding in Massachusetts increased from 14 to 34% between 1990 and 1996.

High productivity in Massachusetts has resulted from relatively high rates of hatching and fledging. From 1992-1995, proportion of eggs hatched and chicks fledged ranged between 0.57 - 0.71 and 0.60 - 0.77, respectively. However, declining trends in both parameters is a concern. We attribute relatively high productivity and rapid population growth of Piping Plovers in Massachusetts to two factors: abundant habitat and intensive management. Management has addressed three categories of limiting factors: human recreation, dune building, and predation.

Massachusetts' beaches are used by millions of recreationists each summer. Without management, large areas of beaches would be functionally unavailable to nesting plovers because of heavy pedestrian use, and birds that did nest would be vulnerable to direct egg mortality or nest abandonment as a result of human disturbance. Unless intensively managed, off-road vehicles (ORVs) can also limit distribution and productivity of Piping Plovers. Adverse effects from ORVs include direct mortality to birds or eggs, physical occupancy of nesting or feeding habitat, and physical degradation of feeding habitat caused by repeated vehicle passes (Leatherman and Godfrey 1979, Strauss 1990, Melvin et al. 1994, U.S. Fish and Wildlife Service 1996). Chicks are especially vulnerable to being run over by ORVs, even when closely monitored and at levels of use as low as ≤ 5-10 vehicle passes per day (Melvin et al. 1994).

Increasingly since the late 1980's, nests and suitable nesting habitat have been protected from human disturbance by warning signs and symbolic twine fencing. These efforts have allowed Piping Plovers to achieve relatively high levels of productivity on beaches where moderate levels of non-motorized recreational use occur (Hoopes et al. 1997). Public education efforts have included on-site wardens, interpretive signs, brochures, educational slide shows and videos, and articles in newspapers and magazines.

Provisions against "take" of adults, chicks, and eggs contained in federal and state endangered species laws have provided strong legal tools to protect Piping Plovers from ORVs. In addition, Massachusetts' Wetlands Protection Act (WPA) has been an important regulatory tool for protecting habitat of Piping Plovers and other beach-nesting birds. Regulations pursuant to the WPA state that "Projects that will alter a wetland resource area shall not have short or long term adverse effects on the habitat of state-listed species". Under the WPA, coastal beaches, dunes, and intertidal areas are all defined as wetland resource areas, and use of ORVs on coastal beaches has been determined to be an activity regulated by the WPA. Since 1991, the WPA has been an effective regulatory mechanism to protect plover and tern habitat from ORVs. Both the U.S. Fish and Wildlife Service (USFWS) and the Massachusetts Division of Fisheries and Wildlife (DFW) have issued guidelines to assist landowners in managing ORVs so as to avoid violations of state and federal laws. In early April, nesting habitat is delineated and ORVs are restricted to discrete travel corridors along the outer edges of that habitat. As soon as chicks hatch, 200 yard-long sections of beach are completely closed to recreational vehicles until the chicks fledge. These temporary vehicle restrictions have been vigorously opposed by ORV user groups and to varying degrees by landowners and municipalities that derive income from sales of beach driving permits. However, management that conforms to these guidelines now occurs on nearly every Piping Plover nesting beach in Massachusetts where ORVs are driven and seems to be slowly gaining acceptance. In 1996, DFW was granted a two-year Section 10 permit from USFWS to allow limited incidental take of Piping Plovers that could result from increased flexibility in recreation management at sites where adequate recovery programs are in place and demographic eligibility requirements have been met.

Restrictions on ORVs also protect other components of the beach and dune community, including nesting and migration habitat for terns and shorebirds, and have allowed natural restoration of beach, dune, and salt marsh vegetation. Recovery efforts for Piping Plovers, however, are an inadequate conservation umbrella for the federally threatened Northeastern Beach Tiger Beetle (*Cicindela dorsalis dorsalis*). Heavy pedestrian and ORV traffic on beaches is believed to have contributed to the near extirpation of this beetle from its range north of Chesapeake Bay (USFWS 1994), primarily through larval mortality caused by sand disturbance and compaction. Larvae inhabit beach substrates year-round, so temporary restrictions on ORV use will probably be inadequate on beaches where tiger beetle restoration is an objective.

Massachusetts' Wetlands Protection Act has also been an effective regulatory tool to prevent or minimize degradation of plover and tern habitat by construction of engineered dunes and use of sand fencing, discarded Christmas trees, and vegetation plantings to trap sand and build dunes. Such activities attempt to counter natural processes of beach and dune erosion and accretion, and often replace relatively flat, sparsely vegetated substrate with dunes that are too steep or vegetated to be suitable nesting or brood-rearing habitat (Melvin et al. 1991, U.S. Fish and Wildlife Service 1996).

Predation is a major factor limiting Piping Plover productivity in Massachusetts. We estimate ≥ 60 of nest losses each year are from predators, primarily red fox (*Vulpes vulpes*) and crow (*Corvus brachyrhynchos*). Causes of chick loss are difficult to identify, but predation is often suspected. Although it is widely assumed that predator populations have increased as a result of human activities in the coastal zone, conclusions about the relative importance of predation as a factor limiting Piping Plovers now versus historically are speculative. Since the late 1980's, managers have increasingly used various designs of wire predator exclosures placed around nests to protect eggs and increase hatching success (Rimmer and Deblinger 1990, Melvin et al. 1992). Drawbacks of exclosure use have been higher rates of abandonment and the appearance of "smart" foxes and crows that seem to identify exlosures as sources of food.

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Coexistence of Outdoor Recreation and Wildlife: A Natural-Lands Manager's Perspective

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Outdoor recreational activities are increasing in popularity throughout the United States (Flather and Cordell 1995). These activities can have a negative impact on natural resources (Knight and Gutzwiller 1995 and references therein). For example, Boyle and Samson (1985) reported more than 80% of studies reviewed that described nonconsumptive outdoor recreation and wildlife interactions having negative impacts. There is, however, value in providing positive outdoor recreational opportunities for enhancing public support for natural lands preservation (Purdy et al. 1987, Knight and Temple 1995). Unfortunately, attempting to balance protection and conservation of wildlife and providing recreational opportunities can be difficult and controversial (Zaslowsky 1995). The solution to providing recreational opportunities while protecting the environment lies in a three pronged approach: information gathering and preparation, alternative development and stakeholder involvement, and finally, providing on-the-ground tools for mitigation (Johnson and Vande Kamp 1996).

The first phase of planning for coexistence involves gathering all the best available information. This requires knowledge about the sensitive resources to be protected. Information on environmental characteristics needs to be gathered to identify how the recreational use impacts the resource through thorough research and observation. The type of recreation mitigated must be understood as well as the patterns of that use (i.e., on/off-trail, seasonality). Visitor use studies can be valuable sources of information for planning (Zeller et al. 1993). Exploring the mitigation tools available (i.e., seasonal spatial/temporal restrictions, trail locations, fencing) and acceptance by the recreationists is critical to an effective strategy.

The second phase is critical to success. This involves developing well articulated natural and recreational resource goals and objectives. In addition, development of alternative strategies (i.e., trail locations, seasonal restrictions) with stakeholder (i.e., agency staff, public) involvement is important at this stage (Tilghman and Murray 1995).

Finally, implementing strategies of coexistence will require a plethora of mitigation tools. Education of the stakeholders (i.e., recreationists) about the negative impacts, for example, is the most crucial tool for a natural lands manager. Recreationists are more likely to support alternatives that involve restrictions to recreation if they understand how they and wildlife will benefit (Friedland et al. 1973, Purdy et al. 1987). Cooperative ventures between recreationists and natural lands managers is an effective means of ensuring the success of mitigation (Selin 1995). For example, using climbers to assist in monitoring cliff nesting raptor closures and educating other climbers is a powerful way to develop support for spatial and temporal use restrictions. When developing recreational trails, natural lands managers can reduce fragmentation by spatially arranging trails to maximize interiors and minimize edges (i.e., trails near roads or at the margins of housing developments). Minimizing the development of social trails (a source of fragmentation) by creative, aesthetically pleasing fencing or warning signs such as "Beware rattlesnake habitat" can be useful. Seasonal spatial and/or temporal restrictions are very useful tools for protecting sensitive individuals or wildlife populations (Richardson and Miller 1997). Finally, enforcement of regulations can be accomplished through the use of uniformed staff such as rangers or natural land managers (Klein 1993, Swearingen and Johnson 1995).

With appropriate preparation, stakeholder involvement, and the use of a variety of mitigation techniques, natural lands managers can successfully reduce the impacts of outdoor recreation and enhance the coexistence with wildlife.

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Motorized Recreation and Effects on Wildlife

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Outdoor recreational activities are increasing in popularity throughout the United States (Flather and Cordell 1995). Results from a national survey indicate that the number of individuals participating in nonconsumptive wildlife-oriented activities nearly doubled between 1980 and 1990 (U.S. Department of the Interior, Fish and Wildlife Service and U.S. Department of Commerce, bureau of the Census 1993).

In particular, recreational activities involving motorized modes of travel are on the rise. Heretofore, some have thought that nonconsumptive outdoor recreation was an environmentally benign activity. Increasing evidence, however, indicates that these activities can affect individuals, populations, and communities (Knight and Gutzwiller 1985).

Along with this is a rising concern among scientists and mangers about the deleterious impacts that motorized recreation may have on wildlife. For example, Boyd and Samson (1985) reported that 73% of studies involving impacts of off-road vehicles and snowmobiles reported negative effects on wildlife. Although much of the information reported in the literature is anecdotal, numerous studies have directly examined the impacts of snowmobiles, four-wheel drive off-road vehicles, and general vehicular traffic on wildlife. Here I summarize studies that deal with land-based motorized recreation on wildlife, examine deficiencies in the studies, and offer suggestions for future research.

As one might expect, different types of motorized recreation may elicit a variety of responses by wildlife. For example, a quiet, slow-moving passenger car may evoke a different response than a loud, fast-moving motorcycle. Of importance, but often lacking in the literature, are comparisons between motorized and nonmotorized activities.

The existing literature reflects that only a limited number of wildlife species have been studied. Most information is based on responses of large, easily observable species while the smaller, inconspicuous species have received little attention. Because there can be considerable interspecific variation in wildlife responses to recreational activities, this information is particularly important.

When attempting to manage for both wildlife and recreationists, the most valuable information is the effect of recreational disturbance on a species' inclusive fitness (survival and reproduction), movements, and habitat use. Unfortunately, much of the literature lacks this information and focuses on immediate behavioral reactions to a disturbance. Thus, we are left to only speculate on whether an immediate reaction, such as fleeing an area, will result in a decreased fitness.

Although numerous studies have addressed the impact that motorized recreation has on terrestrial vertebrates, our knowledge is limited. While more research is needed, sufficient information exists to make management decisions which may reduce the impact of recreational activities on wildlife. Future studies should have sound experimental design (treatments, controls, replicates), include comparisons between types of activities, focus on a diversity of species, and obtain information relating to fitness, movements, and habitat use.

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Nutritional Value of Native and Introduced Plants Consumed by Desert Tortoises

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The flora of the Mojave Desert has changed substantially over the last century, and an important component of this transformation has been invasion by exotic species. Simultaneously, population densities of desert tortoises have declined. A variety of causes have been proposed for this decline, including the possibility of nutritional problems associated with consumption of exotic plant species. Several studies have indicated that wild tortoises do consume, and may even prefer, the introduced and now widespread annual forb *Erodium cicutarium* (red-stemmed filaree or heron's bill) and the introduced annual grass *Schismus barbatus* (split grass). Do these plant foods provide less nutrition to tortoises than do native plants?

We compared the nutritional quality of filaree and split grass with that of the native annual forb *Malacothrix glabrata* (desert dandelion) and the native grass *Oryzopsis hymenoides* (Indian rice grass). Wild tortoises obtained from new construction sites in southern Nevada were housed in outdoor pens in Los Angeles and were offered weighed amounts of freshly collected and quickly frozen food plants, a single species at a time. Three to four successive 10 day periods, each demarcated by feeding the tortoises differently-colored bits of plastic tape, were allowed for the spring forb diet before switching to the summer diet of dry grass for another month of measurements. Only two diets per year could be tested. Food consumption was measured by subtracting the dry weight of uneaten food from that offered daily, and all feces were collected in plastic bags attached to the back end of the tortoise's shells. Apparent digestibility (AD) of dry matter was estimated as the ratio of dry matter retained to dry matter ingested. Samples of food and feces were measured for energy, nitrogen and water content to allow calculation of apparent digestibilities of these nutrients.

Apparent digestibilities of the nutrients in the two forbs were similar (63-70% for dry matter, 69-73% for energy, 72-79% for nitrogen, and 70-75% for water). The two grasses yielded similar proportions of their dry matter (47-50%) and energy (46-48%) to digestion by tortoises, but the native grass provided some net nitrogen (AD = 7%) whereas tortoises eating dry *Schismus barbatus* in summer lost more N in their feces than they were getting in their food (AD = -7%). However, other studies indicate that green (springtime) *Schismus barbatus* provided dry matter, energy and nitrogen in proportions comparable to those of the springtime forbs measured in this study. Thus, the primary differences in nutritional quality of tortoise foods seem to be related to phenological stage (age) and taxonomic affiliation (monocot, dicot) of the food plants rather than their biogeographical history (native or exotic).

Effects of Diet and Hibernation on Growth and Maturation of Desert Tortoises (*Gopherus agassizii*)

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We have initiated a study of the interactive effects of diet and hibernation on the rates of growth and maturation of desert tortoises (*Gopherus agassizii*) from the Sonoran population. Sibling groups of hatchling tortoises are distributed among four treatment groups representing two diets (a salad of chopped mixed produce versus a high-protein, medium-fiber pelleted diet) and two hibernation conditions (2 months hibernation versus no hibernation). The diet treatments were started when the hatchlings were 2-3 months old, and the hibernation treatment began in the second year of the study when the hatchlings were approximately 12 months old.

In the initial year of the study, hatchlings fed the pelleted diet grew larger than did the tortoises fed salad ($p < 0.05$). Variation in growth among sibling groups was also significant ($p < 0.05$).

Community involvement is a central feature of this study. The hatchling tortoises were donated by tortoise hobbyists in Phoenix and Tucson, and a newsletter keeps the donors informed of their progress. The tortoise research project is included on the Zoo's Behind the Scenes program. A week-long cross-curriculum thematic teaching unit for middle and high school students from the Phoenix metropolitan area incorporates information about tortoises into Language Arts, Mathematics, and Science classes. The students make a trip to The Phoenix Zoo to work with the tortoises in the study and learn about the Zoo's conservation programs.

Desert Tortoise Relocation at Yucca Mountain, Nevada

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The desert tortoise is the only threatened or endangered species resident at Yucca Mountain, Nevada, the site being studied by the U.S. Department of Energy as a potential geologic repository for high-level nuclear waste. Twenty-eight tortoises were relocated at that site during 1992-1995 to prevent those animals from being harmed during ground-clearing and construction activities. Most of these tortoises had been fitted with radio transmitters and monitored from one month to three years prior to being relocated as part of a series of studies to evaluate and mitigate impacts of DOE activities. One tortoise was relocated 4.9 km. All others were relocated 2 to 1,640 m and over half of these were released within their home range.

We monitored relocated tortoises for 1 to 36 months after they were moved. Four returned to construction areas, one of which was killed on an access road after returning. The other three were relocated one to seven additional times. Two other relocated tortoises died, 9 and 32 months after begin relocated. Cause of death of these small (47 and 64 mm carapace length) tortoises was not attributable to construction activities or to being relocated.

The tortoise relocated 4.9 km wandered more than 32 km after being released. Less than half of the other relocated tortoises showed movement patterns that differed from the rest of the Yucca Mountain population. Six individuals had larger and four had smaller home ranges compared to nonrelocated tortoises in similar age/sex classes.

Thirteen relocated tortoises were tested for antibodies to *Mycoplasma agassizii* one to four times after being relocated. Three of these tortoises tested positive at least once after being relocated. The overall proportion of positive samples from relocated tortoises (3 of 32 samples; 9%) was lower than the overall rate of positives (18.7%) for all samples (*n* = 283) collected at Yucca Mountain from 1993 to 1995.

Although post-relocation annual home ranges of some relocated tortoises differed, they did not indicate that the tortoises were substantially impacted by being relocated. We conclude that relocating tortoises short distances within or near established home ranges and then intensively monitoring those tortoises was an effective mitigation measure for reducing the likelihood of injury or death of tortoises at Yucca Mountain.

Differences in Burrow Use Between Adult Male and Female Desert Tortoises

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We monitored seasonal use of cover by radio marked adult desert tortoises (*Gopherus agassizii*) at Yucca Mountain, Nevada, to describe the number and types of burrows used and to evaluate differences in cover use between sexes. In general, we found tortoises in burrows most often during the hottest and coldest months and in pallets and away from cover most often during months with moderate temperatures. In addition, we detected differences between males and females in the depth of burrows used and in the types of cover used seasonally.

We found males deeper in burrows and in deep burrows (i.e., burrows > 1 m deep) more often than females during all seasons. In addition, males used more deep burrows per year (x = 4.9, SD = 0.32) than females (x = 3.0, SD = 0.21). Thirty-nine and 27% ofthe burrows used per year by males and females, respectively, were deep.

Males and females used a different number of burrows and different types of cover seasonally. During spring, females used more burrows (x = 4.3 vs. 3.4), were found away from cover more often (25 vs. 21 %), and were found in deep burrows about half as often (17 vs. 33%) as males. This pattern was reversed during fall (September-October), which is when most courtship activity was observed at Yucca Mountain. Females used fewer burrows (x = 4.0 vs. 5.3), were away from cover less often (7 vs. 16%), and were found in deep burrows only slightly less often (37 vs. 40%) than males during fall. Many of these seasonal differences probably were related the annual reproductive cycle and to differences in the timing of hibernation between males and females.

Comparison of Diagnostic Tests for Tortoise Upper Respiratory Tract Disease

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The bacterium *Mycoplasma agassizii* has been shown by experimental infection studies to be an etiologic agent of a chronic upper respiratory tract disease (URTD) of tortoises. Complementary culture, DNA-based (PCR), and immunological (ELISA) tests for *M. agassizii*, necessary to determine the infection and immune status of asymptomatic and URTD-symptomatic tortoises, have been developed. These diagnostic tests are based on different principles, and differ in the types of samples required, cost, and interpretation. The tests were validated in three controlled experimental infection cohort studies including a total of 43 infected and 23 control adult tortoises. Test parameters evaluated were:

— sensitivity, or "if a tortoise is infected, will it test positive?"

— specificity, or "if a tortoise is not infected, will it test negative?"

— positive predictive value (PPV), or "if a tortoise tested positive, was it really infected?"

— negative predictive value (NPV), or "if a tortoise tested negative, was it really not infected?"

For the three experiments, the ranges of results calculated 3 months after experimental infection are shown in the table on the next page. The rate of false positives was 0% for culture and PCR, and 0 - 27% for ELISA. The rate of false negatives was 0 - 17% for culture, 0 - 20% for ELISA, and 36 - 63% for PCR. Importantly, these values varied at different sampling times postinfection. The variation may relect, in part, the progression of URTD: 1) establishment of mycoplasmosis, 2) host responses which reduce the population of mycoplasma and simultaneously cause illness and signs of disease, 3) relaxed host responses after the mycoplasma population is reduced or host defenses become exhausted, and 4) re-expansion of the mycoplasma population after host defenses relax. Culture and PCR can be better than ELISA for diagnosis early in the infection (2 to 8 weeks postexposure), because time is required for a tortoise to respond immunologically. The ELISA can be better than culture and PCR for diagnosis in later stages of infection if the tortoiseresponses decrease mycoplasma numbers. When comparing populations, test parameters also may vary with the true prevalence of infection.

Test	Sensitivity	Specificity	PPV	NPV
Culture	93–100%	100%	100%	83–100%
PCR	37–64%	100%	100%	50–58%
ELISA	89–100%	73–100%	84–100%	80–100%

The greatest risk of transmission of mycoplasmal URTD is from symptomatic,culture-positive, or PCR-positive tortoises. To minimize the spread of infection, before tortoise relocations, potential recipient populations should be tested to estimate the prevalence of infection.Tortoises that test positive should be relocated to vary among populations. Recipient population density should be increased only to the extent that can be sustained by the available habitat. Increased population density promotes the spread of all communicable diseases.

Survivorship and Growth Rates of Neonate and Juvenile Desert Tortoises at Ft. Irwin Study Site

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Since the establishment of Ft. Irwin Study Site (FISS) in 1990, 216 desert tortoises (*Gopherus agassizii*) have hatched inside a 0.4 hectare field enclosure built in natural habitat at U. S. Army's National Training Center, San Bernardino County, California, 40 km northeast of Barstow in the Central Mojave Desert. Mean cohort size was 36 ± 30.6 neonates (range: 6 to 88). Densities inside the enclosure ranged from 150 to 344 juveniles/ha in the original enclosure (FISS I) and 42 juveniles/ha inside a second enclosure (FISS II) built in 1995. Through Fall 1996, overall survivorship was 44%. Mortalities were attributed to: 1) dehydration and malnutrition (10%); 2) avian and mammalian predation inside the enclosure (31%) ;3) predation after experimental release from the enclosure (12%); 4) 1oss due to transmitter failure after experimental release (18 %); and 5) unknown causes (29%). Differential survivorship by cohort year was influenced by avian predation prior to entire roofing of the enclosure in 1990, small initial cohort sizes in 1992 and 1993, and experimental release of 4 and 5 year-old juveniles during 1994 and 1995. Mean annual growth rates were calculated from increase in minimum carapace length (MCL) in spring of one year to spring of the following year. Overall growth rates varied from a maximum of S.3 mm/year to 2.5 mm/year. Mean annual growth rate for juveniles translocated to FISS II in Spring 1995, was twice that of FISS I representative juveniles of the same age-size class 1995 to 1996 (6.3 mm/yr compared to 3.1 mm/yr). Low growth rates could be the result of higher than normal densities inside the enclosures; below average precipitation during some years: intense episodic handling of neonates and juveniles for research studies; degradation of the habitat inside the enclosure from repeated trampling by researchers and seasonal occupation by adult tortoises for the life of the enclosure.

Population Estimation of Desert Tortoises

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Numerous methods have been used to estimate population size of desert tortoises. One square mile study plots were established approximately two decades ago by the Bureau of Land Management in California and later in other States. Data from these plots have been useful in establishing that desert tortoises were indeed declining, and these data were used as evidence that the species needed to be listed as threatened. Subsequently, this method of population estimation has been criticized as not representing random samples of the overall population and the stratified Lincoln Index method of population estimation has very large error bars. The Desert Tortoise Recovery Team recognized the drawbacks of this method, but recommended that the additional data collected at these sites on modes of mortality were valuable. Indirect methods have been used to assess population size, but these methods have fairly low reliability. Small plot methods have been the subject of experimentation as have "distance sampling." These methods each have attributes to make them appealing, and both have drawbacks. The methods used to sample tortoise populations will have to be accurate and inexpensive. Very small plots (e.g., one hectare) have been used to get a single value of the number of tortoises in an area the size of the proposed DWMAs, but no variance around the number can be computed. Distance sampling techniques can estimate a variance around the mean number of individuals, but this method depends strongly on a detectability index which may be difficult to measure. Intermediate-size plots have the advantages of both methods, but some researchers worry that using intermediate sized plots pose yet other logistic problems. The many arguments for and against the various population estimation methods will be discussed.

A Framework for Visitor Management and Resource Protection

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Almost all public land protected areas in the U.S. allow some level of visitation. Visitors come for purposes of recreation, education, research, training, commercial use, subsistence and spiritual renewal and other reasons. Depending on the type of protected area, it should be possible for managers to provide some range of quality visitor experience opportunities that in turn maintain an appropriate level of resource protection. Planning approaches are evolving that better integrate these two goals - both of which are often a part of a public agency's or a given protected area's mission statement. When visitors have a quality experience, they often become constituents that support the area, its management, policies and funding needs. Desired levels of resource protection can be matched with the types of experiences offered visitors if good information about the impacts to be avoided is utilized.

This ideal mix of use and protection is often not attained because: 1) the absence of a planning process that integrates the two (because of the nature of planning models themselves, or because visitor management and resource specialists have often chosen to operate independently); **2)** even where visitor management and resource protection are well planned, the resources and management capability needed to implement the plans may be absent.

This presentation will briefly explore the evolution of visitor management including the concept of carrying capacity. Changes, while not yet widespread, include a perceptible shift from applications largely concerned about recreation to applications that are more comprehensive and better integrate resource protection goals (Manning et al. 1995). Basic elements of the most frequently used planning approaches (see references) - the Recreation Opportunity Spectrum, (ROS); Visitor Impact Management,(VIM); the Limits of Acceptable Change (LAC) and the Visitor Experience and Resource Protection approach (VERP) - can be synthesized to form a framework that can help balance visitor management with resource protection. Later approaches put a strong emphasis on a level of public involvement during the planning process in order meet user needs and develop a sense of ownership about agreed upon goals and practices.

Basic elements of these approaches include: a. agreement about desired future conditions and management goals for the area, b. agreement on a set of generic visitor experience and resource protection opportunity classes (management zones), c. a description of the biophysical, social and managerial setting attributes of each opportunity class that clearly integrates the appropriate level of protection and ecosystem integrity with the types of experiences that are offered to visitors, d. the selection of indicators and standards that connect impacts with the causes of impact and enable managers to know if desired conditions are being achieved, e. the selection of management actions that will likely address the issues and opportunities within the desired future condition statement, and f. a monitoring program based on the indicators and standards selected.

This framework may be made more meaningful or instill more confidence in resource mangers apprehensive about impacts from visitation, if it is accompanied by a review of visitor management and resource protection strategies that might be used in element e., the selection of management actions. Strategies reviewed will include: 1) How to reduce the use of problem areas, 2) How to modify the location of use within problem areas, 3) How to modify the timing of use, 4) How to modify the type of use and visitor behavior, 5) How to modify visitor expectations, 6) How to increase the resistence of the resource, 7) Rehabilitating impacted locations (Cole et al. 1987). Within these strategies lie a host of visitor management techniques like site and route selections, grouIn sum, the tools exist to permit the integration of quality visitor experiences and resource protection in most protected areas, but the particular impacts to wildlife or plant communities that managers are concerned about must be carefully integrated into the planning process, the full range of tools used to achieve management objectives, and resources available to implement the plan. Managers should also be reluctant to encourage visitation if planning has not been done or if they do not have the management capability necessary to achieve desired future conditions.

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The Role of the Burrow in Juvenile Tortoise Life History

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Previous research on juvenile desert tortoises has shown that they can conserve water very effectively during dry seasons; however, water loss rates can be remarkably large and may create situations in which these small reptiles are seriously threatened by desiccation in natural environments. Little is known concerning the role of the burrow in water conservation. Here, I report on burrow use by juvenile desert tortoises at the Fort Irwin Study Site of the central Mojave Desert, California. Preliminary results on burrow locations showed that significantly more juvenile burrows were located under the canopy of shrubs than in open areas and that the frequency of shrubs with burrows was dependent on shrub type (size and species). Larger shrubs (e.g. *Larrea, Lycium)* had more burrows associated with them than smaller shrubs (e.g. *Ambrosia, Ephedra).* Because desert reptiles are often water limited, they must evolve behavioral and/or physiological mechanisms to resist evaporative water loss (EWL) in their dry environment. This spring, in order to determine the extent that the burrows of *G. agassizii* may function to reduce EWL, I will construct artificial burrows of different depths and in different microhabitats and measure temperature and humidity inside these artificially constructed burrows and in natural burrows. Using doubly labeled water, I will measure water turnover rates in juveniles living in artificially constructed burrows.

A Review of Reptilian Keratins

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Cutaneous dyskeratosis, a disorder of free-ranging desert tortoises, is characterized by loss of integrity of the horny layer of the carapace, plastron and thickened foreleg scutes. The disorder is thought to be associated with a defect in keratinization or cornification. This has prompted us to examine the composition of shell keratin of desert tortoises with and without cutaneous dyskeratosis to determine if ultrastructural or biochemical differences can be identified. What follows is a review of reptile keratins and the keratinization/cornification process.

The epidermis of reptiles is covered by a thick outer horny (cornified) layer that protects underlying structures from injury and prevents desiccation. The horny layer is derived by the process of keratinization and cornification of the underlying epithelial cells. Keratin has been defined by x-ray diffraction techniques, ultrastructural analysis, and biochemical studies of the composition and configuration of keratin intermediate filament and matrix proteins. Patterns identified by x-ray diffraction analysis include the α-keratin pattern of mammalian hair and epidermis of amphibians, birds, mammals and reptiles, and the β-keratin pattern of avian and reptilian feathers, beaks, claws, hard scales and shell. Ultrastructural characteristics of the horny a-layer of reptile skin include distinct thickened cellular outlines enclosing bundles of 80 AE filaments, a relatively translucent intracellular matrix and intercellular dense packets of mucus. In the horny β-layer of turtle shell, epithelial cells coalesce into a compact layer with obscure cellular boundaries and a reticulated appearance of 30 AE filaments with interspersed desmosomes. The protein structure of a-type keratin is a modified a-helix (α-helical coiled coil) while that of β-type keratin is a β-sheet. The α and β keratin proteins of turtles are biochemically distinct. The β-keratin proteins range from 6.6-30 kd while a-keratin proteins range from 7.3-46 kd. Although the β-keratin of reptiles only occurs in hard tissue structures (shell, scales, beaks and claws), the only similarity to mammalian hard α-keratins is the presence of a large proportion of zinc-soluble matrix material. Otherwise, the amino acid content, particularly of glycine and cystine residues, is more like that of soft mammalian keratins.

In general, the keratinization process involves 2 phases of cellular differentiation (fibrogenesis and matrix formation) while the third phase, cornification, involves cell surface modification. During fibrogenesis, keratin polypeptides are synthesized intracellularly and incorporated into intermediate filaments (IF). During matrix formation, the IF are organized into a cytoskeleton by matrix proteins (IF associated proteins) and other substances. Cornification continues as cell membranes of α-keratin producing cells thicken and the boundaries of β-keratin producing cells coalesce and are joined at the lateral margins by frequent desmosomal attachments. In α-keratin producing cells of turtle epidermis, a lamellar substance comprised of polar lipids is stored in the cytoplasm in membrane-bound vesicles (lamellar bodies), and is released into the intercellular space to form part of the stratum corneum. Membrane-bound packets of electron lucent material found in β-keratin producing cells just beneath the horny layer of turtle shell eventually enmesh in the horny layer. There is complete dissolution of nucleus and cytoplasmic organelles in fully keratinized cells. Due to extensive disulfide bonding, the final keratin product is insoluble except in certain protein solvents at extreme pH or in the presence of denaturing and reducing agents such as urea and dithiothreitol.

ABSTRACTS FROM THE 1998 DESERT TORTOISE COUNCIL SYMPOSIUM

Cattle, Dung and Tortoises: Symbiosis?

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Free-ranging desert tortoises will eat feces and other "non-nutritive" materials. It has been postulated that tortoises in recent evolution have relied on cattle dung to maintain their populations when food resources were scarce. A scientific response to this hypothesis requires information on the nutritive properties of cattle feces, and specifically, on the ability of tortoises to extract nutrients from cattle feces. For a digestibility study, cattle dung was offered to 14 healthy juvenile tortoises (mass range 328-991 g) as the sole food during a one month adaptation period. Only four animals would eat a sufficient amount to be included in a subsequent four-week digestibility study. Samples of offered dung and all uneaten dung were collected and dried to determine dry matter (DM) intakes. All tortoise excreta were collected for nutritional analysis. During the third and fourth weeks of the trial, average DM intake was not significantly different from fecal excretion (mean difference = -0.44 ± 0.22 SE g/2wk), suggesting a net digestibility of zero. On a DM basis, dung samples contained 50.0 % ± 0.34 acid detergent fiber (ADF), 1.34 % ± 0.012 total nitrogen (TN), and 4.24 ± 0.542 kcal/g gross energy. These constituent levels did not differ significantly from those of uneaten dung. The estimated digestibility of energy and ADF were not significantly different from zero and the estimated TN digestibility was negative. Based on our preliminary trial results, the suggestion that tortoises have benefitted from a symbiotic relationship with cattle and their feces is clearly speculative.

Desert Tortoise Preserve Committee: Accomplishments for 1997

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The major purpose of the Desert Tortoise Preserve Committee, Inc. (DTPC) is to promote the welfare of the California State Reptile, the desert tortoise (*Gopherus agassizii*) in the native wild state in the southwestern United States. In the past, the DTPC has established preserves for desert tortoises in areas of prime habitat in Kern and San Bernardino counties. In addition, the DTPC provided educational information to publicize the uses of the preserve lands.

One long-range objective of the organization is to provide educational programs to people traveling in the desert. The programs will center on the tortoise, but will also include information on desert ecosystems and impacts of human activities on environmental systems. One educational program, Nexus 2000, was started in 1995 to establish facilities along major highways to take advantage of the large number of people using these transportation routes. These facilities are planned to take advantage of the latest technology for multimedia presentations and interactive opportunities for visitors.

To expand the fund-raising potential of the DTPC, a permanent office was located in the City of Riverside in 1997 and an Executive Director was hired to coordinate efforts. The membership of the DTPC will be expanded and further campaign work will be conducted to raise the necessary funds to complete work on Nexus 2000. At the same time, successful mitigation programs undertaken by the DTPC (such as the Harper Lake Road fencing project) will be continued.

Effects on Growth and Survival of Tortoises Voiding Their Bladders During Handling

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Studies in which desert tortoises are handled often result in the side effect of some tortoises voiding their bladders during processing. Water loss could result in serious health threats or compro-

mise normal physiology, especially during the hot, dry summer months. I examined recapture and growth data for tortoises that voided and did not void their bladders when handled during annual surveys (1990-94) of three populations in Arizona: the Eagletail Mountains, Maricopa Co., Granite Hills, Pinal Co., and Little Shipp Wash, Yavapai Co. Proportions of tortoises that voided their bladders at least once when handled during an annual survey ranged from 0-38% and 20-100% among populations and years for individuals ≥180 mm and <180 mm midline carapace length, respectively. Tortoises <180 mm were more likely to void than those ≥180 mm at each population (*G* tests, $P<0.001$).

Recapture rates from one year to the next (a combined measure of capture probability and survivorship) for tortoises <180 mm were only different (*G* test, $P<0.05$ for Granite Hills 1991-92) between the two groups in one out of 11 yearly tests among the three populations. Recapture rates between groups approached significance for Little Shipp Wash from 1991 to 1992 ($0.10>P>0.05$), but all other comparisons were non-significant ($P>0.10$). The pooled data for tortoises <180 mm from Little Shipp Wash indicated that tortoises that voided in one year were less likely to be recaptured in the subsequent year ($P<0.025$). Recapture rates of tortoises ≥180 mm were not different between groups in 12 yearly tests ($P>0.05$), but approached significance for the Granite Hills from 1991 to 1992 ($0.10>P>0.05$). Pooled data for tortoises ≥180 mm from the Granite Hills also indicated that tortoises that voided in one year were less likely to be recaptured in the subsequent year ($0.05>P>0.025$). In order to obtain the most conservative results in this exploratory analysis, Bonferroni adjustments were not made to correct the overall experimentwise error rate. Both the Granite Hills and Little Shipp Wash received less rainfall in the summer of 1991 than the 1990-93 average. Incomplete data were available for the nearest weather station to the Eagletail Mountains, but summer 1991 was relatively wet compared to the long-term average. Analysis of covariance (with carapace length and estimated volume of fluid voided during handling as covariates) indicated that volume of fluid lost did not affect tortoise growth between 1990 and 1994 for tortoises ≥180 mm ($P=0.615$) or <180 mm ($P=0.462$).

The following general conclusions may be drawn from these results: 1) most tortoises that void lose small volumes of fluid; 2) small tortoises are more likely to void when handled than adult tortoises; 3) voiding during handling appears to affect recapture rates (and thus possibly survival) at least during some years; and 4) growth does not appear to be affected by the volume of fluids lost during handling. Therefore, researchers should develop well-defined study objectives that minimize handling time as much as possible in an effort to prevent tortoises from voiding their bladders.

Effects of Microgeographic Differences in Rainfall on the Nutrition and Survivorship of Desert Tortoises in the Mojave National Preserve

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Dispersion of rainfall is one of the important determinants of variation in primary productivity in desert ecosystems. Geographic, elevational and seasonal patterns of rainfall may affect populations of desert tortoises by affecting food availability, which in turn can affect patterns of growth, reproduction and survivorship in these and other desert animals. In Ivanpah Valley, California, rainfall may vary two- to threefold from lower elevation areas to higher elevation areas within a single rainfall event, regardless of season. We quantitatively analyzed the diets of tortoises in areas receiving significantly different rainfall in Ivanpah Valley, California, by analyzing contents of fresh tortoise scat soon after rainfall events. Tortoises in areas receiving significantly more rainfall primarily fed on green perennial grass (*Hilaria rigida*), whereas tortoises in lower rainfall areas fed primarily on dry cactus (*Opuntia* sp.). Differences in food and water availability have also resulted in a recent population die-off of tortoises in lower elevations, whereas populations in higher elevations within the same valley have not experienced this die-off. Microgeographic differences in rainfall, caused by physiographic features of elevation, mountain ranges and other factors, may therefore at times affect nutrition and survivorship of tortoise populations. This variation in resource availability and survivorship cannot be evaluated with present monitoring programs that have unreplicated study sites for a given geographic area.

A Potential Parasite in Wild Tortoises in Arizona: Pinworm? Trematode? Fungus?

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In the fall of 1996 eleven fecal samples from wild Sonoran desert tortoises were preserved in the field using 5% formalin and later examined for intestinal parasites. Direct smear and flotation methods recovered an unusual artifact from 8 of the 11 samples. Initially identified as a trematode egg by parasitologists (based on morphology), the organism is now thought to be a fungal oospore. The ovoid oospores bear a conspicuous operculum at the small end, and measure 42.7 X 27.4 (19.3-52.6 X 13.9-44.3) microns. A water bath was set to incubate the Aeggs@ and recover miricidia, the first trematode life-stage. The Aeggs@ did not hatch or decompose after weeks in water. During this time over a hundred slides were produced (direct smear), for measurement purposes. The oospore was found attached at the operculum to fungal hyphae in several slides. The hyphal connection was fragile, and tapping the cover-slip sometimes dislodged the oospore. The fungus has been found in three separate populations of desert tortoises. The fecal samples testing positive were collected only between late August and September (1996 and 1997), the monsoon season in Arizona. It is possible that oospores are produced during this time on decaying moist vegetation.

Tachygonetris (pinworm) ova were found in all samples. Additional parasites (*Entamoeba spp.*) were found while viewing slides. Since large samples were originally collected and preserved, the samples can be re-evaluated for parasites using ethyl acetate and centrifugation. Results will be presented with results of current incubations of the suspect fungus.

18 Years of Change in Protected and Unprotected Desert Tortoise Populations at the Interpretive Center, Desert Tortoise Research Natural Area, California

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In 1979, a 7.8 km^2 study plot was established at the Desert Tortoise Research Natural Area (DTRNA), eastern Kern County, California. The plot was centered on the interpretive center, which was under construction. The plot contains two subplots, a 4.53 km^2 protected area inside the DTRNA fence and a 3.24 km^2 unprotected area outside the fence. The entire plot was surveyed in 1979, 1985, 1989, 1993, and 1997 with a 60-day spring survey technique, modified to be a 180-day spring survey to take into account the large size of the plot. Since the study was initiated, the numbers of tortoises registered on the entire plot declined from 593 individuals in 1979 to 77 individuals in 1997. Between 1979 and 1997, densities of all sizes of tortoises declined 90% inside the fence and 94% outside the fence. For adults, the declines were 86% inside the fence and 94% outside the fence. Habitat for the tortoises has continued to decline outside the protected area, while recovery appears to be underway inside the fence. Existing management practices appear to be effective in protecting habitat, but are not effective in protecting individual tortoises or populations. The losses of tortoises both inside and outside the fence are due in large measure to landscape-scale problems (raven predation, disease). In addition, human activities on a local scale contribute to additional sources of mortality outside the fence (vandalism, vehicle kills).

Seasonal and Annual Variation in Common Raven Abundance in a Human-dominated Landscape

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Common raven (*Corvus corax*) populations have increased considerably in recent years in the deserts of southwestern United States. The increases are probably caused by an rise in human population densities in the desert and they may be responsible for increased raven predation on juvenile desert tortoises (*Gopherus agassizii*). As subsidized predators, ravens benefit from food, water, and other subsidies provided by human activities. We hypothesized that the human-provided resources are particularly important sources of food and water for ravens during summer and winter, times when natural sources of food and water are scarcer. Thus, we predicted more ravens would be found at primary sources of food and water during summer and winter than fall and spring. We tested this prediction in the west Mojave Desert by censusing ravens at six resource sites (landfill, sewage pond, golf course, towns, and two desert references) in each of three areas (Edwards Air Force Base, Mojave, and Boron). Significantly more ravens were found at landfills and sewage ponds, suggesting that these provide important resources. Although there was considerable variation among seasons and years, the prediction was partially supported. The results lend support to the suggestion that efforts to manage raven populations should focus on reducing availability of resource subsidies.

Longevity of Shrubs in the Warm Deserts of North America

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In arid regions, where variability in growth rings reflects variability in climate, it is often difficult to age-date trees and shrubs by ring counting. This has required researchers interested in the demography of woody plants to exercise considerable ingenuity in determining how long various species can survive. One famous example is the so-called "King Clone," a large clonal ring of *Larrea tridentata* (creosotebush) that has occupied the same site for an estimated 11,700 years. This estimate was made using radiocarbon dates from old wood combined with extrapolations from modern growth rates.

Repeat photography is another technique that has been used to determine longevity of shrubs in the Mojave and Sonoran deserts. In Grand Canyon, for example, photographs taken in 1872 and matched in the early 1990s show that *Ephedra* (Mormon tea), *Acacia greggii* (catclaw), and *Lycium andersonii* (wolfberry) can live for at least 120 years and that *Ambrosia dumosa* (white bursage), *Atriplex confertifolia* (shadscale), *Opuntia erinacea* (grizzly bear prickly pear), and *O. basilaris* (beavertail) can live for more than 75 years.

Long-term vegetation plots are a third source of information regarding longevity of desert shrubs; plots on Tumamoc Hill, Tucson, Arizona, indicate that *Aloysia wrightii* (oreganillo), *Fouquieria splendens* (ocotillo), *Janusia gracilis*, and *Jatropha cardiophylla* (sangre de Cristo) can live at least 72 years.

Estimates of longevity help us better understand the dynamics of desert communities and provide information that can be useful to management and restoration projects.

Bowers, J. E. 1997. Demographic patterns of *Ferocactus cylindraceus* in relation to substrate age and grazing history. Plant Ecology 133:37-48.

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Survey, Monitoring, and Management of the Desert Tortoise at Lake Mead National Recreation Area

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As a cooperator in the multi-park Natural Resources Protection Program desert tortoise project, Lake Mead National Recreation Area has greatly expanded its tortoise management program. Since the initiation of the project in 1994, the park has been active both in surveys and monitoring of the species, and in habitat enhancement and protec-

tion. We conducted cursory habitat surveys across nearly 850,000 acres of potential tortoise habitat and found that the park has a few high-density "hot spots" with many more medium to low density areas. The Nevada portion of the park, north and west of the Colorado River, has higher tortoise densities than the Arizona side, where tortoise sign is rare. We also established 14 square-kilometer monitoring plots throughout the park. Tortoise sightings on the plots varied considerably, although actual population estimates could not be determined due to small sample sizes and low recapture rates. For plots that were visited multiple times, the continual discovery of unmarked tortoises and the low occurrence of recaptures suggests that the number of tortoises occupying a site is probably much larger than our original findings indicate, and additional surveys and monitoring would help to better define the populations. We also built a burro exclusion fence, removed feral burros, and closed and rehabilitated non-system roads in an effort to protect and enhance habitat for the species.

Factors Affecting Alien Annual Plant Abundance at a Site in the Western Mojave Desert: Effects of Human Disturbance, Microhabitat, Topography, and Rainfall

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Four alien annual weeds (the grasses *Bromus madritensis rubens*, *Bromus trinii*, and *Schismus* spp, and the forb *Erodium cicutarium*) have invaded the Mojave Desert. To identify conditions that may have promoted their spread, I evaluated the association of temporal and spatial variation in their biomasses with environmental factors during one high and one low rainfall year. Sampling was stratified to sample all combinations of the following factors: (1) topographic position (upland, washlet); (2) microhabitat (intershrub, north creosote bush canopy, and south canopy); and (3) human disturbance, in the combined form of sheep grazing and off-highway vehicle use (protected, unprotected from disturbance). Biomasses were generally highest in washlets, under creosote bushes, and in the unprotected areas. The distribution of *Schismus* spp and *Erodium cicutarium* varied between years, with greatest amounts under the south canopy during the wet year and intershrub spaces during the dry year. These results suggest that human disturbance and comparatively mesic conditions present during wet years, under shrubs, and in washes, may facilitate annual plant invasions into the Mojave Desert. Relative abundance of aliens was highest during the dry year, suggesting that their dormancy requirements may be less stringent than that of natives, which may explain their population declines following droughts.

Status of Alien Annual Plants and their Environmental Correlates in Desert Tortoise Habitat

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To describe the current status of alien annual plants in desert tortoise habitat, we measured above-ground live annual plant biomass at 8 sites in the Fremont-Kramer, 10 sites in the Ord-Rodman, and 16 sites in the Superior-Cronese Desert Wildlife Management Areas designated in the Recovery Plan for the Desert Tortoise (Mojave Population). These sites respectively represented the western, southern, and central Mojave Desert regions. During the high-rainfall spring of 1995, three alien species accounted for 66% of the total annual plant biomass, *Bromus madritensis* subsp. *rubens*, *Erodium cicutarium*, and *Schismus* spp. Measurements made during a year of low rainfall produced even higher values, suggesting that 66% may be at the low end of the interannual range. The two other alien species that were sampled, *Bromus trinii* and *Bromus tectorum*, each accounted for less than 1%. In contrast to biomass, alien species represented only 5 of 130 (4%) of all annual species that were collected. These data suggest that number of alien species (richness) may be a poor indicator of the extent and impact of plant invasions, and that alien biomass is likely a better measure.

We also evaluated correlations of alien annual plant biomass and species richness with disturbance, soil nutrients, and native plant diversity. In general, alien biomass and richness were positively correlated with variables in the first two categories, and negatively correlated with variables the last category, but analysis of individual species and covariance among species was necessary to minimize confounding variation. The most significant variables were density of dirt roads and frequency of fire, annual rainfall, and native annual plant diversity. Land managers in the Mojave Desert should assess land use practices based on individual alien species, not on alien plants as a whole, and should consider the effects of alien species on each other when evaluating these relationships.

The Relation Between the Geochemistry of Surficial Materials and Desert Tortoise Mortality in Selected Study Sites, southeastern California—a Progress Report

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Since 1989, several dozen ill, dying, or recently dead tortoises have been salvaged from numerous sites in the Mojave and Colorado deserts and necropsied to determine causes of death. Some tortoises were found have elevated levels of one or more elements in the kidneys and(or) livers as compared with control animals (see Jacobson et al., 1991, and Homer et al., 1994; 1996). These elements included Ba, Cd, Cr, Hg, Ni, Pb, and(or) V. Our study is focusing on the geochemical environment where the necropsied tortoises lived. We collected samples of rock, soil, and unconsolidated stream alluvium from 13 study sites and analyzed them for 48 elements (Ag, Al, As, Au, Ba, Be, Bi, Br, Ca, Cd, Ce, Co, Cr, Cs, Cu, Eu, Fe, Hf, Hg, Ir, K, La, Lu, Mg, Mn, Mo, Na, Nd, Ni, P, Pb, Rb, Sb, Sc, Se, Sm, Sn, Sr, Ta, Tb, Th, Ti, U, V, W, Y, Yb, and Zn). In comparison to expected abundances for these elements based on the rock chemistry in the study areas, we found locally elevated concentrations of one or more of 25 elements (Ag, As, Au, Ba, Be, Br, Cd, Ce, Co, Cr, Cu, Fe, Hg, Mn, Mo, Ni, Pb, Rb, Sb, Sr, Th, U, V, W, and(or) Zn). The relatively weak enrichments of most of these elements can be related (1) to the presence of trace elements in alluvial magnetite (a common iron-oxide mineral) or (2) to trace elements in coatings of manganese- and or iron-oxide coatings on sediment grains. We did not find anomalous levels of any one element in all areas containing tortoises having the same disease, indicating that no one element seems to be responsible for a given disease. Additionally, with the possible exception of mercury, we found no significant correlation between elevated levels of a given element in tortoise organs and elevated levels of that element in the surficial environment of the tortoise's habitat. Because the measured element concentrations for most of the elements studied generally represent long-term enrichment over thousands of years, it seems unlikely that recent increases in tortoise mortality are related to enrichments of these elements in surficial materials.

Reproductive Output of Large-For-Age Desert Tortoises (*Gopherus agassizii*)

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Small juvenile desert tortoises maintained on a high plane of nutrition since 1991 had reached an adult body size (> 180 mm carapace length) by 1995. Are such large-for-age (LFA) tortoises reproductively competent? In 24 outdoor pens, ten LFA females and eight LFA males (sex assessed from plasma testosterone and estradiol levels) were paired with ten adult males and eight adult females, respectively, and six adult females were paired with six adult males to serve as a control group. Following initial behavioral observations, follicular development was monitored with ultrasonagraphy in Fall 1995 and Spring 1996, and clutch size was measured with radiography in

Spring 1996. In Spring 1996, all 14 adult females laid eggs. However, only two LFA females produced eggs (one clutch per female, two eggs per clutch). Every adult female had some eggs hatch. Only one of the two clutches from LFA females was found and the eggs showed no signs of development.

LFA females remained paired with adult males throughout 1996 and Spring 1997. In 1997, five LFA females laid a total of six clutches. Eggs from two clutches, both from one LFA female, hatched. LFA females that had laid eggs in 1996 also laid eggs in 1997, but these were infertile. LFA males were reproductively competent but LFA females were not.

Status of the Northern & Eastern Colorado Desert Coordinated Management Plan

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One of three ecosystem plans in progress that address the recovery of the desert tortoise in the California Desert, the Northern & Eastern Colorado Desert Coordinated Management Plan (Plan) focuses on the Northern and Eastern Colorado Desert Recovery Units and a small portion of the Joshua Tree Recovery Unit. The planning area, 5.5 million acres in size and lying in the Sonoran Desert Ecoregion, is bounded by I-40 (north), the Colorado River (east), the Imperial Sand Dunes and Coachella Canal (south), and the West Mojave Plan (west). The planning area does not have urbanization pressures which characterize other parts of the California Desert. The major cooperating agencies are the Bureau of Land Management (lead agency), Joshua Tree National Park, U.S. Marine Corps Air Station in Yuma for the Chocolate Mountains Gunnery Range, U.S. Fish & Wildlife Service, and California Department of Fish & Game (which has provided the lead wildlife biologist). Additional cooperators to the Plan include other Federal, state, and local agencies as well as many interest groups. Plan scope is ecosystem comprehensive. Plan decisions will amend existing land use plans of the cooperating Federal agencies for the tortoise and other species and habitats and may be of use by other agencies and companies with interests in the planning area.

Work on the Plan in the last year was focused on completing the collection of data and the mapping of plant communities. The latter included an accuracy assessment, collection of additional habitat data for species-habitat modeling, and correcting the map with the accuracy information. From the accuracy assessment exercise we found plant communities to be accurate to varying degrees with an overall accuracy of about 50%. Plant communities and overall map accuracy after corrections were made is greatly improved. All spatial data has been GIS digitized to aid in modeling, analyses, and Plan development.

Species-habitat-ecological processes models are currently being run. They will help define and map areas of relative biodiversity importance. The California Wildlife-Habitat Relationship System (WHR), developed by the California Resources Agency, is the modeling technique employed. It has been tailored to the particular species and habitats found in the planning area. Modeling results will be used in analyzing use-biodiversity conflicts and aid Plan development. Model maps will be completed prior to April, 1998. The basis for modeling is plant communities and includes natural and artificial water sources, species accounts and known occurrence of wildlife and plant species of concern, habitat data collected during the accuracy assessment noted above, detailed information on the desert tortoise and bighorn sheep, a characterization of the important ecological processes, and various physical features. Physical features data available include elevation, slope, aspect, landforms, and lithology. Criteria for assigning relative biodiversity value to habitats have been developed for species uniqueness, rarity, or range limits; ecological processes; habitat fragmentation; species richness/diversity; and exotics. A different modeling protocol was developed to predict the occurrence of rare plants. It is based on a limited set of considerations: elevation range, plant community, landform and distance from known occurrences of the same species.

Major scheduled milestones for remaining work on the Plan are as follows:

April, 1998— Complete value and conflict analyses; develop Plan and decisions

August, 1998— Issue draft Plan/EIS; 90-day public review

February, 1999— Issue Proposed Plan/EIS; 30-day public review

April, 1999— Sign Record of Decision

The Plan lead, Dick Crowe, may be contacted for further information at the above address and by calling (909) 697-5216.

Survey of Upper Respiratory Tract Disease in Gopher Tortoises in Florida

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From 1995 to 1997, two-hundred and thirty-seven blood samples were collected from 234 gopher tortoises (*Gopherus polyphemus*) on 42 sites in Florida to determine exposure to the pathogen (*Mycoplasma agassizii*) that causes upper respiratory tract disease (URTD). Twenty-seven (12%) of the gopher tortoises were seropositive, 9 (4%) were suspect, one was seronegative but culture-positive, and the remaining 197 (84%) were seronegative. Of the three gopher tortoises that were sampled twice, one remained seronegative and the other two seroconverted from negative or suspect to positive. The 27 seropositive gopher tortoises and one culture-positive tortoise were from six locations: an old refuse dump, a state park, and a military reservation in northern peninsular Florida; an airport and a state park near Orlando; and a nature park in St. Petersburg. Forty-six (20%) of the gopher tortoises showed one or more clinical signs of URTD. Palpebral edema and ocular discharge were the most common signs.

Proposed Management Plan for Desert Tortoise Habitat on the Arizona Strip

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The Desert Tortoise (Mojave Population) Recovery Plan (U. S. Fish and Wildlife Service, 1994) describes a strategy for the recovery and delisting of the Mojave population of desert tortoises. This strategy includes: (1) identification of six recovery units, (2) establishment of a system of Desert Wildlife Management Areas (DWMAs) within recovery units, and (3) development and implementation of specific recovery actions within DWMAs.

In the Northeastern Mojave Recovery Unit, the *Recovery Plan* recommended establishment of the Piute-Eldorado, Coyote Springs, Mormon Mesa, Beaver Dam Slope, and Gold Butte-Pakoon DWMAs. A portion of the proposed Ivanpah DWMA in California is also included in this recovery unit. These areas involve seven primary jurisdictional units: four BLM resource areas, Lake Mead National Recreation Area, Mojave National Preserve, and the Fish and Wildlife Service Desert National Wildlife Refuge. There are additional lands managed by various agencies, including the states, counties, military, Indian tribes, as well as private lands.

The Arizona Strip BLM has developed a proposal that is designed to address tortoise recovery goals and objectives. The Proposed Action implements many of the recommendations of the *Desert Tortoise (Mojave Population) Recovery Plan*, and is designed to complement actions proposed by adjacent BLM districts. BLM proposes to designate three Areas of Critical Environmental Concern (169,300 acres, 264.5 sq. miles) to be managed primarily for recovery of desert tortoises, and modify the prescriptions for the Virgin River ACEC. BLM would implement management prescriptions within the four ACECs.

Short-term Effects of Fire on Desert Tortoises at Saguaro National Park

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Wildfires are known to kill individual desert tortoises, but effects of fires on tortoise populations are largely unstudied. The Mother's Day Fire (8 May 1994) burned approximately 138 hectares (340 acres) of desert tortoise habitat on the Rincon Management Unit of Saguaro National Park. On standardized surveys conducted in June 1994, we found six live and seven dead tortoises, five of which were apparently killed by the fire. We estimate this fire-caused mortality to be approximately 12% of the adult tortoise population that inhabited the area prior to the burn, a catastrophic loss estimated at six times the expected annualized mortality rate for a sustaining population of this long-lived species. All live desert tortoises appeared to be healthy and continue to be monitored and compared to tortoises in an adjacent unburned site. Fires also may have longer lasting effects on tortoises due to habitat alteration. Approximately one square kilometer plots (0.6 x 0.6 miles) in burned and nearby unburned habitats were intensively surveyed for tortoises during summer 1996. Using radiotelemetry in 1997, we tracked tortoises in burned and unburned areas.

The Use of Steep Slopes by Desert Tortoises (*Gopherus agassizii*) in the Western Mojave: Notes on Ecology and a Discussion of G_0

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Radio tagged tortoises were located at three sites with steep slopes (Barstow Marine Corps Logistics Base [MCLB], Fort Irwin National Training Center [FINTC]), and Marine Corps Air Ground Combat Center-Lava [MCAGCC-L]) on a weekly schedule, to investigate the physical features of areas in which these animals are found. A total of 546 locations were made from March 28th to September 17th of 1997. These locations consist primarily of full season records for 29 individuals (14male, 15female), and include 140 recognizable cover sites. Animals were found to utilize slopes from 0° to 33°. Significant variation was found among sites, and among tortoises within sites. No significant difference was found between sexes. The three sites were found to differ in the percent composition of five substrate particle size classes. The percent of substrate particles of cobble and boulder size ranged from 0% and 0% respectively, for locations at both MCLB and FINTC, to as high as 70% and 40% for locations at MCAGCC-L. Additionally, the direction in which the cover site opened was recorded for all permanent/semi-permanent cover sites. This direction was found to be dependent on the aspect of the slope. The location of the animal (above or below ground), and a suit of environmental variables, for the purpose of estimating G_0, were also recorded. The predictive capacity of these variables will be discussed.

Effects of Military Activities and Dust on Creosote Bushes

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Because creosote bush (*Larrea tridentata*) is the dominant evergreen shrub of many desert communities in the Southwest, what happens to this woody plant species during human disturbance has profound effects on this ecosystem. Military training on these desert landscapes has two easily demonstrated impacts on the local plants, breakage and crushing of shoots by heavy vehicles and coating resinous leaves by dust. Studies conducted at Fort Irwin National Training Center in the central Mojave Desert, where tank warfare is rehearsed, have provided quantitative data for physical damage to creosote bushes from different levels of military training. At high disturbance by vehicles, nearly all individuals showed measurable breakage and greater than 50% of the plants lost the original canopy, whereas less damage and more intact shrubs appeared at sites with less vehicular traffic. Creosote bush has a characteristic pattern of resprouting and can recover from surface traffic damage, amazingly returning to its original canopy design within five years. New shoots of resprouts are markedly different in physiological and morphological traits than canopy old growth. Heavy dust does not kill creosote bush, but leaves dusted by road traffic showed net photosynthesis reduced to 21% of controls and leaf temperature substantially increased. Dust seems to reduce plant carbon gain by impairing tolerance to water stress and decreasing water-use efficiency, but creosote bush can recover from heavy coating with clay particulates by experiencing new growth and shedding old leaves. Studies are underway to determine at what level or periodicity of military training death of creosote bush is observed, because that signals the point when the plant community cannot return to its original condition, given that reestablishment by seedlings is exceedingly rare. Loss of creosote bushes, with important aboveground biomass, also probably corresponds with a loss of fertile islands and associated animal habitats.

The West Mojave Plan: Accomplishments and Goals

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The West Mojave Plan is a multi-species regional habitat conservation plan. It is being prepared by a consortium of 28 cities, counties, federal and state agencies and special districts. The plan will present a consistent program for compliance with the California and federal endangered species acts while contributing to the recovery of desert tortoise populations within the rapidly urbanizing Western Mojave Recovery Unit. The Plan is being drafted by an interagency planning team with the assistance of a "Supergroup" composed representatives of agencies and organizations with a stake in the future management of the recovery unit. The plan will enable the agencies and local jurisdictions to obtain programmatic incidental take permits and assurances, and programmatic biological opinions, from the United States Fish and Wildlife Service (FWS) and the California Department of Fish and Game (CDFG).

During the past year, a team of twenty biologists was organized by the United States Geological Survey's Biological Resources Division and tasked to prepare a species account, an analysis of threats and habitat needs, management recommendations, a bibliography, and hard-copy maps of species range and occurrence for each of the 98 special status plants and animals being studied by the plan. A geographical information system (GIS) computer map data base was prepared which includes nearly a gigabyte of biological, resource and jurisdictional information. In addition, a document titled *Current Management Situation* was completed which catalogued the plans, policies and programs currently being applied by each of the 28 participating agencies to the desert tortoise and other special status plants and animals.

The CMS, together with the biological data base and GIS maps, are presently being evaluated by a team of FWS and CDFG biologists and botanists. That team will determine whether existing programs could support the issuance of incidental take permits, assurances, and biological opinions. Where program modifications are necessary before permits could be issued, the FWS and CDFG team will recommend appropriate measures for adoption by the agencies. These findings and recommendations will be set forth in an evaluation report.

Desert tortoise management treatments, and prescriptions affecting other species, will be developed by the Supergroup using the GIS and textual data base, the CMS, and the evaluation report. The Supergroup will accomplish this through "task groups," scheduled to meet during the early summer of 1998. Thereafter, the planning team will prepare a Draft Plan and Draft Environmental Impact Report and Statement (EIR/S) for release late in 1998. Following a 90-day public review, a Final Plan and Final EIR/S will be prepared. It is anticipated that the West Mojave Plan could be ready for agency adoption in May 1999.

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Does Dietary Nitrogen Intake Influence the Reproductive Output of Female Desert Tortoises (*Gopherus agassizii*)?

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Nitrogen may be a limiting resource for the production of eggs by female desert tortoises. We evaluated the influence of dietary nitrogen intake upon reproductive output in Spring 1996 by: 1) measuring the food and nitrogen intakes (g dry) of 24 females fed six pelleted diets (i.e., four females per diet; 0.5, 1.0, 1.5, 2.0, 2.5, and 3.0 % N, DMB; all diets contained 0.4% potassium), 2) detecting ovulation and shell formation using ultrasonagraphy, and 3) measuring clutch size (number of eggs per clutch) using radiography. Some females ovulated and formed eggshells before consuming much diet during the spring. Dietary treatments did not affect the hatching success of incubated eggs but showed a significant effect upon the number of eggs produced per female. Many measures of reproductive output (e.g., size of first clutches) were correlated to body mass but not to food or nitrogen intakes. Egg mass (fresh or dry), water content, and composition (dry mass of yolk, white, or shell) were not affected by dietary treatment or correlated to female body size, food intake, or nitrogen intake. Ten of the 24 females were fed their respective diets through another reproductive cycle (until July 1997). The number of eggs that they produced in the second reproductive season was correlated to female body size and their nitrogen intake since Spring 1996. Remarkably, four of six additional females that were fed the lowest N diet (0.5 % N) from July 1996 to July 1997 still managed to produced eggs in 1997.

The Ord Mountain Pilot: A New View on Vehicle Route Designation

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Completion of a 100% route inventory by Denver's National Applied Research Science Center (NARSC) photogrametric staff provided the foundation for designation of a vehicle route network within the West Mojave Desert portion of the California Desert Conservation Area (CDCA). The Ord Mountain Pilot Unit (126,000 acres), containing numerous sensitive resources and designated desert tortoise (*Gopherus agassizii*) critical habitat, was used to develop a Geographic Information System (GIS) methodology for route designation applicable to the entire West Mojave Desert.

Utilizing biological screening components routes were evaluated, coded with resource and access values, and designated "open" or "closed" based on those criteria. Critical screening components incorporated the Desert Tortoise Emphasis and Non-Emphasis Zones (DTEZs) indicative of tortoise habitat quality. Desert tortoise transect data including corrected sign, landform, elevation, and slope were correlated to determine tortoise emphasis zones rated high, medium, and low, relative to tortoise recovery value. Tortoise non-emphasis zones were identified on the basis of elevations greater than 4000 feet or landforms exceeding 30 degrees slope.

Route designation was completed by a Bureau of Land Management (BLM) interdisciplinary team providing site-specific knowledge and following management prescriptions outlined in "West Mojave Route Designation Ord Mountain Pilot Unit Biological Resource Screening Components" (BLM 1997). Concurrently, interest group representatives made route proposals on hard-copy maps containing the same data. While the Off Highway Vehicle (OHV) representatives' proposal closed few existing routes, the BLM and Desert Tortoise Council proposals were very similar. Accepted by planning partners, this GIS methodology will be expanded to the 9.2 million acres of desert encompassed by the West Mojave Coordinated Management Plan.

Age Class Structure of a Desert Tortoise (*Gopherus agassizii*) Population in the Tucson Mountains of Saguaro National Park

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In 1996 and 1997, 102 tortoises were marked during two 45-day censuses on a one square kilometer plot in the Tucson Mountains as part of a three year project to study the desert tortoise at Saguaro National Park. Frequency of observation of individual tortoises was correlated with both body size and with average distance from the edge of the plot. The relationship between body size and number of prominent growth rings indicates a growth rate similar to that obtained from recapture data if each ring is counted as one year. Most tortoises greater than 20 years could not be aged precisely because inner rings were worn away and outer rings could not be resolved however it was clear that they were at least 20 years old. The age distribution was evaluated alternatively by calculating a Lincoln Index estimate for each age class and by using simple models to adjust the age frequency distribution for effects of body size and distance to the plot boundary. Preliminary results indicate possible high variability of annual productivity and a low mortality rate for juvenile and immature tortoises. The age distribution of tortoise shell remains recovered in the Tucson Mountains indicates that egg and hatchling mortality is highest although sample sizes are small. Validity of age determination from growth rings needs to be tested in other populations where many annual recaptures of young tortoises are expected. Methods for the adjustment of age distributions need to be refined.

Effects of Body Size on Courtship Behavior in the Desert Tortoise, *Gopherus agassizii*

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An analysis of courtship behavior of the desert tortoise, *Gopherus agassizii*, was conducted at the Desert Tortoise Conservation Center near Las Vegas, Nevada. From Fall 1996 to Fall 1997, 18 male and 18 female desert tortoises were housed in outdoor semi-natural enclosures. Fifty randomly selected pairings were chosen from this group and their interactions were recorded on video camera. To determine the effects of body size on courtship behavior, I recorded duration of Phases I (trailing), II (subduing), and III (mounting), total duration of courtship, number of times the male bites the female, number of times the male rams the female, and number of times the mounted male fell off the female. Preliminary results suggest that with an increasing ratio of male to female mass, number of bites increases ($p<0.05$). Additionally, number of rams is positively correlated with number of bites ($p<0.05$). Results from this study will add to current knowledge of tortoise reproductive behavior. If differences in behavior between smaller (younger) and larger (older) males are observed, translocation practices may begin to take into account the size of the released tortoises. For example, if only young males are released, they might not mate successfully until they are older, resulting in a decline in birth rate. In order for translocated populations to endure, older individuals might need to be released in addition to younger ones.

A Review of Reptilian b-Keratins

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Cutaneous dyskeratosis, a disorder of free-ranging desert tortoises, is characterized by loss of integrity of the horny layer of the carapace, plastron and thickened foreleg scutes. The disorder is thought to be associated with a defect in keratinization or cornification. This has prompted us to examine the composition of shell keratin of desert tortoises with and without cutaneous dyskeratosis to determine if biochemical or ultrastructural differences can be identified.

Keratin comprises a diverse group of molecules that have been characterized by x-ray diffraction techniques, biochemical studies of the composition and structure of keratin intermediate filament and matrix proteins, and ultrastructural analysis. Patterns identified by x-ray diffraction analysis include the a-keratin pattern of mammals (also found in soft epidermal stratum corneum of reptiles and birds), and the b-keratin pattern of avian feathers and reptilian shells, beaks, claws, and scales. The unique protein structure of a-type keratin is a modified a-helix (a-helical coiled coil) while that of b-type keratin is a b-sheet. Recently, it has been demonstrated that the framework of b-keratin filaments is composed of twisted b-sheets, each containing four segments of polypeptide chains. Biochemically, the only similarity between reptilian hard b-keratin structures (shell, claws, etc.) and mammalian hard a-keratin structures (hooves, quills, etc.) is the presence of a large proportion of zinc-soluble (high sulfur) matrix material. In general, the keratinization process involves intermediate filament (IF) and matrix formation while cornification involves cell surface modification. Pre-keratin polypeptides are synthesized intracellularly and incorporated into intermediate filaments (b-keratin IF are .4.0 nm while a-keratin IF are .7.0 to 8.0 nm). The IF are organized into macrofibrils by matrix proteins (IF associated proteins). There is complete dissolution of nucleus and cytoplasmic organelles in fully keratinized cells. Cornification of b-keratin structures continues as the boundaries of keratinized epithelial cells coalesce. Numerous desmosomes anchor the undulant base of the horny layer of tortoise shell to the underlying layer of keratinized epithelial cells. Due to extensive disulfide bonding, the final keratin product is insoluble except in certain protein solvents at extreme pH or in the presence of dissociating and reducing agents, such as urea and dithiothreitol respectively.

Molecular Systematics, Polyploidy, and Paleoecology of *Larrea*

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The genus *Larrea* dominates the warm deserts of North and South America. *Larrea* includes four species in South America and one species in North America. The North-South disjunction has interested scientists since the 1800's, but there are also many other unique features in Larrea that give it a selective advantage in deserts. *Larrea* species are extremely drought tolerant, very long-lived, allelopathic, clonal and exhibit hybridization and polyploidy.

The origin and timing of the disjunction of *Larrea* have been inseparable issues, since the time of the disjunction relates to theories about the origin of *Larrea*. The use of packrat middens to date the distributions of *Larrea* in the North American deserts during the Late Pleistocene and Holocene suggest a South American origin. The purpose of this research was to examine the evolutionary and biogeographic history of the genus *Larrea*. This was accomplished by investigating the patterns of genetic variation in chloroplast DNA and by analyzing temporal and spatial distributions of the three geographically distinct polyploids of *L. tridentata*.

The phylogenetic relationships, based on chloroplast DNA restriction site analysis, were congruent with morphological studies. Cytoplasmic gene flow was postulated to account for identical haplotypes shared between *L. nitida* and *L. cuneifolia* from South America. *L. nitida* is thought to be the putative maternal donor of the chloroplast. Two distinct chloroplast haplotypes were found in North American *L. tridentata*, and one of those haplotypes was also found in South American *L. divaricata*. Low levels of genetic variation in chloroplast DNA were detected throughout the genus. This low variation could be a result either of extremely long generation times or of relatively recent diversification.

Three morphologically cryptic ploidy levels have been identified by Yang in *L. tridentata* (creosote bush): diploid (2n=26) in the Chihuahuan Desert, tetraploid (2n=52) in the Sonoran Desert, and hexaploid (2n=78) in the Mojave Desert. We determined ploidy levels within the southwestern deserts using guard cell size, based on work of J. Masterson. Mean guard cell sizes (“ 1 SE) in the central Chihuahuan Desert were 225”9 Fm^2, in the Sonoran Desert 376"15 Fm^2, and in the Mojave Desert 490"13 Fm^2. Mean guard cell area was therefore significantly different among populations in the three deserts; however, the population boundaries of the ploidy levels were not distinct.

Polyploidy changes across the range of *L. tridentata* from the end of the glacial maximum to the present were inferred from measurements of guard cells of *Larrea* leaves preserved in pack rat middens. In the warm deserts of North America. Diploids and tetraploids were both present in the lower Colorado River Valley 10,000 to 21,000 years before present (B.P.), and were replaced by tetraploids and possibly hexaploids before 8,100 yr B.P. Hexaploids were present in the Mojave Desert by 6,500 yr B.P.

Growth Patterns of the Desert Tortoise in an East Mojave Population

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Growth was monitored on 127 tortoises in an eastern Mojave Desert population from 1988 to 1995. Nearly all annual growth occurred between early April and mid-June. Smaller tortoises had a larger growth rates. Between 125 and 184 mm in carapace length, the mean growth rates was 10.80 mm ± 0.660. Above 184 mm, growth rates decreased in a more-or-less linear fashion until tortoises reached approximately 235 mm (males) or 208 mm (females), at which point growth was less than 2 mm per year. For females, this growth cessation point was coincident with increased reproductive output. Both among and within gender, the larger size that a tortoise obtains, the greater its growth rate at some point. There was no significant difference in growth between immature males and females, but adult males experienced significantly higher growth rates than adult females, following a growth spurt at supposed sexual maturity. Drought negatively affected growth in all groups. For immature tortoises, mean growth in the best years was 14.7 mm, but only 3.6 during a drought; for adults, growth was negligible during drought. Age was predicted from size using von Bertalanffy growth curves.

Geo- Bio- Chemistry of the Desert Tortoise: Trace Element Composition of Carapace and Scute by Neutron Activation Analysis

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The desert tortoise (*Gopherus agassizii*) is a federally listed threatened species in the Mojave and Colorado desert portions of its range in the Southwest. Diseases contributing to accelerated tortoise mortality include upper respiratory tract disease, cutaneous dyskeratosis (lesions of the scutes, the horny plates covering the shell), and degeneration of the liver and kidney. Necropsies by B. L. Homer and colleagues indicate elevated concentrations of several potentially toxic metals in the liver and kidney of some animals. We are investigating the abundances and sources of trace elements, including potentially toxic metals, in desert tortoise shell and scute by instrumental neutron activation analysis (INAA), and by lead isotopic analysis, which should enable us to distinguish natural and anthropogenic sources of lead.

Our initial, reconnaissance INAA investigations have two purposes: to learn which chemical elements can be measured in desert tortoise bone and scute, and to determine overall abundance levels. Two tortoises from the northern Colorado Desert were analysed: a healthy subadult male (killed on a highway) and a diseased subadult female. Gamma ray counts were performed at <1 hour, and 5, 7, 14, and 60 days after irradiation. At least 33 elements, including many of the potentially toxic metals, can be measured with acceptable accuracy and precision in tortoise bone, scute, or both.

Provisional inferences from these initial analyses are: (1) The more electropositive ("lithophile") transition elements (Sc, Ti, V, Zr, Hf, Ta, rare earth elements, Th, U) are more readily accommodated in the apatite of bone than in the keratin of scute. (2) Although desert tortoises spend much of their time underground in burrows, the data tentatively suggest minimal elemental input to the scute through contact with soil or bedrock. (3) Trace element abundances in tortoise bone are generally similar to those in human bone; tortoise scute is likewise fairly similar to human nail material. (4) Scute from the diseased tortoise shows relative depletion in most of the elements determined. Whether this apparent difference is an effect or a cause of disease, or simply variation between two individuals, remains to be determined.

A Comparison of Distance Sampling and Strip Transects for Estimating Desert Tortoise Sign: Implications for Sampling Desert Tortoise Populations on Landscape Scales

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The use of distance sampling for estimating desert tortoise populations is briefly reviewed and forms a foundation for the current study. Data for this study was obtained from the eight 9 km^2 study plots in the southern Mojave Desert established at Marine Corps Air Ground Combat Center and Joshua Tree National Park in 1995. An experimental design was developed to sample live tortoises, carcasses, burrows, and scats using distance sampling as the population (in the statistical sense) estimator. Tortoise, burrow, and scat densities were estimated at nested multiple-scales to produce an unbiased desert tortoise distribution/density surface for the landscape. This analysis and protocol was presented at the Desert Tortoise Council Symposium in 1997. The experimental design and resulting database provided an opportunity to directly compare distance sampling and strip transects of varying widths for estimating burrow and scat densities on landscape scales at plots that varied enormously in desert tortoise abundance. The tested hypothesis was: Tortoise sign density estimates using distance sampling should be independent of and indeed similar at any surveyed band width; while wide strip transects should underestimate tortoise sign density, because all sign within the transect are not detected by the surveyor. However, as strip transect widths approach the detection function parameter calculated from distance sampling, the two methods should yield comparable results. The optimal strip transect width for estimating scat densities should be much narrower than the corresponding transect band for burrows, because scats are much more difficult to observe than burrows. The data strongly and unequivocally support the posed hypothesis. Distance sampling is time intensive because the perpendicular distance between each located object and an established line transect must be accurately measured. The data from my protocol suggest that distance sampling need only be used on actual tortoises. Tortoise sign densities can be adequately estimated from strip transects whose optimal widths are separately calculated for burrows and scats from an initial pilot study using distance sampling. This pilot study is necessary, because optimal strip transect width is habitat and to some extent year specific. For example, in a highly productive year the increase in vegetation and litter would require narrower strip transects for burrows and scats.

Plasma Corticosterone and Androstenedione in Male and Female Desert Tortoises During the Reproductive Cycle

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Blood samples were collected by jugular puncture at monthly intervals from April to October from 20 adult male and 30 adult female desert tortoises. The tortoises were maintained in pens 15 m x 30 m with natural vegetation and small artificial sod plots at the Desert Tortoises Conservation Center, Las Vegas, Nevada. Water and alfalfa hay were supplemented. Progesterone, testosterone, estradiol, thyroid hormone, corticosterone and androstenedione and lipids and calcium were analyzed in all of the plasma samples. Part of this study was published earlier (Rostal et al. Herp. Monogr. 8:72-82, 1994). Plasma corticosterone in male tortoises ranged from 0.580 ng/ml to 5.990 ng/ml and showed a significant seasonal pattern. Mean corticosterone in males was significantly higher in August and September than in April, May and June. Female values ranged from 0.200 ng/ml to 4.080 ng/ml. The mean monthly values for female tortoises were significantly lower than that of the males in every month, and the seasonal pattern was different. Peak values in the females occurred in April, and lower mean values were seen for all other months. Plasma androstenedione in males showed a somewhat similar cycle in that higher values were seen in August through October. Female samples are currently being analyzed and will be presented.

Geographic Variation and Environmental Determinants of Reproductive Output in the Desert Tortoise

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Three study sites were established in California in the spring of 1997 as part of a multi-year study to examine variation in reproductive output of desert tortoises: Joshua Tree National Park (JTREE), Mojave National Preserve (MOJAVE), and an area of land leased by the Bureau of Land Management (BLM) for wind energy production near Palm Springs (MESA). At MESA, 9 out of 10 monitored females produced a total of 72 eggs. Of these females, 6 produced second clutches and one produced a third clutch. Clutch size ranged from 2-8 eggs. Modal clutch size was 4 eggs. Mean clutch sizes were 4.33 and 5.00 eggs for first and second clutches, respectively. First clutch size was positively correlated with carapace length ($\underline{r}^2$=0.29) but not significantly ($\underline{P}$=0.14). When all clutches were considered, a significantly positive relationship was detected ($\underline{r}^2$=0.26, $\underline{P}$=0.04) The earliest date of egg laying occurred between April 18-23. The last clutch was oviposited sometime after July 3. At JTREE, only 1 of 8 females produced a single clutch (5 eggs). At MOJAVE, 12 of 18 monitored tortoises produced 43 eggs in 12 single clutches with no subsequent clutches. Clutch size ranged from 1-7 eggs with modal clutch size of 3-4 eggs. Mean clutch size was 3.58 eggs. Larger females produced larger clutches and the relationship between the two variables was almost significant (r^2=0.32, P=0.055). Most of the variation observed appears to be related to differences among sites in rainfall and associated production of annual food plants.

Root Communications and the Structures of *Larrea* Dominated Plant Communities

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Results of spatial pattern analyses and experimental studies of the structures of desert shrub communities have suggested that roots of some shrubs may interact by mechanisms other than simple competition for limiting resources. Experimental studies using root observation chambers to observe the effects of encounters between individual roots on root elongation rates have revealed two mechanisms of inter-root "communications". *Ambrosia dumosa* roots appear to possess a contact-inhibition mechanism, which causes inhibition of root elongation upon contact between roots of separate plants from the same population and even of the same genotype. This mechanism includes self/non-self and population level recognition systems, and the fact that only roots in contact with neighboring roots are inhibited conveys a detection and avoidance capability on a whole root system level. *Larrea tridentata* roots inhibit root elongation of either *Larrea* or *Ambrosia* roots in their vicinity, with or without contact. Results of experiments employing activated carbon to remove root exudates support the hypothesis that the communication mechanism of *Larrea* involves the release of a readily diffusible, generally inhibitory substance by *Larrea* roots into the soil.

The possible implications of these communication mechanisms for the structures of desert plant communities were investigated by employing new optical and computing technology to precisely measure and to compare and contrast the detailed structures of simple, *Larrea tridentata* dominated communities located in four geographically separated deserts: Mojave, Colorado Sonoran, Arizona Sonoran, and Chihuahuan. In each of these deserts we measured sites in communities dominated by *Larrea* and one or a few other species. Codominants were different at each site. Analyses show that while intraspecific distributions of *Larrea* were similar at all sites, relationships between *Larrea* and its codominants were widely different among sites, varying from strong segregation in the Colorado Sonoran site to strong aggregation in the Chihuahuan site. Mechanisms possibly underlying these structural differences will be discussed.

Which Method is Better? A Comparison of Mile^2 and Kilometer^2 Overlapping Desert Tortoise Census Plots at Saguaro National Park

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A desert tortoise census within a mile^2 study plot in Saguaro National Park (Rincon Mountain Unit) conducted in 1989 is compared with a census in a purposely overlaid kilometer^2 plot conducted in 1996 and 1997. Strategies, techniques, results, intrinsic advantages and limitations of each method, and conclusions are presented and discussed.

Mojave Desert Landscapes, Soils, Hydrology, and Ecological Processes

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Recent linkages of ecological investigations to geosciences research on landscape dynamics and soils have proven essential for interpreting many ecological phenomena that occur on the extensive alluvial piedmonts or "bajadas" of the southwestern deserts. These piedmont environments are typically complex mosaics of alluvial deposits varying in geological age and parent materials. Soil-forming processes including accumulation and vertical redistribution of clay minerals and calcium carbonate in distinct soil horizons lead to increasing soil profile development over time. The degree of soil development has a profound impact on soil water balance. Soil characteristics that modify infiltration of water at the surface and recharge of subsoil horizons exert a major control on plant physiological responses and ultimately composition of vegetation. Varying soil hydrological dynamics also affect animal populations directly through limitations different kinds of soils impose on burrowing activities and indirectly by controlling the production of both herbage and seeds used by herbivorous and granivorous animals. Linking ecological studies of the desert tortoise with detailed knowledge of geological landscapes and soils could contribute to a better understanding of factors that limit this desert reptile.

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Conservation and Management Implications of Upper Respiratory Tract Disease to Gopher Tortoises

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When tortoises are impacted by human activities, decisions must be made regarding their disposition. The choices open for a particular population of tortoises depend on the location; historical, current, and future site use; surrounding land use patterns; importance of the population in maintaining genetic variability; and political and social factors. No one prescription will be ideal for all situations, and it is difficult, if not impossible, to develop a set of prescriptions that will cover all permutations of the above factors. However, guidelines for making decisions can be developed, and some are presented in this talk. The following points must be considered when making conservation and management decisions relative to URTD in gopher and other tortoises: 1) Goals must be clearly established. 2) Personnel must have appropriate training to recognize URTD, collect necessary samples, and interpret results. 3) Clear questions must be formulated. 4) Survey and monitoring programs must be developed and implemented, and precautions taken to ensure detection and prevent spread of URTD. 5) Management options must be weighed, and plans formulated and implemented that are consistent with established goals. 6) The results of ongoing and new research must be evaluated and incorporated into management plans as the information becomes available.

Plant Composition and its Effects on the Desert Tortoise

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Among desert animals tortoises appear to be uniquely constrained by their simple renal tubules and lack of salt glands, making excretion of electrolytes such as potassium especially demanding. However, many desert plants are high in potassium. Ingested potassium is excreted predominantly as urates and fluid urine, but this also entails substantial excretion of both nitrogen and water. Thus these constituents of food may be particularly important. An index, the potassium excretion potential (PEP), is proposed to account for the relative amounts of potassium, nitrogen and water in foods. A high PEP indicates a surplus of nitrogen and water relative to potassium. Analytical data reveal that: 1) some plant families (e.g., legumes and cacti) typically have high PEP, 2) shrubs usually have negative PEP (i.e. more potassium than can be excreted), 3) PEP varies greatly according to phenological stage, 4) PEP may differ from year to year, likely due to differences in plant water balance, 5) PEP may vary among plants on different soils, 6) PEP in dried, senescent plants (such as grasses) is altered by weathering. The stable isotopes of carbon and nitrogen in plants also warrant investigation. It may prove possible to document historical diet shifts (e.g., from perennial grasses such as bush muhly to annual grasses such as red brome) and to assess the importance of legumes in tortoise diets from the isotope levels in tortoise tissues, including museum specimens. This may prove helpful in assessing past and present impacts of livestock grazing on tortoise populations.

Lower Cost Techniques for Road Revegetation on Desert Tortoise (*Gopherus agassizii*) Habitat in the West Mojave

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Need for widespread road revegetation on disturbed desert habitat is pushing restorationists to improve effective lower-cost techniques. Over the last two years Round River has been further exploring the effectiveness of vertical mulching, pitting, and imprinting. In spring 1997, on the Copper Mountain Mesa Project we relied mostly on the local plants for seed recruitment. Vertical mulching and imprinting were utilized to create microsites that catch and hold blowing seed, therefore encouraging germination and plant establishment. Early results on this project suggest that vertical mulch, imprints, and pits serve to discourage vehicle use, trap seed, increase water infiltration and retention, and improve conditions for native revegetation. During the Shadow Mountains Project in winter 1996, roads on the Fremont-Kramer Critical Habitat Unit were ripped with a bulldozer. Road ends were pitted, camouflaged, and blocked by vertical mulching using Joshua tree (*Yucca brevifolia*), cholla cactus, (*Opuntia* spp.), white bursage, (*Ambrosia dumosa*), creosote bush, (*Larrea tridentata*), big galleta grass, (*Hilaria rigida*), and other native species. Early monitoring in Fall 1997 showed areas vertical mulched and pitted to be discouraging vehicles and encouraging revegetation. Native perennial species such as *Larrea*, *Ambrosia*, and indigo bush (*Psorothamnus fremontii*) are slowly establishing. Non-native and wide-spread filaree (*Erodium cicutarium*) and fiddleneck (*Amsinckia intermedia*) also are coming in, but do not seem to be significantly impeding native growth. Vertical mulching, pitting, and imprinting continue to show promise as effective, lower-cost habitat rehabilitation alternatives to costly live-planting and often ineffective direct seeding.

Transfer and Persistence of Maternal Antibodies Against *Mycoplasma agassizii* in Desert Tortoise Hatchlings

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This study investigated: I. Vertical transmission of *Mycoplasma agassizii* from mother desert tortoises (*Gopherus agassizii*) to their hatchlings through the eggs, II. Transfer of specific maternal antibodies, and III. Persistence of maternal antibodies in hatchlings over time. Plasma of 20 captive reared desert tortoise hatchlings from 4 clutches of 4 *M. agassizii*- seropositive females clinically sick with Upper Respiratory Tract Disease (URTD) and 19 hatchlings from 4 *M. agassizii*- seronegative clinically healthy females was sampled at 4, 8, 12, and 29 months and examined by ELISA for *M. agassizii*-specific antibodies. Yolk, egg shell membranes, and nasal lavages tested negative for *M. agassizii* by polymerase chain reaction (PCR). There was no indication of an active mycoplasma infection in yolks and hatchlings. Offspring of sick females had significantly higher specific antibody levels than offspring of healthy females. The difference between offspring of sick females and offsprings of healthy females was still significant in one year old hatchlings.

It was concluded that *M. agassizii* was not transmitted through the egg. Desert tortoise females transfer antibodies to their offspring. The transferred specific antibodies were still detectable after one year.

Based on the results of this study, it should be possible to artificially incubate eggs and raise healthy desert tortoises form females infected with *M. agassizii* to conserve genetic material and restock populations of this threatened species. Transferred specific antibodies can potentially interfere with sero-diagnostic tests, i.e. hatchlings with high antibody levels could potentially be misclassified as having been infected with *M. agassizii.*

Movement and Dispersal Orientation of Neonatal and Juvenile Desert Tortoises

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Sixteen neonates and 14 four and five-year old juvenile desert tortoises (*Gopherus agassizii*) were released from an *in situ* field enclosure in natural habitat at the U.S. Army's National Training Center in the central Mojave Desert of California where they were hatched and maintained. Juveniles were released in late Spring 1994 and 1995. Neonates were released within 2 weeks of emergence from their nests in Fall 1995 and 1996. I measured the straight-line distance traveled and direction of dispersal on the first day after release and after the period when there was no further movement away from a burrow and dispersal appeared suspended by winter hibernation or summer estivation. Mean distance traveled by neonates on the first day (48.5 ± 51.2 m) was further than by juveniles (36.0 ± 32.6 m) and three times as far on the final day (147.4 ± 102.8 m compared to 52.0 ± 70.6 m). Movements of neonates were longer and occurred over a shorter period, only 2 weeks compared to 4 weeks for juveniles before settling into a burrow with no further dispersal for the season. Mean circular angle of dispersion was similar for both groups on the first day: juveniles = 163° ± 76° and neonates = 168° ± 103°: and on the final day: juveniles 174° ± 73° and neonates = 222° ± 80°. There is a strong trend for dispersal to the southwest through southeast directions, but this was not significant ($P = 0.05$) due to low concentration. It is likely greater dispersal of neonates is facilitated by residual yolksac lipid reserves. The reason for the uniformity of dispersal direction is not known at this time.

The Important and Continuing Role of Mycoplasmas in Respiratory Diseases of Various Animal Hosts

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Mycoplasmas (members of the class *Mollicutes*) are unique bacteria, being the smallest, self-replicating organisms currently known. They lack the usual cell wall outer structure of most other bacteria, have very small amounts of genetic material (DNA), usually require cholesterol for growth and membrane function, are filterable through the usual bacteriological filters (450 nanometers), and are very dependent upon the host for nutritional support. The important mollicutes include helical wall-less prokaryotes (genus *Spiroplasma*) found in some plants and many different insect hosts, the non-culturable phytoplasmas that are plant pathogens in a variety of hosts, and members of two genera (*Mycoplasma* and *Ureaplasma*) that most often colonize and induce disease in vertebrate hosts. Most *Mycoplasma* species are quite host specific, but exceptions occur. The oral cavity and urogenital tract of man and animals are the most common sites of mycoplasma colonization, with a considerable number of species in both locations considered as normal flora.

Mycoplasma pneumoniae is an important agent in human acute respiratory disease in children and adults, with recent evidence that *Mycoplasma fermentans* might also be a respiratory pathogen in man. *Ureaplasma urealyticum* and *Mycoplasma hominis* can be important respiratory pathogens in human neonates. Other *Mycoplasma* and *Ureaplasma* species are pathogenic for the respiratory tract of an ever-expanding number of domestic and wild animal hosts, including avian, bovine, caprine, canine, equine, feline, murine, ovine, porcine, and reptilian hosts.

Mollicutes involved in respiratory disease are inhabitants of mucous membranes and host acquisition occurs through direct oral to oral contact with other infected hosts. Respiratory infections are also transferred via contact with respiratory aerosols, fomites from infected persons or convalescent carriers. Colonization of the respiratory tract by mycoplasmas is mediated through attachment to host target cells, frequently involving specialized attachment proteins (adhesins) on the organisms. This is followed by an induction of a broad range of host immuno-regulatory events (cytokine production and direct effects on host lymphocytes/macrophages), which may either minimize disease through host defense mechanisms or lead to lesion development. Host responses may vary from secondary complications to a variety of extrapulmonary sites, to chronic respiratory disease, or to infections with no obvious signs and symptoms. Exacerbation of infection in a host frequently occurs through intercurrent infections, environmental stress, or in immune deficiencies.

Acquisition of certain pathogenic mycoplasmas into the urogenital tract, or an increase in numbers of mycoplasmas considered as normal flora, can have important consequences in both male and female human or animal hosts. Infections vary from acute localized infections (urethritis, vaginitis, pelvic inflammatory disease) to major effects on reproductive functions (infertility) and to intrauterine or neonatal infections.

Effective control of mycoplasma infections involves chemotherapy with broad spectrum antibiotics (tetracyclines or macrolides) in conjunction with a competent host immune response. Antibiotics that inhibit bacterial cell wall synthesis (penicillin, etc.) are not effective. Widespread chemotherapeutic approaches do not appear to be practical in controlling mycoplasma infections in most wild animals, and possibly in some domesticated animals. Detection of infected hosts, through proper and effective diagnostic procedures (cultural and serological techniques), and removal of such hosts to confinement areas for possible treatment regimens might be effective in some animal populations. There is little evidence at present that such infections can be controlled through immunization procedures.

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A Search for Mycoplasmas in *Ornithodoros parkeri* Ticks Collected from the Desert Tortoise (*Gopherus agassizii*) in the Mojave, Colorado, and Sonoran Deserts

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Mollicutes are a group of about nine distinct genera of wall-less bacteria occurring in a variety of plant, insect and animal hosts. Two species in the genus *Mycoplasma* have been identified as etiologic agents in respiratory disease of tortoises. *Mycoplasma agassizii* is pathogenic for both the desert (*Gopher agassizii*) and gopher (*Gopher polyphemus*) tortoise in Southwestern and Southeastern United States, and in tortoises in France. A currently unnamed *Mycoplasma* species (strain HB29) has been isolated from desert tortoises with respiratory disease in California, and identified in a single Florida gopher tortoise with a respiratory infection. Experimental transmission of *Mycoplasma agassizii* from tortoise to tortoise through an infectious nasal discharge has been documented.

Ticks are an important vector for transmission of numerous infectious bacterial agents, including spirochete infections (Lyme disease and relapsing fever due to *Borrella* infections), tularemia, and various rickettsial infections. In addition, special mollicutes of the genus *Spiroplasma*, a group of helical wall-less prokaryotes occurring widely in insects have been found in two tick hosts (*Ixodes pacificus, Haemaphysalis leporis-palustris*) in the US. Previous studies have documented the frequent occurrence of ticks, specifically *Ornithodoros parkeri*, as ectoparasites of tortoises. Also, tick transmission of mycoplasmas involved in bovine pleuropneumonia disease in Africa has been demonstrated in some earlier experimental studies but not confirmed under natural conditions. In view of this association between ticks and bacterial/mycoplasmal agents, it was thought worthwhile to attempt cultivation of the two *Mycoplasma* species from ticks infesting tortoises.

Four hundred fifty nine ticks (all *Ornithodoros* *parkeri*, J. Oliver, pers. comm.) were collected from *Gopher agassizii* tortoises in the Mojave, Colorado, and Sonoran deserts in California, Arizona, and Nevada from March 18 to November 14, 1997. Eighty three percent of the ticks (382) came from the Desert Tortoise Conservation Center in Las Vegas. Upon arrival by express air mail with information on tortoise number and health profile forms and other collection data, the ticks were assigned pool numbers and immediately placed in a sterile mortar with a small piece of dry ice. After carbon dioxide anaesthesia, the ticks were ground with a pestle in a small amount of sterile sand and about 2 ml of SP-4 mycoplasma medium. This formulation contains 17% sterile fetal bovine serum and 500 units/ml of penicillin G to suppress bacterial growth. The tick triturate was then drawn into a sterile syringe and the contents passed through a sterile, 25mm bacteriologic filter (450 nm) into a 4ml screw cap glass vial containing about 1.5 ml SP-4 broth. Vials were incubated at 30°C and examined periodically for turbidity or pH changes in the medium. Each fresh lot of the SP-4 broth was tested to confirm the ability to grow the two *Mycoplasma* species identified in tortoises.

No *Mycoplasma* or *Spiroplasma* species were isolated in cultivation attempts from the ticks examined in this study. Although a preponderance of the ticks originated from one location, the disease is apparent in many of the tortoises at this location. These findings would seem to suggest that tick transmission of the mycoplasma infection is an unlikely event.

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Evolutionary Implications of Cenozoic Climates for the Desert Tortoise

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The history of climate and vegetation for the last 60 million years provide insight into the ecology and physiology of the modern *Gopherus agassizii*. Both *Gopherus* and evidence for tropical deciduous forest appeared in the fossil record in the Eocene (55 mya, million years ago). Climates were tropical with only wet and dry seasons and little temperature difference. Tortoises were likely active in warm-wet periods, inactive in warm-dry periods, ate fresh and dried understory warm-season herbs and grasses, and primarily used sheltersites to avoid predators. The uplift of the Rocky Mountains and the Sierra Madre Occidental in the late Oligocene-middle Miocene (25-15 mya) established the modern biotic and climatic provinces in North America. New climate-limited biomes (thornscrub, grassland, conifer forests, tundra,etc.) formed along environmental gradients. The modern subgenera (genera) diverged primarily involving enhanced burrowing behavior in *Gopherus* compared to the more conservative *Xerobates*. With the development of colder temperatures at higher latitudes and elevations, temperate winter and a four-season climate developed. In these areas, tortoise seasonal activity patterns, diet and behavior were little changed except that part of the extended inactive period due to cold (hibernation) and sheltersite were increasingly important environmental buffers. The drying trend that resulted in the formation of the Sonoran Desert (by 8 mya) resulted in the modern five-season climate (winter, spring, foresummer, summer, fall). Selection likely intensified spring inactivity and foresummer estivation. The reversal to more tropical climates in the Pliocene (5-2.4 mya) and the northward expansion of the Gulf of California (Bouse Formation) would not have resulted in major life history evolution. In the Pleistocene, new climatic regimes developed with much cooler summers and the cool season greatly expanded in spring and fall resulting in a general contraction (for the first time) of monsoonal rainfall from the tropical oceans and widespread expansion of Mediterranean climates and biotas. For 85-90% of the last 2.4 mya, glacial climates allowed woodland and chaparral to expanded into desert elevations; Mohave Desert species such as

Yucca brevifolia (Joshua tree) were widespread. The Mohave Desert climate can be viewed as a reversal to the original Eocene two-season regime (wet, dry) with two devastating differences: (1) the rains fall in the cool season instead of the warm season leaving the summers very hot and dry and (2) winter temperatures are cold. Tortoises adapted to this new environment in several important ways: (1) building more extensive burrows to buffer extreme cold, heat, and aridity, (2) shifting primary activity period from hot-wet summer to relatively-cool spring rainy season, (3) shift of diet from tropical subshrubs, herbs and grasses to spring annuals, mostly of temperate origins, and (4) a related shift from general consumption to general avoidance of dried plant foods. In this deep historical context, it is clear that the Mohave desert tortoise is the most recently evolved North American tortoise and likely the only one to have adapted to a winter rainfall climate.

Climatic Effects on Survival and Reproduction of the Desert Tortoise (*Gopherus agassizii*) in the Maricopa Mountains, Arizona

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Between 1987 and 1994, the desert tortoise population at the Maricopa Mountains declined from over 140 to approximately 20 individuals. An eight year drought, detected by the Palmer Drought Severity Index, coincided with the period when tortoises died. Mortality occurred disproportionately on hotter, drier and less vegetated S and SW exposures, while tortoises in the Maricopa Mts. preferentially utilized N and NE slopes. Ecological correlates including high sahuaro mortality and changes in other indicator species during the study support the climate hypothesis. Adult tortoises, especially females, suffered the highest relative mortality rate. Tortoises with high-domed shells suffered higher mortality than flatter tortoises during the drought at the Maricopa Mts. The diet was composed mostly of woody perennials, in contrast to other Arizona populations, which have higher quantities of succulent and energy-rich annual plants in the diet.

Reproduction was investigated to assess drought effects on the potential for population recovery. Shelled eggs were first detectable in the Maricopas on June 5 and oviposition was completed by July 24, in 1994. The number of females reproducing at the site of population collapse was significantly lower than at a nearby control site (Espanto Mt.) without high mortality. At Espanto, environmental stressors appeared less severe. Other than proportion of females reproducing, fecundity of the Maricopa and Espanto females was comparable to previously studied Sonoran tortoise populations. Body weight gradually declined during the arid premonsoon season, then dropped substantially at oviposition, and was quickly restored after heavy precipitation. Recovery of this population will be slow due to the apparently low reproductive rate.

Survey, Monitoring, and Management of the Sonoran Desert Tortoise at Saguaro National Park

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We conducted survey transects and density plot censuses for Sonoran desert tortoises at Saguaro National Park (SNP) from 1995 to 1997. Surveys (n=30) were used to determine presence or absence of tortoises. Transects were divided into habitat types including slopes, bajadas, and high elevations. Tortoises occupied all habitat types except for high elevation sites in the Tucson Mountains. Mark and recapture techniques were used to estimate population densities for km^2 plots (n=3) at SNP. Numbers of tortoises registered per census at each plot ranged from 34 to 82 at SNP. GPS was used to document tortoise locations. This research provides SNP with detailed information on the quality and quantity of habitat and tortoises that can be used for management, long term monitoring, and interpretation. Management considerations of this sensitive species at SNP include poaching, release of captive pets, fire, road mortality, and abandoned mines.

Research, Monitoring, and Management of the Desert Tortoise in Organ Pipe Cactus National Monument, Arizona

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Organ Pipe Cactus National Monument lies in southwestern Arizona, on the U.S.-Mexico border, near the geographic center of the Sonoran Desert. The monument is comprised of approximately 133,600 hectares (330,000 acres), 95% of which is designated wilderness. Topography ranges from rugged mountains to steep bouldery slopes, to bajadas grading downslope to broad desert valleys. Vegetation varies from relatively dense and diverse Sonoran Desertscrub, Arizona Uplands Subdivision, to monotypic creosotebush flats and other Lower Colorado River Subdivision plant associations. In recent years, the monument has sought to clarify the status and distribution of desert tortoises and their habitat. This was pursued through inventory and monitoring activities, and use of geographic information system technology. Survey transects in 1988 and 1995, and monitoring plot data gathered in 1996 and 1997, have confirmed that tortoises are widespread in typical habitat, at densities in the range of 25-30 per km^2. Tortoises were also found lower on bajadas and valley floors than expected, probably because of the availability of microhabitats in incised arroyos for shelter sites and burrows. GIS data management has allowed estimation of the distribution, quality, and quantity of tortoise habitat, using the parameters of slope, elevation, and vegetation. Management of the tortoise in Organ Pipe Cactus National Monument involves a number of issues, including: poaching; abandonment of pet tortoises; invasion by non-native plants (e.g. buffelgrass); roadkill; and habitat impacts from increasing off-road travel related to border activities (e.g. drug smuggling and interdiction, illegal immigration and interdiction).