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Subject: **MECHANISTIC INVESTIGATION OF THE DISTRIBUTIONAL LIMITS OF THE DESERT TORTOISE**
PALEN SOLAR POWER PROJECT
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Enclosed for filing with the California Energy Commission is the original of the **MECHANISTIC INVESTIGATION OF THE DISTRIBUTIONAL LIMITS OF THE DESERT TORTOISE**, for the Palen Solar Power Project (09-AFC-7).

Sincerely,

Marie Mills

Marie Mills

University of Nevada, Reno

Mechanistic investigation of the distributional limits of the desert tortoise *Gopherus agassizii*

A dissertation submitted in partial fulfillment of the
requirements for the degree
Doctor of Philosophy in
Ecology, Evolution, and Conservation Biology

by

Kenneth E. Nussear

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Dissertation Adviser

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ABSTRACT

The severe climatic conditions and low resources associated with desert environments, result in selective pressures that potentially influence morphological, physiological, and behavioral adaptations in desert-dwelling animals, thus defining species distributions. Many factors act simultaneously to influence the natural distributions of tortoises. The factors limiting tortoise distribution may include: biogeographical and historical limitations to dispersal, the biophysical environment, local precipitation, and forage availability. Interactions among limiting factors will define the time and space constraints on habitat use. These constants define the realized niche, and help us to know the fraction of the *available* habitat that is actually useable. This understanding is critical to conservation of rare and endangered species.

I investigated the mechanisms contributing to the distribution of desert tortoises by manipulating their distribution at the northeastern limits to the range, and measuring responses to different habitats and thermal environments. I measured critical temperatures during hibernation, and characteristics of the shade resources used during the active season. I also measured the production of eggs, and movements of animals displaced into atypical habitats to understand ecological constraints to distribution. Aspects of the thermal environment were addressed by experiments that sought to understand the mechanisms of heat exchange for tortoises, and by modeling tortoise activity as a function of the environmental variables.

Tortoises at four study sites transecting the northeast Mojave desert had similar minimum body temperatures that were well above critical temperatures for this species. Tortoises that were translocated into Great Basin scrub/woodland habitats appeared to select shrubs for shade differently than shrub presence. Tortoises avoided the most abundant shrub (*Artemisia* spp.) as a resource for shade, and did not establish home ranges in Great basin scrub habitats. The use of shade in relation to summer thermal environment appears to be critically important to understanding the distribution of desert tortoises. Finally, I examined the mechanisms of heat exchange by manipulating carapace coloration and measuring responses of behavior, body temperatures, and heating rates. Shell coloration had little influence on the thermal biology of desert tortoises. That result that differed from the current paradigm typically used to predict the operative temperatures available to ectothermic vertebrates.

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Introduction to the Dissertation

What are the relationships between habitat requirements and distributional limits of the desert tortoise (*Gopherus agassizii*)? Factors limiting the geographic distributions of species have long been debated in ecology, and those debates have focused on the relative importance of biotic and abiotic influences to species abundance and distribution (Andrewartha and Birch 1954, MacArthur 1958). Both biogeographic and ecological processes can influence distribution and abundance, and ecology can be dominated by physiological tolerances to abiotic conditions in extreme environments, such as deserts. Thus, understanding the underpinnings of distributional limits generally requires knowledge of mechanisms for several processes acting simultaneously.

Species distribution may be explained by a nested arrangement of several limitations to distribution (Grinnell 1917, Brown et al. 1996). First, there may be biogeographic limitations acting on broad scales, for example species may be absent from an area simply because they have not dispersed there, or they may have occurred there historically, but were displaced due to changing climatic conditions (Brown 1971, VanDevender et al. 1976). Other limitations to distributions, such as the abiotic characteristics of the habitat sustaining a species have lead to the concept of a species niche (Grinnell 1917, Hutchinson 1959, Brown et al. 1996).

Thermal biology is often important to species distributions. This importance was recognized by early researchers (Darwin, 1859, Grinnell, 1917), but became prevalent in the 1940's (Cowles and Bogert 1944, Woodbury and Hardy 1948, Norris 1953, Norris 1967), as we came to understand the importance of the thermal environments of reptiles. Gates (1962), Norris (1967), Porter and Gates (1969), and Tracy (1976) added mathematical descriptions of the interactions between organisms and their environments. Their work led to the definition of "climate space" as the combinations of temperature, insolation, wind, and humidity in which animals could exist (Porter and Gates 1969). Climate space is essentially a numerical quantification of four dimensions of Hutchinson’s (1959) fundamental niche (Brown: in Real and Brown 1991, p 450). The thermal environment defines one aspect of a species fundamental niche, and it may be considered as a resource of space and time, over which both biotic and abiotic interactions may occur that ultimately influence species distribution (Tracy and Christian 1986).

In addition to historical limitations to species distribution are limitations imposed by the thermal environment *within* otherwise suitable habitats. A hierarchical approach may be one logical way to explore the ways in which environmental variables are important in determining range limitations of desert tortoises and differences in the climate space for tortoises across their range. The hierarchy must include ultimate mechanisms (e.g. evolutionarily) at one extreme, to proximate mechanisms (e.g. physiology, behavior, etc.) at the other.

However, proximate and ultimate factors are both important at each level. Each level of the hierarchy is defined by factors influencing the fitness of animals at different temporal scales.

The first level of such a hierarchy consists of the primary limitations to distribution. Primary ecological limits are conditions causing the death of individuals (e.g. conditions causing freezing or overheating). Extreme events occurring at a frequency shorter than the lifetime of individuals may extirpate organisms from an area, and exclude recolonization of the habitat from nearby populations, in the absence of local adaptation to extreme conditions (Kirkpatrick and Barton 1997).

Secondary mechanisms include variables acting indirectly over long periods of time, such as extended periods of drought, long periods of limited activity time, or high levels of predation on one size class of a population (Doak et al. 1994). For example, animals must be able to be active for long enough periods of time to acquire energy needed for growth and reproduction. Like other ectotherms, tortoises may experience constraints on activity time due to the influence of climatic conditions in different portions of their range. Reductions in daily and annual periods of activity may occur if the hospitable conditions reduce climate space by the regular occurrence of extreme environmental conditions somewhere within tortoise distribution. The thermal environment may be temporally inhospitable, resulting in limitations on the time needed to acquire enough energy to survive and reproduce regardless of the amount of food available.

Tertiary mechanisms may not cause mortality of individuals directly, but may reduce recruitment of young. Thus, environmental limitations may prevent egg production by females (Henen et al. 1998) or the development of eggs or juveniles. Limitations may include changed quality and/or quantity of food and water resources for growth (Turner et al. 1986, Mueller et al. 1998) and egg production (Henen 1997, Henen et al. 1998). Limited food and water resources can occur during periodic droughts (Nagy and Medica, 1986, Henen et al. 1998).

Quantifying the thermal environment and its effects on ecological performance measures is critical to a robust understanding of ecological constraints and opportunities induced by the thermal environment (Tracy 1982, Grant and Dunham, 1988, Huey and Kingsolver 1989, Huey 1991). Many aspects of the thermal biology of desert tortoises have been investigated (McGinnis and Voigt 1971, Marlow 1979, Naegle 1976, Zimmerman et al. 1992, 1994, Hillard 1996, Henen et al. 1998), but few studies have been connected to understanding the geographical distribution of desert tortoises.

Several attempts have been made to quantify the niche of the desert tortoise (Schamberger and Turner 1985, Weinstein and Berry 1988). These studies have used habitat modeling, using atmospheric data and characteristics of the habitat that correlate with tortoise density as a method of predicting "good tortoise habitat." These models have been difficult to validate using independent data, so the limits to their usefulness have not been determined (Weinstein and Berry 1988). These models do not incorporate the mechanistic interactions between the tortoise and its environment, but rather depend on non-mechanistic correlations with measurable variables. Using current tortoise densities to predict tortoise distribution may be problematic, as areas within the range could have low densities due to stochastic historical incidents, such as recent drought, or disease. This correlation approach does not directly consider the thermal biology of these organisms, and, therefore, is not likely to be a dependable predictor of appropriate habitat (Huey 1991).

Porter and Tracy (1983) quantified environmental parameters and calculated the climate space for the desert iguana (*Dipsosaurus dorsalis*) in three habitats: (1) at a site in California where the species "can" and does exist, (2) at a nearby site in Nevada, where the species could likely exist but does not, and (3) at a site in Washington where it would not be likely to exist, and does not. This study showed that the temperatures and time combinations available for activity that could be experienced by adult animals were seemingly sufficient for growth and successful reproduction at all three sites. However, the combinations of soil moisture and temperature needed for the successful hatching of desert iguana eggs was likely to limit their distribution. The conditions of the soil in the areas where the lizards did not occur naturally had soil moisture/temperature combinations that were either too dry, or too cold (Nevada site), or both (Washington site) to allow enough time for eggs to complete incubation before the onset of winter. This study demonstrates that quantification of the interaction of the environment and the habitat of a species can result in testable predictions about the limitations to species distributions as a function of the environment and the physiological properties of the organism. This study is important because it recognized that different life stages of the organism have very different physiological requirements (Porter and Tracy 1983, Hillard 1996).

Tortoises may cope with differences in climatic conditions in different habitats by changing their thermal preferences, physiology, and behavior (Nagy and Medica 1986, Curtin 1998, Henen et al. 1998). Different amounts of activity time available (at both a daily and seasonal time scale) imposed by the thermal environment as a function of elevation may be reflected in measurable differences in the ecology of the animals and consequent fitness levels. More specifically, tortoises may experience limited time for activity if the climate space for tortoises is reduced by extreme environmental conditions found at different geographic locations. These changes in ecology, induced by the thermal environment, may result in differences in the daily and seasonal activity time, movement patterns, microhabitat selection, burrow use, reproduction, bodily growth, and survivorship of the desert tortoise in different environments.

Significance of Research

A mechanistic investigation of the distributional limits of the desert tortoise is important for several reasons: (1) We can learn much about the ability of desert tortoises to acclimatize to different environmental conditions, and (2) we can gain insight into the mechanisms limiting the successful dispersal and establishment of this species into new habitats. (3) We can then make recommendations to management and regulatory agencies as to how habitat determinants should be used to improve desert tortoise conservation efforts.

APPROACH

When I began my dissertation research, I proposed to study factors contributing to the geographical distribution of desert tortoises, including: 1) how tortoises respond (as measured by activity time, movement, shade use, survival, and reproduction) to different thermal environments and to differences in availability of food and water resources occurring over elevational clines, and 2) the mechanisms underlying thermal energy balances between tortoises and their environments, and the relative importance of the different modes of energy exchange.

The four chapters comprising this dissertation address these research objectives yet are written as focused articles on four different topics.
These chapters are entitled:

1. TRANSLOCATION AS A CONSERVATION TOOL FOR DESERT TORTOISES

This chapter details aspects of a large translocation project that funded the research in all chapters, enabling me to measure the activity, movements, shade use, survivorship, and reproduction of translocated as well as resident desert tortoises at several sites within and outside the geographic distribution of desert tortoises. From this work, we not only learned much about the responses of desert tortoises to being translocated back into the wild, but also of their responses to atypical habitats and elevations.

2. Hibernation in the Mojave desert tortoise

This chapter describes an investigation into the timing and possible mechanisms controlling the hibernation of desert tortoises across an elevational/latitudinal cline. From this work, we gained insight into the role of the thermal environment (with respect to the hibernation period) for tortoises at several sites within and near the northern limits to tortoise distribution, and the effects that result in the amount of time that tortoises are active during the rest of the season. We found that tortoises are very likely not limited in their northern extent by cold temperatures, as their hibernation temperatures were similar at every site. Nevertheless, tortoises at warmer sites tended to have shorter hibernation periods, and thus, longer periods of activity throughout the rest of the year.

3. THE RELATIONSHIP BETWEEN THE ABSORPTANCE OF THE CARAPACE AND THE THERMAL BIOLOGY OF THE DESERT TORTOISE.

This chapter addresses the mechanisms of energy exchange with respect to the thermal environment for desert tortoises. The results of this study have fundamentally changed the way we think about the interactions of these organisms and the thermal environment. Specifically, we found that the absorptance of the carapace of desert tortoises to solar radiation is far less influential to their energy balance than physics alone would predict. In fact, the carapace of tortoises appears to act as an insulator to solar energy. This finding caused the calculation of a climate space for these organisms to be far more difficult.

4. CAN MODELING OF DESERT TORTOISE ACTIVITY BE USED TO IMPROVE POPULATION DENSITY MONITORING FOR DESERT TORTOISES?

This chapter attempts to use various metrics of the environment to predict the surface activity of desert tortoises. I then ask whether modeling could be used to enhance current monitoring efforts that are being conducted by the U.S. Fish and Wildlife Service. The approach used consisted of an Artificial Neural Network model of activity, using inputs of 18 measures of the physical environment. The above ground activity of tortoises (which is important to quantify for density sampling) was difficult to predict with sufficient precision to have confidence in the model either to improve monitoring, or to model the activity time for tortoises during the active season. Further, we found that tortoise activity was not repeatable on consecutive days with similar environmental conditions. This calls into question whether a predictive model of the environment can be used to predict climate space for these animals.

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Chapter 1. Translocation as a conservation tool for desert tortoises

ABSTRACT

Desert tortoises are being displaced by expanding metropolitan areas in the Mojave Desert. Because desert tortoises are a threatened species, there is potential conservation value if they can be returned to the wild at designated translocation sites or in reclaimed habitat. We translocated tortoises to five sites in the northwestern Mojave in Nevada and Utah to evaluate the efficacy of translocation as a conservation tool in a variety of habitats. The sites were located at several elevations, and extended to habitats beyond those typically associated with tortoises. We measured survivorship, reproduction, movements, and microhabitat use by translocated and resident animals. Survivorship was not significantly different for translocated and resident animals within and among sites and was greater during non-drought years. The number of eggs produced was similar for translocated and resident animals, but differed among sites. Animals translocated to atypical habitat generally moved until they reached typical tortoise habitat if possible. Even when desert tortoises are translocated to typical tortoise habitat, they tended to move greater distances in the first year than did native tortoises, but their movements in the second year after translocation were indistinguishable from those of native tortoises. The large

movements of translocated tortoises have implications important to management decisions. Managers must ask, how large must a translocation site be? Will roads need fencing to prevent the loss of animals? How much area will be needed to contain the translocated animals? Our data suggest that translocation can be effectively used as a conservation tool for the desert tortoise, if they are translocated into typical Mojave Desert scrub habitats, and if the site is of sufficient size.

Introduction

Desert tortoise populations in the Mojave desert have experienced declines in population size in recent decades (U. S. Fish and Wildlife Service 1994). As a result, populations north and west of the Colorado River were listed as threatened in 1990 by the U.S. Fish and Wildlife Service (U. S. Fish and Wildlife Service 1994). The decline in numbers of this species has been attributed to human-induced habitat loss and degradation, as well as disease (U. S. Fish and Wildlife Service 1994). Areas managed for tortoise recovery, called desert wildlife management areas (DWMAs), were designated to minimize human impacts on desert tortoises by restricting human use while maintaining distinct population segments of tortoises, which are distinguished genetically, ecologically, and with respect to conservation urgency (U.S. Fish and Wildlife Service 1994). Outside of DWMAs many tortoises have been adversely affected by urban development. These animals are frequently captured and placed into holding facilities, where some animals are used in research, zoo, education, and adoption programs (Clark County 1991).

The number of humans in Clark County, Nevada increased from fewer than ten thousand in the 1940's to more than 1.3 million by 2000, and grew at an average rate of 5,000 people per month during the 1990's (U.S. Census Bureau. 2003). This rate of human population growth, and the resultant environmental impacts, indicates a need for effective conservation measures to protect the listed desert tortoise populations. One conservation measure has been to remove tortoises from natural habitats prior to urbanization. In Clark County, Nevada, and Washington County, Utah, this practice resulted in the accumulation of displaced tortoises in holding facilities, which caused a need either for larger holding facilities, or a method of reintroducing these animals into the wild.

To date, few studies of the effects of translocation on desert tortoises have been conducted, and no study has been extensive enough to evaluate translocation thoroughly as a conservation tool for this species. The results of previous efforts are reported in government documents (Berry 1974, Berry 1975, Berry 1976), as anecdotes, (e.g. see Cook et al. 1978) or unpublished accounts (Crooker 1971, Bryan and West 1972, McCawley and Sheridan 1972, Cook et al. 1978, Corn 1991, SAIC,1993). Thus, the potential for success of translocation in this species had not previously been thoroughly examined, and as a result translocation as a tool for conservation has remained controversial (Berry 1986, Dodd and Seigel 1991, U. S. Fish and Wildlife Service 1994).

The success of a translocation study is typically taken to be the ability of the translocated or augmented population to become self-sustaining in the long-term (Griffith et al. 1989, Dodd and Seigel 1991, Fisher and Lindenmayer 2000). Success, however, may be measured at several temporal scales, which may be important precursors to judging the long-term success of a translocation program (Tasse 1989, Dickinson and Fa 2000, Fisher and Lindenmayer 2000). For example, there may be some level of initial mortality above which a translocation study is judged to be unsuccessful (Platenberg and Griffiths 1999). In addition, other goals may be used to judge success in the short-term, such as the colonization of a particular site (Lohoefener and Lohmeier 1986), the social integration of translocated animals into the existing population (Berry 1986, Reinert 1991), and the ability of the animals to find mates and reproduce (Berry 1986, Pedrono and Sarovy 2000).

Our project was designed to assess the feasibility of and the habitat requirements for translocating desert tortoises. Our goals were to assess the extent to which translocated animals would accept and thrive in new habitat, find forage and shelter, integrate into existing tortoise populations, and produce offspring that could ultimately contribute to growth of the population. We assessed success of translocation by measuring these attributes in the field.

We quantified survivorship, reproduction, microhabitat use, and movements (one index of behavior, which may be especially important to land managers). Knowledge of how translocated tortoises move about after translocation is important to plan appropriately for any needed fencing of reserve areas or to determine the size of translocation release areas. Important in all of these measures of success are comparisons between translocated and resident animals in the area. These comparisons allow the effect of translocation to be statistically separated from factors normally expected in resident populations in particular areas.

MATERIALS AND METHODS

STUDY SITES

Five study sites (Fig. 1) were selected to represent the known range of elevation (500 to 1500 m) of extant desert tortoise populations in the northeastern portion of their geographical range (Germano et al. 1994).

One site, Bird Spring Valley (BSV, 35.9727 N; 115.3363 W; 997 m), was well within the geographic and elevation range known for this species. This site was southwest of Las Vegas, NV where tortoises were common (~ 30 per sq. km, Burge and Bradley 1976). The habitat was characterized by Mojave Desert scrub (Turner 1982) where the most abundant shrubs (as measured by their frequency of occurrence) were *Ambrosia dumosa (40%), and Larrea tridentata (13%). Ephedra nevadensis, Ceratoides lanata, and Lycium andersonii* each comprised about 5% of the perennial species. *Yucca schidigera* and *Y. brevifolia* occurred sparsely at the site. Eighteen percent of the area was covered by shrubs. The valley was an extensive bajada that ranged in elevation from 900 m to 1300 m and was of relatively even terrain. Mountainous peaks bordered Bird Spring Valley to both the east and west.

The Lake Mead site (LM) was a peninsula at the northern end (Overton arm) of the Lake Mead National Recreation Area, near Overton, NV (36.4839 N; 114.3492 W; 552 m). This site was located 105.8 km northwest of the Bird Spring Valley site (Fig. 1). It was 550 m lower in elevation, and characterized by a hotter climate than at Bird Spring Valley. Tortoises were present at the site, but at very low densities (~ 5 per sq km). Vegetation was Mojave Desert scrub (Turner 1982) with the most abundant shrubs at the site being *Ambrosia dumosa* (47%), *Larrea tridentata* (12 %), and *Ephedra californica* (11 %), with *Krameria parvifolia*, *Hilaria rigida*, and *Tetradymia spinosa* in heterogeneous patches. *Yucca* spp. were absent at this site. Twenty percent of the area was covered by shrubs.

There were three sites located in southwestern Utah, near the city of St. George. These sites were near the northern latitude limits to tortoise distribution and the elevation at these sites ranged from 1000 to 2000 m, which exceeded the upper elevation limits of the known range of desert tortoises (Fig 1.) (Germano et al. 1994). The St. George site consisted of two translocation release points into atypical habitats, with a third site (within typical tortoise habitat) serving as an elevation control for the northern latitude.

The Shivwits site (SHIV; 37.2267 N; 113.8386 W), was within the elevation range known to be hospitable to tortoises (~ 900 m to ~1300m). However, the dominant vegetation differed from that typically associated with desert tortoises. The site was within the ecotone between Mojave Desert scrub and Great Basin conifer woodland (Brown 1982). The perennial vegetation was dominated by *Coleogyne ramosissima* (35%), *Artemisia filifolia* (18%), *Gutierrezia sarothrae* (17%), and *Prunus fasciculata* (10%). Forty-two percent of the area was covered by shrubs.

Pahcoon flat (PAH, 37.2240 N; 113.8404 W) ranged in elevation from 1350 m to 2000 m, which was above the elevation typically associated with desert tortoises at similar latitude. This site was characterized as Great Basin conifer woodland dominated by *Artemisia tridentata* (44%), *Gutierrezia sarothrae* (27%), and *Coleogyne ramosissima* (20%). *Cowania mexicana* (4%) and *Juniperus scopulorum* (2%) were also at notable densities at the Pahcoon site. Forty-one percent of the area was covered by shrubs

The Sandstone Mountain site (SSM) had the same elevation range as Shivwits, but the vegetation was characterized as Mojave Desert scrub (Turner 1982). The most frequent perennials were *Coleogyne ramosissima* (26%), *Gutierrezia sarothrae* (25%), *Ambrosia dumosa* (9%), *Ephedra* species (7%), and *Artemisia filifolia* (7%). *Larrea tridentata* was present at Sandstone Mountain, but at a low frequency (3%). Twenty-seven percent of the area was covered by shrubs. There were few native tortoises located at this site, although tortoises existed in dense populations across the Virgin River, a few kilometers from this site.

PRIMARY PRODUCTION SAMPLING FOR ANNUAL VEGETATION

Primary production was sampled during the peak production of spring annuals in each year along twenty 200 m transects. Each transect began at a random point and extended in a random direction. Twenty quadrats (1 m^2) were sampled at random distances along each transect. This number of quadrats was chosen to minimize the within-transect variance, while minimizing the sampling effort (Simard et al. 1992, Catchpole and Catchpole 1993). The amount of annual vegetation (biomass) in each quadrat was ranked using calibration methods similar to those of Andariese and Covington (1986) and Tausch (1989). In this method, the amount of vegetation in each quadrat was subjectively ranked on a scale of 1 to 10. Separate ranks were made for standing green annuals and standing dry annuals for each quadrat. This effectively separated the new growth of the year from what had grown and was still standing from the prior year. Subjective ranks were used to quantify production in mass per unit area using a calibration curve based on the biomass of plants determined by clipping the above ground vegetation from representative quadrats along each transect. Calibration curves were constructed separately for each vegetation type (dry or green), each site, each year, and for each person sampling annual vegetation. Clipped plants were sorted into standing green annuals and standing dry annuals for each quadrat. All plants were dried at 45 °C to constant mass on three successive weighings and then the mass was recorded for each clipped quadrat. The mass of the plants in each clipped quadrat was regressed against the subjective ranks to generate an equation expressing the ranks as a function of measured plant biomass (Andariese and Covington 1985, Singh et al. 1990). The linear regressions for all sites and all years yielded significant positive correlations between the two measures of production.

PERENNIAL PLANT SAMPLING

Perennial plants were sampled once at each site using line-transects to assess perennial plant frequency, plant cover, height, and two perpendicular width measurements. Perennial plants were sampled by selecting 20 random points at each site. Each random point was used as the starting point for a 200 m random transect in a random direction. Cover was calculated using the line-intercept method (Canfield 1941). For each perennial plant that intersected the transect, the two points along the measuring tape that the plant crossed were recorded. Absolute cover for each species was calculated as the sum of all intercept distances for a given species divided by the total transect length (Canfield 1941). Total cover for the sites was calculated by summing the cover for each species. Average shrub volume was calculated as the average of the products of the measured height, and two widths for individuals of each plant species that intersected the transect.

Relative frequency for each species was calculated as the percent of individual plants intercepted by the transects belonging to a given species divided by the total number of perennial plants intersecting the 20 transects.

TRANSLOCATION

Experimental animals

All experiments using animals were conducted according to IACUC guidelines (University of Nevada IACUC Protocols #A95/96-19, A98/99-19, A98/99-29, and A95/96-28).

The tortoises released in Nevada were acquired from the Desert Tortoise Conservation Center (DTCC), a facility administered by Clark County, Nevada, which is located southwest of Las Vegas, Nevada. Tortoises released in Utah were acquired from the Washington County Temporary Care Facility (TCF), in Saint George, Utah. Tortoises in these facilities were generally acquired as they were displaced by urban expansion in their respective counties. Some of the animals were cleared from construction sites as new development occurred, others wandered into human developments and were turned in to the facilities, and a few animals that were previously kept as pets were later turned in to the facilities. Translocated tortoises were held in captivity for varying amounts of time. The details of the time in captivity for each release cohort are given below.

General Translocation Procedures

All tortoises translocated during this experiment were tested for an immune response to *Mycoplasma* using an ELISA test developed by the University of Florida. *Mycoplasma agassizii* is an organism that has been implicated as a cause of upper respiratory tract disease (URTD) (Brown et al. 1994).

On the day of release, all tortoises were provided drinking water for 15 to 20 minutes, and then released by being placed in an unoccupied tortoise burrow, in a burrow excavated with a power auger, or in the shade of a shrub, depending on the availability of natural burrows, and the severity of the daily ambient temperature at that time (Lohoefener and Lohmeier 1986, Corn 1991). Tortoises released under shrubs were generally released in areas where natural burrows were rare, and they were only released during early spring. This procedure was adopted after we noted that tortoises placed in natural or artificial burrows always left that burrow immediately and did not return to that burrow thereafter. During the first releases at Bird Spring Valley in 1997 all released animals were observed for the entire day of release to ensure that there were no immediate signs of heat stress (Cook 1983). In later releases, tortoises were only observed for approximately 30 minutes after release (the earlier observations showed that no tortoises were threatened by adverse conditions after released).

At Bird Spring Valley and Lake Mead, the tortoises released in January of 1998 were taken from the Desert Tortoise Conservation Center while hibernating and placed into burrows that were then covered with a piece of ¼ “ fiber-board (i.e. Masonite) (Corn 1991). The boards did not prevent tortoises from escaping, but were meant to encourage the animals to remain in hibernation. The tortoises placed in the covered burrows were monitored for 30 minutes to ensure that they did not leave the burrows immediately after release. The animals were then monitored weekly using radio-telemetry. The majority of the tortoises remained in their release burrows until early March of 1998. On March 11 of 1998 the boards were removed from all burrows.

Nevada Sites

1997 Bird Spring Valley

In 1997, sixty tortoises were released in Bird Spring Valley, NV. These included 30 adult females ranging in carapace length (CL) from 195 to 283 mm, 20 adult males (CL range 202 - 323 mm), and 10 subadult tortoises (CL = 128 - 183 mm). The tortoises had been maintained at the DTCC from 181 to 1246 days prior to translocation. Tortoises were released between April 21, 1997 and June 5, 1997 in groups of five to ten animals per week.

1998 Bird Spring Valley

In January of 1998, thirteen additional tortoises were released in Bird Spring Valley. These included 10 females (CL range 234 - 281 mm) and 3 males (CL = 235 - 255 mm). The tortoises had been maintained at the DTCC 123 to 293 days prior to translocation. The tortoises were translocated on January 27, 1998 while still hibernating. This release was conducted to serve as a temporal counterpart to our low elevation release (at Lake Mead), which had to be aborted in spring of 1997 due to unseasonably hot temperatures at the Lake Mead site during the release period.

1998 Lake Mead

In January of 1998, thirty tortoises were released at the Lake Mead site. These included 15 females (CL range 213 - 261 mm), 10 males (CL = 215 - 297 mm), and five subadults (CL = 138 - 192 mm). The tortoises were maintained at the DTCC from 136 to 2292 days prior to translocation. The tortoises were translocated on January 23, 1998 while still hibernating.

Saint George

1998 Shivwits/Pahcoon

In spring of 1998, seventeen tortoises were released at Shivwits between April 23 and May 2 of 1998. This group of animals included five females (CL range = 204 - 270 mm), nine males (CL = 203 - 308 mm), and three subadults (CL 155 - 178 mm). The animals released at Shivwits had been maintained in the TCF for 203 to 705 days prior to translocation.

Eighteen tortoises were released at Pahcoon flat between April 29 and May 21 of 1998. These included six females (CL = 202 - 252 mm), nine males (CL = 219 - 296 mm), and three subadults (CL = 165 - 200 mm). The animals released at Pahcoon had been held in captivity for 219 - 708 days prior to translocation.

1999 Sandstone Mountain

In the spring of 1999, 17 tortoises were released at Sandstone Mountain between April 26 and May 17 of 1999. The tortoises included seven males (CL range = 197 - 298 mm), four females (CL = 180 - 245 mm), and six subadults (CL = 165 - 204 mm). The tortoises released at Sandstone Mountain had been held in captivity for 15 to 588 days prior to translocation.

RESIDENT ANIMALS

Resident animals represented an “experimental control” for comparison of reproduction, movement, survivorship, and habitat selection with that of translocated animals. Resident animals were included in the study at the Bird Spring Valley and Lake Mead sites. The Saint George sites lacked sufficient numbers of residents to make statistical comparisons with translocated animals. We were able to gather data on egg production from animals at a site (Area 31) in St. George adjacent to the Sandstone Mountain site (Fig. 1). This site was within the Red Cliffs Reserve, and was similar in elevation, physiognomy and climate to the Sandstone Mountain site.

Resident animals were incorporated into the study at Bird Spring Valley beginning in 1996. Forty-three residents were equipped with radio-transmitters in 1996 (see below), and 17 additional animals were added in 1997. Up to 60 residents were tracked at any one time at Bird Spring Valley. Due to radio failures, the numbers of resident animals that were tracked in a given year fluctuated from 48 to 60. The residents tracked for all years combined consisted of 42 males with a range of carapace lengths (CL) from 194 to 280 mm (mean = 236.58 mm ± 21.9) and 45 females ranging in carapace length from 198 to 254 mm (mean = 227.5 mm ± 12.7).

At the Lake Mead site, resident animals were incorporated in the study beginning in 1998. A total of 17 residents were monitored at the site. The residents at this site were comprised of 11 males ranging in carapace length from 238mm to 298 mm and 7 females ranging in carapace length from 198 mm to 285 mm.

RADIO TELEMETRY

Movements of all tortoises were monitored by using radio telemetry using AVM models G3, SB2, or SB2-RL transmitters for adults depending on the release year, and model SM1-H, which was a lighter transmitter, for subadults. Resident animals had transmitters attached as the animals were encountered. Transmitters were attached in a manner similar to that described in Boarman et al. (1998). The body of the transmitter was attached with epoxy to the first costal scute, usually on the left side of the animal, to provide the best positioning of the antenna. The antenna was then affixed (with epoxy) to the center of each costal scute from front to rear, wrapping around the back of the animal and continuing forward on the opposite side. Silicone was used to secure the antenna in the scute margins to allow for growth of the animals (Boarman et al. 1998). All tortoises were numbered with a paper tag covered with clear epoxy, and notched on the marginal scutes by creating a small groove using a triangular file (Cagle 1939).

Tortoises were located using radio telemetry with hand-held radio receivers (e.g., Telonics TR-2, Mesa AZ). The animals were located weekly and their positions were recorded in Universal Transverse Mercator (UTM, WGS84) coordinates using Global Positioning System (GPS) receivers (Garmin GPS III+, Olathe, KS). Equipment failure and logistical constraints altered the telemetry schedule for some animals. The microhabitat (i.e. whether the tortoise was in a burrow, in a pallet, in the open, or under vegetation) occupied by the tortoise was also recorded each time a tortoise was located. If the tortoise was found under vegetation, the species of plant, the height of the plant (cm), and two perpendicular width measurements (cm) were recorded.

MOVEMENT

Tortoise activity was characterized from successive weekly tortoise locations for the year. We calculated the start-to-end-distance, which was the straight line distance from the point of release (or the hibernation burrow) to the hibernation burrow for the next winter. We also calculated the maximum distance from the origin, which was taken as the straight line distance from the point of release (or hibernation) to the farthest point traveled to for that year.

Movement was analyzed using nested split-plot analyses with movements (maximum and start-to-end distances) as response variables, and translocation group (e.g., residents, translocated 1997, and translocated 1998 for Bird Spring Valley and Lake Mead), year, and the translocation-by-year interaction as factors in the models using JMP 4.0.4 (SAS Institute, 2001). Individual tortoises were nested within translocation groups, and this variable was treated as a random factor in the analysis. This analysis was chosen over a standard repeated-measures analysis in order to generate the independent contrasts on the translocation-by-year interaction that were of particular interest in this study (SAS Institute pers. com.). Animals with fewer than six observations for the year were not used in the movement analyses as these were typically animals that had radio failure or that were lost before the end of the year. Additionally, because radio-transmitter failure occurred frequently for subadults, only adults were used in the analyses. The start-to-end and maximum movement distances were log transformed to comply with normality assumptions of the error variance in General Linear Models. Goodness of fit tests and residual plots were used to evaluate other assumptions of the models.

There were no residents at the St. George study site with which to compare movement patterns. Therefore, analyses of maximum and start-to-end distances over time were conducted to examine any trends of these movement metrics. These analyses were conducted using a nested split plot analysis with start-to-end and maximum distances as the response variables, and with year and gender as factors in the model, with individual tortoises nested within gender as a random effect. Post-hoc analyses of significant “year” effects were conducted using Tukey's HSD.

Two additional analyses were conducted to explore the overall pattern of movement distances over time found in translocated animals generally, while controlling for differences associated with the different study sites. We conducted an analysis of variance using the annual site means (for all sites) of maximum movement distance for translocated animals as the response variable, and “time since translocation” (years) and site as predictor variables in the analysis. A similar analysis was conducted using the start-to-end distance as the response variable and “time since translocation” (years) and site entered as predictor variables in the analysis. The analyses were conducted using JMP 5.0 (SAS Institute 2003). The effect of “time since translocation” on maximum and start-to-end distance was displayed using leverage plots to examine the time effect after accounting for any effect of site (Sall 1990; Fig. 5 and 6).

SITE FIDELITY

We tested for the use of home ranges using a site fidelity test (Hooge and Eichenlaub 2001) with which we tested tortoises’ fidelity both to the initial location for each tortoise and to the harmonic mean of all locations for each tortoise. To conduct the site fidelity test it is necessary to compute the sum of all distances from the test locations of animals (initial and harmonic mean) to all other locations for that tortoise. This collective distance was compared to the sum of distances to points from random simulations. Patterns of the movements for each animal in each year were categorized using the site fidelity test in the Animal Movement Extension 2.04b (Hooge and Eichenlaub 2001) for Arcview 3.2 (ESRI, Redlands, CA). All random movement simulations were run with the starting point and the harmonic mean of all points, and with 1000 random iterations of the same number of locations as the actual data for each tortoise (Hooge and Eichenlaub 2001).

The site fidelity test created 1000 random walks with random angles using the distances between the observed relocations. The mean squared distances (MSD) from the initial location were calculated for the animal telemetry locations, and for each of the random walks. The tests were categorized as “constrained” (i.e., had a home range) when the MSD for the animal was less than 95% of the MSDs for the random walks; “random” (i.e., not different from the average random simulation) when the MSD for the animal was within 5 and 95% of the MSDs for the random walks; and “dispersed” (i.e., more directional displacement than the average random simulation) when the MSD for the animal was greater than the MSD for 95% of the random walks.

Contingency analyses were conducted on the counts of animals in each of the site fidelity categories resulting from the site fidelity analyses (JMP V 5.0, SAS Institute 2003). The simulations starting from the initial animal location for the year, and the harmonic mean of location for the year resulted in the same categorization in each case, and thus all analyses were conduced using the harmonic mean categorizations of site fidelity. The analyses for Bird Spring Valley and Lake Mead were conducted comparing the site-fidelity category of residents to those of translocated animals of both translocation groups (1997 and 1998) for each year. The random-walk movements for tortoises at the Lake Mead Site were restricted to locations on land as desert tortoises are not known to swim. Utah sites did not have resident animals for comparison, so analyses were conducted for each site over time to examine the changes of the site fidelity patterns from year-to-year.

AREA USED

A measure of the area used by the translocated tortoise population was conducted for two of the sites (Bird Spring Valley and Shivwits) to represent two possible patterns in area covered by the displaced animals. The area used by tortoises was measured by creating an adaptive kernel analysis of all of the points for the release of tortoises, their positions during the first year, and their positions during the second year. All analyses were conducted with the Animal Movement Extension (Version 2.04b, Hooge and Eichenlaub 2001)) for Arcview (Version 3.2, ESRI, Redlands CA) using a 95% adaptive kernel, and the default values for the smoothing factor (H).

SURVIVORSHIP

Survivorship of animals in the study was summarized for each site in each year. In 1997 at Bird Spring Valley there was sufficient mortality to analyze whether prerelease conditions, or the time of the year that tortoises were released influenced survivorship. Logistic regressions were conducted to analyze whether the time in the DTCC, or the date of the year (Julian Date) influenced survivorship (JMP V 5.0, SAS Institute 2003).

REPRODUCTION

Egg production was measured by x-radiographing female tortoises between April and August of each year. This time was chosen because it bounded the part of the year when desert tortoises are known to lay eggs (Henen 1997, Turner et al. 1986). The tortoises were x-rayed every two weeks and the number of eggs and the number of clutches that tortoises produced each year were counted. A portable x-ray machine (MinXray Model P300, MinXray Inc., Northbrook Il.) was taken to each study site. Female tortoises were located, transported to the x-ray station, x-rayed, weighed, measured, returned to their original location, and released within a maximum of two hours of capture. The radiographs were imaged using Kodak X-Omatic film cassettes (Eastman Kodak Company, Rochester, New York) and x-radiation at a setting of 75 KVP and exposure times of 0.08 s (Hinton et al. 1997).

The numbers of eggs and clutches produced per year were analyzed using a univariate repeated-measures analysis of covariance, where body mass was the covariate, and site and translocation group were between subject factors (Superanova V 1.11, Abacus Concepts 1989). The univariate analysis was used because data for all tortoises were not available for all years. Due to the paucity of females available for our study in Utah, we combined the Shivwits and Pahcoon sites for analyses of reproduction.

Perennial Plant Shade Use

The use of perennial plants for shade by tortoises and the relative frequency and relative cover of those plant species at the study sites are given in tables 2 and 3. Perennial plants used by tortoises for shade were totaled by species and are expressed as relative use (%). Species accounting for less than five percent of use, frequency, or relative cover were combined into one category called “other”.

Use of perennial plants as shade resources by residents and translocated tortoises was compared (residents and translocated) and combined for years in which the translocation groups did not differ in their use of plant species for shade.

Comparisons of the volume of plants for each species selected by tortoises to the average volume of the plant species available in the environment for each site were conducted using an ANOVA with the group (Site or Tortoises) and species of shrub, as well as the interaction of these two as factors in the model. Independent contrast analyses were conducted when the interaction was significant to identify which species contributed to the differences between the volumes of the used and available shade resources. Plant species that contributed less than five percent to frequency and use were omitted from the analyses.

RESULTS

PRIMARY PRODUCTION

The production measurements for the sites had standard deviations that were as large as the means in many cases. This was because the spatial distribution of annual plant growth was patchy. In general the time over which green plants were available for sampling was shorter at the Lake Mead site, and was increasingly longer for the Bird Spring Valley site, and longest at the Utah sites. This pattern of the availability of green vegetation was not quantified in this study, but because of the variability in production measurements this observation may explain the differences in egg production at the different study sites better than measurements of peak production.

Bird Spring Valley

The estimates of production had high variation. The peak production of spring annuals on a g/m^2 basis was similar for 1997 and 1998 (Table 1). Despite similar winter rainfall in 1999 relative to that in 1997, there was almost no measurable primary production for 1999. This result differed from the 1999 pattern at Lake Mead.

Lake Mead

The Lake Mead site had slightly more production in 1998 than in 1999, but the high variation in this measure obscured any differences. The amount of winter precipitation was similar at the Lake Mead and Bird Spring Valley sites, yet there was some production at Lake Mead in 1999, even with little rainfall, while at Bird Spring Valley that year, under similar amounts of rain, there was almost none (Table 1).

St. George

Pahcoon had extremely high production in 1998 compared to all of the other sites. Production during that year was about six times higher than at any other site during any year. Unfortunately the Pahcoon site was burned in an unintended fire set by the BLM in 1999, after which we stopped sampling primary production at the site.

The other two sites in Utah had primary productivity that was closer to the levels measured at the Nevada sites. The primary productivity at Shivwits was highest in 1998, during a season preceded by high winter rains, and decreased each year thereafter.

The Sandstone Mountain study site had somewhat lower productivity than Shivwits in 1999, and also decreased in the 2000 season. This result was despite fairly high and consistent rainfall for the two years.

SURVIVORSHIP

Survivorship is presented below by years for each study site.

Bird Spring Valley

In 1997 at Bird Spring Valley, of the 53 resident tortoises that were monitored for the entire year, eight died. For seven of these, predation was the suspected cause of death, because in the days prior to their death, the animals were in good health, not suffering from loss of mass or obvious signs of disease, and generally behaved normally. The dead animals were found within a few days of the last time that they were seen, and their bodies were severely disarticulated. The plant matter in the gut of the tortoise was often present at the site of the body, indicating that the animals were eating. The other tortoise that died in 1997 had dyskeratosis of the shell and symptoms of URTD, and probably died of complications associated with these diseases. This animal was losing mass, and had reduced activity compared to other tortoises at the study site. Its body was found intact with no evidence of predation or scavenging.

In the same year, seven of 48 translocated tortoises monitored for the entire year died. All of these tortoises exhibited signs of predation and had no symptoms of disease, suggesting predation was the cause of death.

Neither time in captivity (χ^2 = 0.01, df = 1, P = 0.92), nor the date of the year that animals were released (χ^2 = 1.05, df = 1, P = 0.33) significantly predicted mortality for 1997 in Bird Spring Valley.

In 1998, none of the 55 residents died, but three of the 66 translocated animals died. One of these deaths was likely due to predation, while the cause of the other two deaths is unknown.

Two of the 47 residents tracked died in 1999, one death was known to be due to overexposure to the summer environment. The animal was found upside-down in the open, fully exposed to the sun. The body was found intact, with no signs of predation or scavenging. The cause of the other death was unknown. None of the 47 translocated animals at this site died in 1999.

There was no year in which statistically differential mortality occurred between the resident and translocated animals at Bird Spring Valley.

Lake Mead

One resident tortoise died at the Lake Mead site in 1998, two days after it had been observed to be healthy. Its body was severely disarticulated, and It was surrounded by footprints that appeared to be from a large canid. Two translocated animals died in 1998. One was due to overexposure to the sun, and the other cause was unknown, but could have been due to overexposure to the cold, as it was in mid-winter.

No animals (resident or translocated) died in 1999 at Lake Mead.

As with Bird Spring Valley, there were no differences in the number of deaths between resident and translocated animals at the Lake Mead site in any year.

Shivwits/Pahcoon

Three of the 36 translocated tortoises were killed in a fire that burned the Pahcoon release site in 1998. The fire resulted from a prescribed burn that escaped containment by the Bureau of Land Management. Another tortoise died for unknown reasons in 1998.

During the 1999 season, one translocated tortoise did not emerge from its burrow after hibernation. The tortoise was found alive in its hibernation burrow, which had been crushed by cattle. The tortoise had skin lesions and myiasis. The animal was removed from the study and considered dead, because we were certain that it would have died had it been left in the crushed burrow for a longer period.

No monitored tortoises died at the Shivwits or Pahcoon sites in 2000.

Sandstone Mountain

One of the 17 translocated tortoises at Sandstone Mountain was lost in 1999 and was later found at the bottom of an abandoned mine shaft (see below). Another translocated tortoise was found dead in debris deposited by floodwaters in a large wash. This animal presumably drowned as a result of being caught in the wash during heavy rainfall.

Beginning in the spring of 2000, 14 animals were still being tracked at the Sandstone Mountain site. In April of 2002, two tortoises were found in an abandoned vertical mineshaft (about 10 m deep). They were removed from the mineshaft by volunteers from Washington County, UT. For the purposes of the translocation study these tortoises were considered to be dead.

MOVEMENT

Analyses for trends in maximum and start-to-end movement distances generally showed a pattern of decreasing movements over time for translocated animals (Fig. 2, 3, and 4). The movements of resident animals at Bird Spring Valley and Lake Mead were relatively consistent from year-to-year. The movement indices of translocated tortoises were the same as those for resident animals after one or two field seasons (Fig. 5 and 6). The details of these analyses are given in the sections below.

Movement analyses for translocated animals all sites combined

The analysis for the maximum movement distances (of all translocated tortoises combined) yielded a significant negative relationship of “years since translocation” on maximum movement distances ($F_{1,5}$ = 20.4 P = 0.006, Fig. 5).

There were also significant differences among sites ($F_{4,5}$ = 13.0, P = 0.008), however the time by site interaction was not significant ($F_{4,5}$ = 4.3, P = 0.07).

A similar analysis using start-to-end distances as the response variable yielded similar results. There was a significant negative correlation of “years since translocation” on start-to-end movement distances ($F_{1,5}$ = 9.7, P = 0.03), even after accounting for significant differences among sites ($F_{4,5}$ = 8.07, P = 0.002, Fig. 6). There was no significant site by time interaction ($F_{4,5}$ = 3.84, P = 0.09).

Nevada Sites

Maximum Distances

At the Bird Spring Valley study site, animals translocated in 1997 moved greater maximum distances than did residents in 1997 (mean maximum distance 1484 m vs. 461 m, t = -8.79, P < 0.001). However the tortoises translocated in 1997 did not move significantly further than did resident animals in the following two years (1998, 691 m vs. 560 m, t = -1.52, P = 0.13; 1999, 383 m vs. 483 m, t = 1.6, P = 0.11). Similarly, tortoises translocated in 1998 moved greater maximum distances than did residents in 1998 (1832 m vs. 560 m, t = -5.8, P < 0.001), but not in the following year (1999 maximum movement distances = 439 m vs. 483 m, t = 0.45, P =0.66) (Fig. 2).

At the Lake Mead study site, animals that were translocated in 1998 moved further on average than did resident tortoises (971 m vs. 388 m, t = -2.7, P = 0.01), but did not move further then resident tortoises in the following year (1999) (327 m vs. 301 m, t = -0.25, P = 0.81)(Fig. 2).

Start-to-end distances

At the BSV site in 1997, tortoises translocated in 1997 ended the season further from their initial locations on average than did residents (781 vs. 156 m; t = -4.6, P < 0.001). In 1998 the start-to-end distances moved by the tortoises translocated in 1997 were still significantly greater than those of resident animals (258 vs. 67 m; t = -3.45, P < 0.001), however in 1999 the tortoises translocated in 1997 had start-to-end movements indistinguishable from those of residents (150 vs. 84 m; t = -1.5, P = 0.15).

The tortoises that were translocated in 1998 at BSV exhibited a similar pattern of initially higher start-to-end distances compared to residents (696 vs. 67 m; t = -5.09, P < 0.001), and their start-to-end distances were indistinguishable from those of residents in 1999 (187 vs. 84 m; t = -1.34, P = 0.18) (Fig. 3).

Tortoises translocated to Lake Mead in 1998 ended the season further from their starting positions than was the case for resident animals in 1998 (660 vs. 208 m; t = -2.2, P = 0.04). By 1999, the tortoises that were translocated to the site in 1998 had start-to-end movement distances that were indistinguishable from those of residents (84 vs. 90 m; t = 0.12, P = 0.9).

Utah Sites

The movement patterns in maximum and start-to-end movement distances at the sites near Saint George, Utah (Fig. 4) were similar to those measured for the translocated animals at the Nevada sites (Fig. 2 and 3) in that most of the translocated animals in Utah had decreasing maximum distance and start-to-end movement distances over time (Fig. 4), the notable exception being animals at the Shivwits site, that did not decrease movement distances with time.

Maximum Distances

The overall analysis of maximum movement distance for tortoises at Pahcoon was significant ($F_{16,28}$ = 15.2, P < 0.0001), as was the effect of year on maximum movement distance ($F_{2,28}$ = 82.1, P = < 0.0001). The significant year effect was due to decreasing maximum movement distances in each successive year from 1998 to 2000 (Fig. 4, Tukey's HSD, Q = 2.27). In addition, there was a significant effect of gender, as males moved greater distances than did females (Males = 4151 m vs Females 1862 m, $F_{1,28}$ = 54.8, P < 0.0001).

The overall analysis of maximum movement distance for tortoises at the Shivwits site was not significant ($F_{16,36}$ = 0.3, P = 0.99). This indicated there was no significant change in maximum distances moved over time for tortoises at this site (Fig. 4), nor were there significant effects due to gender.

The overall analysis for the maximum movement distances over time for tortoises at the Sandstone mountain site was significant ($F_{11,19}$ = 8.4, P = 0.003).

There was a significant effect of year ($F_{1,19} = 6.6$, $P = 0.03$) which was a result of decreasing maximum distances moved at the site from 1999 (mean = 1811 m) to 2000 (mean = 490 m).

Start-to-end distances

The overall analysis for start-to-end movement distances at the Pahcoon site was significant ($F_{16,28} = 16.3$, $P < 0.0001$). The year effect was significant, due to the fact that the start-to-end movement distances decreased from 1998 to 1999 (mean = 5835 m vs. 1545 m, Tukey's HSD Q = 2.67). However, there was no significant decrease from 1999 to 2000 (mean = 1545 vs. 493, $P = 0.09$).

The Shivwits site had no significant differences in start-to-end movement distances overall ($F_{16,36} = 0.35$, $P = 0.98$). This result indicated no effect of year or gender in the analysis.

The overall analysis for the Sandstone mountain site was significant ($F_{11,19} = 69.9$, $P < 0.0001$). This reflected a significant effect of year, with decreased start-to-end movement distances from 1999 to 2000 (mean = 1185 m vs 198 m, $F_{1,19} = 5.2$, $P = 0.05$). There was no significant effect due to gender ($F_{1,19} = 0.55$, $P = 0.48$).

Site Fidelity

In general, site fidelity categories correspond with different patterns of habitat use with respect to area. Site fidelity patterns that were categorized as constrained were typified by a classical use of a home range (Burt 1943), in which movements had a smaller areal extent than that of random movements. Tortoises that had site fidelity classified as “random” were similar in areal extent to the random simulations of moment. Dispersed site fidelity patterns indicated movement patterns that were more linear than those of the random movement simulations, suggesting that animals were dispersing from an area.

Bird Spring Valley

At Bird Spring Valley in 1997, a greater proportion of the resident tortoises had constrained movement patterns than did tortoises translocated in 1997, which exhibited more random movement patterns (Table 6).

In 1998, there were significant differences in site fidelity among resident animals in Bird Spring Valley, and tortoises translocated in 1997, as well as those translocated to the site in 1998. The resident animals in that year had the highest proportion of animals with constrained movement patterns recorded for any year, and tortoises that had been translocated a year previously (1997) had a nearly equivalent level of constrained movements to that of resident tortoises. Tortoises translocated in 1998 exhibited similar proportions of random and constrained patterns to those of the first season in the field for the animals that were translocated in 1997, and had the greatest level of random classifications for that year. By 1998 at Bird Spring Valley, all three treatment groups of animals had similar proportions of random and constrained movement patterns (Table 6).

Lake Mead

At the Lake Mead site there were no significant differences in site fidelity among the residents and the tortoises translocated in 1998. Both groups exhibited similar proportions of random and constrained movement patterns, which were also similar to the proportions recorded at Bird Spring Valley for resident animals. In 1999 both resident and translocated animals had a very low number of animals that were classified as dispersed.

Utah Study Sites

The sites located in Utah had no residents for comparison, so site fidelity patterns were analyzed for translocated animals at each site over time (Table 7). At the Pahcoon site in 1998, significantly more animal's movement patterns were classified as random than either of the other categories, a large proportion of them were classified as dispersed, while none were constrained. In the following year (1999), there was an increase in the number of constrained animals (five out of thirteen), with similar proportion of animals classified as random and dispersed. By the year 2000 at the Pahcoon site, there were more animals classified as constrained, and only two of ten animals were either dispersed or random.

The tortoises at the Shivwits site had a similar pattern in site fidelity to that seen at the Pahcoon study site. In 1998, there were more animals with dispersed movement patterns, and fewer animals with constrained patterns. In 1999, there was an even distribution of animals in each site fidelity category. In 2000, there were significantly more animals that were categorized as constrained than either random or dispersed (Table 7).

At the Sandstone Mountain site tortoises were more constrained than at any other site, and this was the case compared to both resident or translocated animals. In addition, the site fidelity pattern did not change among years. Tortoises at this site initially had very high site fidelity (i.e. a high proportion of animals had constrained movement patterns), and retained high site fidelity for both years (Table 7).

AREA USED

Tortoises at Bird Spring Valley were released into an area of 10 km^2 and their movements collectively expanded to fill an area of 18 km^2 during their first season in the field (an increase in area of 80%). In the period between the first season after translocation (December of 1997) until the end of the second season after translocation (December of 1998), translocated tortoises collectively expanded to fill an area of 24 km^2 which was an increase of 140% over the original area occupied by the translocated population, but only a 33% increase over the end of the previous season (1997) (Fig. 7).

Tortoises at Shivwits were initially released into an area of approximately 0.5 km^2 in 1998. By the end of their first season in the field, these animals collectively had expanded to fill an area of 26.7 km^2 during the first season. By the end of the second season (December of 1999) the translocated tortoises had expanded to an area of 64 km^2, which was an addition of 140% from the previous year, or a total expansion of 127 times the original release area (Fig. 8).

REPRODUCTION

Nevada Sites

Number of eggs produced by tortoises

Translocated and resident animals produced the same number of eggs during any given year at each study site ($F_{2,110} = 0.03$, $P = 0.98$). Carapace length was not correlated with the number of eggs produced among all sites and years ($F_{1,110} = 0.32$, $P = 0.58$). There was a significant "number of eggs" by "site" interaction ($F_{2,110} = 3.6$, $P = 0.03$). This was due to differences in the number of eggs produced by tortoises within sites changing among years (Table 5).

NUMBER OF CLUTCHES

Translocated and resident animals produced the same number of clutches at each site within a given year ($F_{2,111} = 0.74$, $P = 0.48$); and there were differences in the number of clutches among sites and years ($F_{2,111} = 3.1$, $P = 0.05$, Table 5).

Utah Sites

There was no overall significant effect due to translocation (i.e. translocated animals vs. resident animals) on the number of eggs produced by animals at the Utah sites ($F_{2,24} = 1.0$, $P = 0.4$). There was a significant year by translocation interaction ($F_{3,24} = 3.1$, $P = 0.05$) due to the low numbers of eggs produced by the animals at Sandstone Mountain in 1999. At the Sandstone Mountain site, there were only four translocated females in 1999, and three did not produce any eggs. This low sample size probably accounts for this difference rather than a biologically meaningful phenomenon. Further, animals translocated to areas of creosote scrub habitat (Sandstone Mountain) did not lay a statistically different number of eggs compared to tortoises translocated to the higher-elevation sage-scrub habitat (Shivwits and Pahcoon; $F_{1,7} = 0.4$, $P = 0.6$).

SHADE PLANT SELECTION

Nevada sites

Lake Mead

Resident and translocated tortoises at the Lake Mead site used species of shade plants in similar numbers in 1998 ($\chi^2 = 4.2$, df = 6, $P = 0.65$), and in 1999 ($\chi^2 = 6.4$, df = 7, $P = 0.5$). Combining all tortoises over both years at the Lake Mead site there were five plant species that were used for shade in excess of five percent over all 226 observations of animals seeking shade under shrubs: *Ambrosia dumosa* - 32%, *Ephedra spp.* - 30%. *Larrea tridentata* - 11%, *Krameria parvifolia* - 8%), and the perennial grass *Hilaria rigida* – 5%. Fourteen percent of shade use observations were on plant species that were classified as “other” (Table 2).

In some cases, plants appeared to be selected as shade resources in proportions different from their frequency of occurrence at the site. For example, *Ambrosia* was used for shade (32% of observations) less frequently than its frequency of occurrence (48%), and *Ephedra spp.* comprised 30% of the observations of shade use, yet its frequency of occurrence was 11% (Table 2). The remaining species generally appeared to be used for shade in similar proportions to their occurrence at the site.

Shrub volume used by tortoises for shade differed from the average volume of four of the six plant species in the environment (Table 4). For each of the four species the tortoises chose shrubs for shade that were larger than the average for the species.

Bird Spring Valley

Translocated and resident animals used plants for shade in similar numbers during 1997 ($\chi^2 = 13.4$, df = 7, $P = 0.06$). During 1998 resident animals used shrubs for shade in similar proportions to translocated animals, regardless of whether they were released in 1997 ($\chi^2 = 9.2$, df = 6, $P = 0.16$), or in 1998 ($\chi^2 = 7.7$, df = 6, $P = 0.26$). In 1999 resident animals differed in their use of shade plants compared to tortoises translocated in 1997 ($\chi^2 = 29.5$, df = 6, $P < 0.0001$), and 1998 ($\chi^2 = 23.2$, df = 6, $P = 0.0007$). The differences in shrub selection in

1999 between residents and tortoise translocated in 1997 were due to residents selecting *Ambrosia* and *Yucca schidigera* more frequently, and *Coleogyne* less often than the translocated animals. Additionally, tortoises translocated in 1998 selected *Coleogyne* and “Other” species more frequently than did residents in 1999.

When combining data at Bird Spring Valley for all tortoises for 1997 and 1998, tortoises (resident and translocated) appeared to use shade plants differently than frequency of occurrence. The percentage of observations under *Ambrosia,* and *Ceratoides* lower than their frequency of occurrence, and the percentage of observations under *Ephedra spp.* and *Yucca schidigera* appeared higher than their frequency of occurrence (Table 2).

Shrub volume also predicted use by tortoises for shade (Table 4). The plants selected for shade by tortoises had significantly greater volume than the average for each species.

Utah Sites

At the Utah sites, there were no resident animals with which to make comparisons. Thus, all of the of the shade resources selected by the animals are presented relative to indices of their occurrence in the environment (table 3).

Sandstone Mountain

At the Sandstone Mountain site *Coleogyne (40%)* and *Larrea (17%)* appeared to be used for shade to a greater degree than their occurrence (25%, and 3.4%

respectively). Six percent of the observations of tortoises in the shade were under *Gutierrezia* spp., while it consisted of 25% of the shrubs encountered on the transects (Table 3).

The average shrub volume for some perennial species used by tortoises differed from their volume at the site ($F_{4,720}$ = 4.3, P = 0.002). Tortoises selected larger plants of three species (*Coleogyne*, *Ephedra spp.*, and *Gutierrezia*), than their average volumes at the site (Table 4). The sizes of *Ambrosia* and *Larrea* plants used for shade by tortoises were similar to the site average for both plant species (Table 4).

Shivwits

Tortoises at the Shivwits site appeared to avoid *Artemisia filifolia* (1% use) and *Gutierrezia* (2 % use) when considering their abundance at the site (18% and 17% relative frequencies). *Juniperus* (20% use) and *Quercus* (12% use) appeared to be used more often than their relative frequencies (2% and 0.3% respectively) (Table 3).

The volumes of plants used for shade by tortoises differed from the species averages at the site ($F_{5,367}$ = 2.75, P = 0.02). Tortoises used larger individuals of *Coleogyne*, and *Prunus* plants than the average size of these species at the site (Table 3). Tortoises used plants of *Artemisia filifolia*, *Gutierrezia*, *Juniperus*, and *Quercus* that were similar in volume to the site averages for these species (Table 4).

Pahcoon

Tortoises used species of plants for shade that appeared to be different than the relative frequency of most plant species at the site. However, because tortoises dispersed from the original release site, we also sampled plant frequency and cover at the locations of individual tortoises at the conclusion of the study. Relative to the plant frequencies for species encountered on transects at the end of the study tortoises appeared to select *Juniperus* (8 % use), and the "Unknown" species group (15% use) more frequently than their occurrence (2 % and 4 % respectively) on the transects near the animals. *Gutierrezia* (0% use), and "Other" (18% use collectively) plant species appeared to be selected less frequently their frequency in the habitat (11% and 37%)(table 3).

The volumes of the plant species used for shade were similar to their respective volumes in the habitat when compared to both the Pahcoon release site ($F_{4,426}$ = 1.6, P = 0.18), and to the transects conducted at individual tortoise locations ($F_{6,793}$ = 1.4, P = 0.23) (Table 4).

DISCUSSION

TRANSLOCATION

Our study demonstrates that desert tortoises can be translocated without significant adverse effects. Indeed, by the end of our three-year study, translocated tortoises were indistinguishable from resident animals with respect to all of our measures of success. Importantly, translocated animals had similar survivorship, and produced the same number of eggs each year as did resident animals, even in the first year after translocation.

SURVIVORSHIP

Survivorship of translocated animals was not significantly different from that of resident tortoises. During 1997 (a drought year), tortoises at Bird Spring Valley experienced the highest levels of mortality for any of the sites in any year (15 %). However, neither the release date nor the length of time spent in captivity was a predictor of the survivorship of translocated tortoises. This was an important result as animals released at Bird Spring Valley in 1997 spent an average of 1.5 years in captivity. Thus, we were encouraged that animals given food and water supplementation while in captivity for long periods were equally able to survive as animals that spent less time in captivity.

The dates over which animals were released ranged from 4/21/97 to 6/5/97, (a 45 day period). Over this time, environment temperatures increased greatly, which could have caused additional stress to animals released later in the season, as tortoises may have been unfamiliar with the shade resources and cover sites needed to protect them from temperature extremes. However, we did not find evidence that the release date influenced survival over the range of days tortoises were released. On the other hand, summer releases have been reported to be potentially lethal to translocated animals (Cook 1978).

In general, it appears that most mortality was due to canid predation, rather than disease or stress due to translocation (Woodbury and Hardy 1948, and Peterson 1994). Most of the dead tortoises were found eviscerated but with their shells intact, and canid foot prints typically surrounded the carcass. Tortoise gut contents, consisting of considerable amounts of vegetation, often remained near the carcasses, thus starvation seemed an unlikely cause of death. However, it is possible that the animals suffered from dehydration (Nagy and Medica 1986, Peterson 1994, Longshore 2003).

Translocation of desert tortoises has been judged as successful previously (Cook et al. 1978) with an overall survival of 79%, and their study animals increased in body mass in the first year after translocation. All of the six deaths in that study were due to the animals' inability to avoid excessive thermal conditions at the time of release. This was largely due to tortoises being released in June and July of 1977, which are among the hottest times of the year (Cook et al. 1978). In fact, three of the six deaths occurred on the day of release, while the other three died within two weeks of release. A second group of translocated animals released in May of 1978 had 100% survivorship (Cook et al. 1978).

The Honda corporation funded a desert tortoise translocation study (SAIC 1993), but flaws in the experimental design severely limit the conclusions that can be drawn from the study. For example, there were fenced treatment plots without replication, and tortoises were considered to be dead if the animals were missing from the plot for a given time period, rather than when carcasses were actually found. Thus, when an animal escaped from one of the fenced plots, or when an animal could not be found because of radio transmitter failure, the tortoise was presumed to be dead. This assumption clearly biased estimates of mortality, elevating estimates to as high as 57%, when in fact a mortality rate of 14% among translocated animals was supported by definitive evidence (SAIC 1993).

BEHAVIOR : MOVEMENT

We were interested in movement from the perspectives of individual behavior, and the area needed to translocate tortoises. Earlier translocation studies on desert tortoises indicated that animals may move away from the release site after translocation (Berry 1974, Berry 1975, Berry 1976, Cook,1983, Berry 1986), and/or return to the site from which they were taken (Corn pers. comm.). While large movements or site abandonment by translocated tortoises have been recorded for desert tortoises (Berry 1986, This study), and gopher tortoises (Diemer 1984, Burke 1989), releases of other tortoise species reported different results. For example, released captive-bred ploughshare tortoises (*Geochelone yniphora*) had little movement, or homing tendency (Pedrono and Sarovy 2000).

Two measures of movement; the distance from the release (or hibernation) site to the last position measured (start-to-end distance), and the furthest distance an animal was found from its starting location for the year (maximum distance) provided information relative to an animals' site fidelity, and how widely the animal ranged. For example an animal that has a large maximum distance, but a small start-to-end distance can be interpreted to be wide ranging, but also to have some fidelity to the site (e.g., overwintering near the same location). Conversely, an animal with both a large maximum distance and a large start to end distance would indicate an animal that is dispersing.

Translocated animals initially moved great distances (regardless of the measure of movement used) compared to residents. The distances that the translocated tortoises moved decreased over time, becoming similar to the distances moved by resident animals in two or three field seasons (Fig. 2 and 3). When combining movement data translocated tortoises at all sites showed a significant decline in movement distances over time, becoming similar to the movement distances of residents in approximately three years (Fig. 5 and 6).

The patterns of movement at the sites consisting of atypical tortoise habitat in Utah (i.e. Great Basin scrub) were qualitatively similar to movements at sites with typical habitat (i.e. Mojave desert scrub), but with important differences. The tortoises released at the Shivwits and Pahcoon sites in Utah had movement distances that were three to four times those observed at at sites with typical tortoise habitat. For example tortoises at the Pahcoon site had average movement distances of 6 km during their first season in the field, and took two seasons before their movements were similar to those of Nevada residents (Fig. 2, 3 and 4). These longer movements generally took these animals from the higher elevation site, dominated by Great Basin scrub, to a habitat more typical of higher elevation Mojave desert scrub (Brown 1982, Turner 1982).

At the Shivwits site, there was no simple route to habitat containing Mojave vegetation. Tortoises at this site spent all three seasons that we monitored them in blackbrush- and sagebrush-dominated habitat, and their movement distances remained high relative to other translocated animals at any of the sites for all three seasons (Fig. 2, 3, and 4).

Site fidelity analyses yielded a result that was consistent with that of the two movement indices. For translocated animals at each site there was a general transition from random or dispersed movement patterns to more constrained movement patterns over time (Tables 6 and 7). Some sites had animals with linear movement patterns that were classified as dispersed. The numbers of animals exhibiting dispersed movement patterns decreased over time generally from the first to the second season. There were a few animals that never settled down to become associated with a location, and whose movement patterns remained classified as dispersed for the entire study period (Table 7).

The combined interpretation of the concomitant reduction of both indices of movement, as well as the conversion of movement patterns from dispersed and random movement patterns to constrained patterns indicates that the translocated animals adopted new home ranges (Burt 1943).

AREA USED

The amount of area used by the translocated animals may be important from a management perspective when translocating tortoise populations. Tortoises translocated to areas within typical tortoise habitat may expand to areas upwards of 250% of the original area, while animals released to atypical habitat may expand to areas many times that size, and create management challenges.

The animals at Bird Spring Valley underwent an initial period of expansion of the area used by the translocated animals, however the increase during the second year was relatively minimal (Fig. 7). This was concordant with the indices of movement for the animals during the first and second seasons (Fig. 2 and 3). The areas used by translocated animals at Lake Mead and Sandstone Mountain had similar extent. Thus, we suggest this result illustrates the level of expansion that might be expected for translocated animals that are moved within typical tortoise habitat.

The area used by translocated tortoises at Shivwits expanded more than for the area used by translocated tortoises at Bird Spring Valley (Fig. 7 and 8). The area used increased greatly during the second season after release, and had little indication of slowing as movement distances remained high during the third season after release (Fig. 4). This pattern of expansion also occurred at the Pahcoon site, and may represent the behavior of animals released into atypical tortoise habitat.

REPRODUCTION

Earlier studies (SAIC 1993) suggested that the physiological stress associated with translocation might cause female tortoises to reduce reproductive investment after translocation (Henen 2002). However, translocated tortoises in our study produced the same number of eggs as resident animals during their first year after translocation, and indeed for every year thereafter at every site. The successful first year reproduction by translocated animals may have been influenced in part by the food supplied to the tortoises while in their pre-translocation holding facilities (Henen 1997, Henen 2002). The number of eggs produced by tortoises differed among sites and years, which could be an indication of the relative austerity of the sites (Henen 1997, Henen 2002). For example, tortoises at the Lake Mead site produced approximately half the number of eggs as animals at Bird Spring Valley in each year. In 1998, which was a year of high rainfall and elevated levels of primary production animals at Lake Mead and Bird Spring Valley produced double the number of eggs as in the previous year, yet Bird Spring Valley tortoises still out performed the Lake Mead tortoises in egg production by the same amount as in the previous year.

Interestingly, the numbers of eggs produced by animals at the Utah sites in all years was as high as the best year at Bird Spring Valley (1998). In addition, even the animals that were translocated to the upland sage-dominated sites produced large numbers of eggs per year, despite their apparent dislike of the habitat as measured by the movement patterns.

SHADE SELECTION

Translocated animals rarely differed from residents in their selection of shade resources at the Lake Mead and Bird Spring Valley sites, with the exception of 1999 at Bird Spring Valley. The differences in the species selected for shade use in that year indicated that translocated animals were at slightly higher elevations than the resident animals at the site, which was likely due to their encroachment into the foothills (Fig. 7) as their area use expanded (mountains bordered the site on two sides). The differences in shade choice among translocated tortoises and resident animals in 1999 were due to higher use of *Coleogyne* (which is typical of higher elevation sites in the Mojave) by translocated tortoises (Woodbury and Hardy 1948).

There were apparent differences among the shrub species available and those selected at each site (Tables 2 and 3). *Ephedra spp*. was frequently used for shade, and used to a greater degree than its relative frequency at the Nevada sites (Table 2). *Ambrosia dumosa* was one of the most common species used for shade at many of the sites (e.g. Lake Mead, Bird Spring Valley, Sandstone Mountain, Tables 2 and 3), yet it did not seem to be used to the extent of its occurrence at the Nevada sites. Bird Spring Valley was the only site that contained *Yucca schidigera*, and it was used for shade to a greater degree than its occurrence. Interestingly, *Larrea tridentata* is often considered to be the preferred shade resource for desert tortoises (e.g. Morafka and Berry 2002), however its proportion of use appeared to be about the same as its occurrence at the Nevada sites (Table 2).

The Utah sites provided the opportunity to introduce tortoises into habitats that they normally do not occupy (Germano et al. 1994). The Sandstone Mountain site was the one site in Utah that was most similar to the Nevada sites when considering perennial vegetation, but it had more of the plant species typical of higher elevation Mojave, such as blackbrush (*Coleogyne*) and sagebrush (*Artemisia*) (Woodbury and Hardy 1948, Mozingo 1987). Despite the typical negative association between the presence of black brush and desert tortoises, (Medica pers. comm. Tracy pers. comm.) tortoises at Sandstone, and eventually Pahcoon used this shrub as a shade resource in high proportions (Table 3).

The animals at the Pahcoon site were unique compared to the four other sites in that most animals left the site of release and dispersed widely. The vegetation at the release site (and available for choice as a shade resource) appeared to be different from vegetation available later in the study. And in fact, comparisons of shade selection by tortoises relative to that of the release site appeared to differ in frequency for nearly every species (Table 3). When comparing the perennial plant transects that were conducted at the tortoise locations, there were far fewer apparent differences among plants that were selected as shade resources, and their frequency of occurrence (Table 3).

Artemisia spp. were used in very low percentages relative to their frequency at the three sites where these species were present (Table 3). Indeed, tortoises appeared to avoid these species for use as shade resources.

CONCLUDING REMARKS

Using translocation for conservation of desert tortoises is simultaneously a biological, an economic, and a political decision. The conservation of habitat should always take precedence for conservation planning (Reinert 1991), but when habitat is lost due to political or economical decisions, only two choices remain: 1) leave tortoises in harm's way to die (no conservation), or 2) collect the animals assuming that they may be useful for conservation in the future. Collected animals are frequently adopted to backyards, used as captives for public education and outreach, and for scientific research. Tortoises are also deposited in large pens that are not relied upon for recovery of the species, but may be helpful for those purposes in the future. These activities may increase public understanding, and therefore, support for conservation efforts (U. S. Fish and Wildlife Service 1994, Primack 1993). The research and education value also serves to increase our understanding of the ecology of these animals. However, as more-and-more tortoises accumulate, facilities for housing them can become saturated. Then agencies managing these animals are forced to expand existing research and/or holding facilities, to euthanize the tortoises (which is generally politically and ethically untenable), or to return the animals to the wild in some responsible fashion. The only situation in which these animals can ultimately contribute to conservation and recovery of the species is to return them to the wild. Thus, translocation can be especially valuable to deal with animals that have already been displaced from natural habitat (i.e. “taken” animals under the Endangered Species Act). Indeed, translocation really is the last and only biological and economic alternative under these circumstances. The protocol by which we have translocated tortoises has been successful by all reasonable short term measures. Below are several issues that we think should be considered for future translocation efforts of this species. Many of these issues are supported by data from this or other tortoise translocation studies, however some of these are opinions based on our experience with translocation, and the ecology of desert tortoises.

1. Tortoises tend to move great distances in the first season after translocation. They do not exhibit home ranges in their first season, but rather engage in more linear movement patterns. By the second season, translocated tortoises tend to establish home ranges. However, this “settling” process (Berry 1986) takes longer or may not be reached for tortoises translocated to atypical tortoise habitat (e.g., different vegetation). This may be important when selecting a translocation site, or when selecting where to release animals within a large site (Berry, 1986). Care should be taken to ensure that tortoises are not

translocated to areas adjacent to roads with heavy traffic, or to areas in which it is undesirable for translocated tortoises to wander into, unless those boundaries are fenced.

2. Tortoises should be released in spring or fall, avoiding the summer months (Cook 1983), as tortoises may be subjected to inhospitable thermal environments when released in the summer months. Animals that are initially released in inhospitable climates may fail to find adequate shelter from extreme environments, and therefore be subjected to lethal extremes (Cook, 1983). Tortoises should be well hydrated prior to release so that they have adequate water stores to sustain them though their initial acclimatization to their new habitat (Field 1999). Analyses of data from seasonal releases in Clark County, NV are pending, and should give insight into favorable seasons for releasing tortoises.

3. Care should be taken to disperse translocated animals, such that clumped groups do not cause increased aggressive social interactions, especially among male tortoises. We did not find evidence that translocation caused intensified aggressive interactions or disturbance of the social structure of wild tortoises in this study, however avoiding situations leading to these adverse behaviors seems warranted (Berry 1986), for example, when translocating tortoises in to areas of extraordinarily high densities.

4. Research on carrying capacity of desert tortoises in different habitats should help us understand how many animals can be moved to a given habitat

and under what conditions. The research should lead to an ability to model "carrying capacity" of a proposed translocation site, so that too many tortoises are not relocated into areas unable to support their numbers (Berry 1986).

5. At each of our study sites translocated tortoises produced the same number of eggs as resident animals. Thus, translocated animals may contribute to recruitment of hatchlings to the population. Adult female tortoises may be especially valuable members of the population (Doak et al. 1994) and would be a preferred demographic group when considering candidates for translocation (Berry 1986).

6. Tortoises translocated to areas near their native habitat may exhibit homing toward those areas (Corn pers comm., Berry 1986, SAIC 1993). It would be beneficial to translocate tortoises to areas that are distant from their original habitat, while maintaining the animals within genetically similar populations (Berry 1986, Reinert 1991).

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TABLES

TABLE 1.

Estimates of the biomass per square meter (mean ± SD) of annual vegetation at each site, and for each year. Cumulative precipitation (mm) for the Summer (May – September) and Winter (October – April) preceding the time the biomass was sampled. Precipitation data were taken from the nearest National Weather Service weather station for each site.

Year	Site	Green Biomass g/m²	Standing Dry Biomass g/m²	Winter Rain (mm)	Summer Rain (mm)
1997	BSV	4.3 ± 5.8	3.0 ± 4.4	36	33
1998	BSV	5.6 ± 4.8	0.3 ± 0.5	115	76
1999	BSV	0.1 ± 0.5	1.5 ± 2.3	45	54
1998	LM	6.4 ± 5.1	0.5 ± 1.9	117	34
1999	LM	3.7 ± 5.7	0.3 ± 1.2	44	95
1998	PAH	38.3 ± 23.3	1.8 ± 2.5	335	193
1999	PAH	Burned	Burned		
1998	SHIV	6.5 ± 1.5	1.2 ± 0.3	335	193
1999	SHIV	2.7 ± 4.2	1.0 ± 2.4	180	145
2000	SHIV	0.1 ± 0.1	0.4 ± 0.3	175	108
1999	SSM	1.4 ± 3.8	11.2 ± 18.2	136	150
2000	SSM	0.5 ± 0.4	0.2 ± 0.1	155	129

BSV – Bird Spring Valley, Nevada
LM – Lake Mead, Nevada
PAH – Pahcoon, Utah
SHIV – Shivwits, Utah
SSM – Sandstone Mountain

TABLE 2.

Frequency and use of plants by tortoises for the Bird Spring Valley and Lake Mead sites. Plants comprising less than 5% of relative frequency or percent use were combined into the last category labeled “Other”.

	Lake Mead		Bird Spring Valley	
Species	**Frequency (%)**	**Use(%)**	**Frequency (%)**	**Use (%)**
AMDU	47.7	32.3	0	12.1
LATR	12.2	11.1	12.6	24.4
EPSPP	11.2	30.1	0	25.5
KRPA	6.5	8	--	--
LYAN	--	--	4.9	9.2
GRSP	--	--	3.6	6.2
HIRI	6.3	5.3	--	--
TESP	6.3	2.2	--	--
CELA	--	--	6.5	0.4
YUSC	--	--	1.2	7.4
Other	9.7	11.1	21.1	14.6

Species codes are given in Appendix 1.

TABLE 3.

Frequency, cover, and use of plants by tortoises for the Sandstone Mountain, Shivwitts, and Pahcoon sites. Plants comprising less than 5% of relative frequency, or cover, or percent use were combined into the last category labeled “Other”.

	Sandstone mountain		Shivwitts		Pahcoon Release Site		Pahcoon (Animals)	
Species	**Frequency (%)**	**Use (%)**	**Frequency (%)**	**Use (%)**	**Frequency (%)**	**Use (%)**	**Frequency (%)**	**Use (%)**
CORA	25.5	39.6	34.7	33.7	19.7	44	34.8	44.0
GUSA	25.2	6.0	17.1	2.2	27.4	0	11.5	0
UNK	4.4	6.0	8.2	11.4	0	15.7	3.8	15.7
ARTR	--	--	--	--	44.1	0.8	0.1	0.8
PRFA	--	--	9.7	3.3	1.6	9.0	4.1	9.0
JUSC	--	--	1.8	20.1	2.4	9.7	1.5	9.7
ARFI	6.9	2.2	18.2	1.09	--	--	--	--
LATR	3.4	17.2	--	--	--	--	--	4.0
EPSPP	7.5	10.5	--	--	--	--	--	--
AMDU	9.2	6.0	--	--	--	--	--	--
THMO	--	--	--	--	0	2.0	7.1	2.0
QUTU		--	0	12.0	--	--	--	--
COME	--	--	--	--	3.9	0.8	0.1	0.8
Other	17.9	12.7	10.0	16.3	8.7	20.1	37	18.1

Species codes are given in Appendix 1.

TABLE 4.

Volume of plant species used for shade by tortoises at each site, and the average volume of each species used for shade at each study site. Asterisks indicate significant differences between the average shrub volume at the site and the average shrub volume used by tortoises for shade resources.

	LM		**BSV**		**SSM**		**SHIV**		**PAH**		**PAH (torts)**	
Species	**Vol (m3)**	**Use Vol (m3)**	**Vol (m3)**	**Use Vol (m3)**	**Vol (m3)**	**Use Vol (m3)**	**Vol (m3)**	**Use Vol (m3)**	**Vol (m3)**	**Use Vol (m3)**	**Vol (m3)**	**Use Vol (m3)**
AMDU	* 0.2	0.4	*0.1	0.5	0.2	0.2	--		--	--	--	--
ARFI	--	--	--	--	--	--	1.6	1.8	--	--	--	--
ARTR	--	--	--	--	--	--	--	--	0.9	4.8	3.2	4.8
CELA	--	--	* 0.1	0.3	--	--	--	--	--	--	--	--
COME	--	--	--	--	--	--	--	--	18.6	5.8	12.6	5.8
CORA	--	--	--	--	* 0.6	1.2	* 0.6	1.5	1.4	1.7	--	--
EPSPP	* 0.4	1	* 0.2	1.1	* 0.5	1.6	--	--	--	--	--	--
GRSP	--	--	* 0.4	9.7	--	--	--	--	--	--	--	--
GUSA	--	--	--	--	* 0.1	0.2	0.2	0.3	--	--	--	--
HIRI	* 0.3	0.5	--	--	--	--	--	--	--	--	--	--
JUSC	--	--	--	--	--	--	87.8	48.4	27.1	54.2	95.7	54.2
KRPA	1	1.01	--	--	--	--	--	--	--	--	--	--
LATR	3.6	3.4	* 1.1	4.5	24.7	17.4	--	--	--	--	12.9	15.8
LYAN	--	--	* 0.2	0.8	--	--	--	--	--	--	--	--
PRFA	--	--	--	--	--	--	* 1.3	10.5	5.2	9.7	4.7	9.7
QUTU	--	--	--	--	--	--	26	35.9	--	--	--	--
TESP	* 0.1	0.5	--	--	--	--	--	--	--	--	--	--
THMO	--	--	--	--	--	--	--	--	--	--	0.3	0.8
YUSC	--	--	* 0.9	4	--	--	--	--	--	--	--	--

LM = Lake Mead
BSV = Bird Spring Valley
SSM = Sandstone Mountain
SHIV = Shivwits
PAH = Pahcoon (release site)
PAH (torts) = Pahcoon transects at tortoises

Species codes are given in Appendix 1.

TABLE 5

Average number of eggs, and number of clutches produced by females at each study site for each year of the study. Animals within sites are summarized by treatment groups. The columns labeled CI indicate the 95% confidence interval for the mean number of eggs, and mean number of clutches.

Site	Year	Treatment	Num Eggs	CI	Num Clutches	CI	N
BSV	1997	Res	2.54	0.89	0.46	0.18	26
BSV	1998	Res	6.00	0.98	1.24	0.23	33
BSV	1999	Res	4.39	1.11	0.83	0.21	33
BSV	1997	T97	2.82	1.92	0.58	0.29	11
BSV	1998	T97	4.73	1.83	0.63	0.26	22
BSV	1999	T97	3.25	1.60	0.43	0.24	20
BSV	1998	T98	7.00	4.80	0.88	0.58	7
BSV	1999	T98	5.67	3.74	0.63	0.52	6
LM	1998	Res	2.80	1.90	1.00	0.62	5
LM	1999	Res	3.80	2.27	0.25	0.49	5
LM	1998	T98	3.21	2.11	0.64	0.39	14
LM	1999	T98	7.00	2.19	1.75	0.43	14
Area 31	1998	Res	7.50	2.39	1.40	0.48	10
Area 31	1999	Res	7.33	2.32	1.39	0.35	12
Area 31	2000	Res	5.00	1.03	0.92	0.38	10
SH/PAH	1998	T98	5.29	2.86	1.40	0.48	7
SH/PAH	1999	T98	5.60	7.46	0.83	0.79	5
SH/PAH	2000	T98	6.00	2.25	0.86	0.67	4
SSM	1999	T99	1.50	8.61	0.33	0.65	4
SSM	2000	T99	6.00	13.15	0.75	0.94	3

LM = Lake Mead
BSV = Bird Spring Valley
SSM = Sandstone Mountain
SHIV = Shivwits
PAH = Pahcoon (release site)

TABLE 6.

Site fidelity for resident and translocated tortoises at Nevada sites (Bird Spring Valley and Lake Mead) for 1997 - 1999. The grouping column indicates rows that differ in proportions of animals movements that were categorized as Constrained, Random, and Dispersed within sites and years.

Site	Year	Group	Constrained	Random	Dispersed	Grouping	P
BSV	1997	RES	32	19	0	A	0.0027
BSV	1997	T97	9	22	0	B	
BSV	1998	RES	47	6	0	A	<0.001
BSV	1998	T97	26	16	0	B	
BSV	1998	T98	3	10	0	C	
BSV	1999	RES	31	18	0	A	0.55
BSV	1999	T97	21	15	0	A	
BSV	1999	T98	5	6	0	A	
LM	1998	RES	7	2	4	A	0.167
LM	1988	T98	10	1	16	A	
LM	1999	RES	8	5	0	A	0.95
LM	1999	T98	15	9	0	A	

BSV = Bird Spring Valley
LM = Lake Mead

TABLE 7.

Site fidelity for resident and translocated tortoises at Utah sites (Pahcoon, Shivwits, and Sandstone Mountain) for 1998 - 2000. The grouping column indicates rows that differ in proportions of animals movements that were categorized as Constrained, Random, and Dispersed.

Site	Year	Group	Constrained	Random	Dispersed	Grouping	P
PAH	1998	T98	0	7	4	A	0.01
PAH	1999	T98	5	6	2	B	
PAH	2000	T98	6	2	2	C	
SHIV	1998	T98	1	11	6	A	0.001
SHIV	1999	T98	8	5	2	B	
SHIV	2000	T98	11	3	2	C	
SSM	1999	T99	11	5	1	A	0.40
SSM	2000	T99	12	3	0	A	

PAH = Pahcoon
SHIV = Shviwits
SSM = Sandstone Mountain

FIGURES

FIG. 1.

The study sites are indicated by the black circles on the map of the southwestern United States. The site southwest of Las Vegas, Nevada was Bird Spring Valley. The Lake Mead site on the northern end of Lake Mead. In southwest Utah the Pahcoon and Shivwits sites are the two sites farthest to the west, which appear to be a single location at this scale, and the Sandstone Mountain site is furthest to the east. The center site in Utah is Area 31, where egg production for resident animals was measured for comparisons with translocated animals in Utah.

FIG. 2.

Means of maximum distances moved (m) by tortoises at the Lake Mead (top panel) and Bird Spring Valley (bottom panel) sites. Error bars are 1 SE of the mean. Residents are indicated by black filled bars, animals translocated in 1997 are indicated by white bars, and animals translocated in 1998 are represented by gray bars.

FIG. 3.

Means of start-to-end distances moved (m) by tortoises at the Lake Mead (top panel) and Bird Spring Valley (bottom panel) sites. Error bars are 1 SE of the mean. Residents are indicated by black filled bars, animals translocated in 1997 are indicated by white bars, and animals translocated in 1998 are represented by gray bars.

Fig. 4.

Means of maximum distances moved (m) (top panel) and start-to-end distances moved (m) (bottom panel) by tortoises at the Pahcoon, Shivwits, and Sandstone Mountain study sites. Error bars are 1 SE of the mean. Pahcoon is indicated by the dark gray filled bars, Shivwits is indicated by the white bars, and Sandstone Mountain is represented by the light gray filled bars.

Fig. 5.

Leverage residual plot of maximum distances moved for animals at each study site as a function of years since translocation. The gray bar with solid black line near the bottom of the graph indicates the average maximum distance and the standard error of that response over three years for resident animals at the Lake Mead and Bird Spring Valley sites combined. Dashed lines indicate the 95% confidence limit to the linear regression line. Significance for the relationship is indicated by the P value in the upper right corner of the graph.

Fig. 6.

Leverage residual plot of start-to-end distances moved by animals at each study site as a function of years since translocation. The gray bar with sold black line near the bottom of the graph indicates the average start to end distance and standard error of that response over three years for resident animals at the Lake

Mead and Bird Spring Valley sites combined. Dashed lines indicate the 95% confidence limit to the linear regression line. Significance for the relationship is indicated by the P value in the upper right corner of the graph.

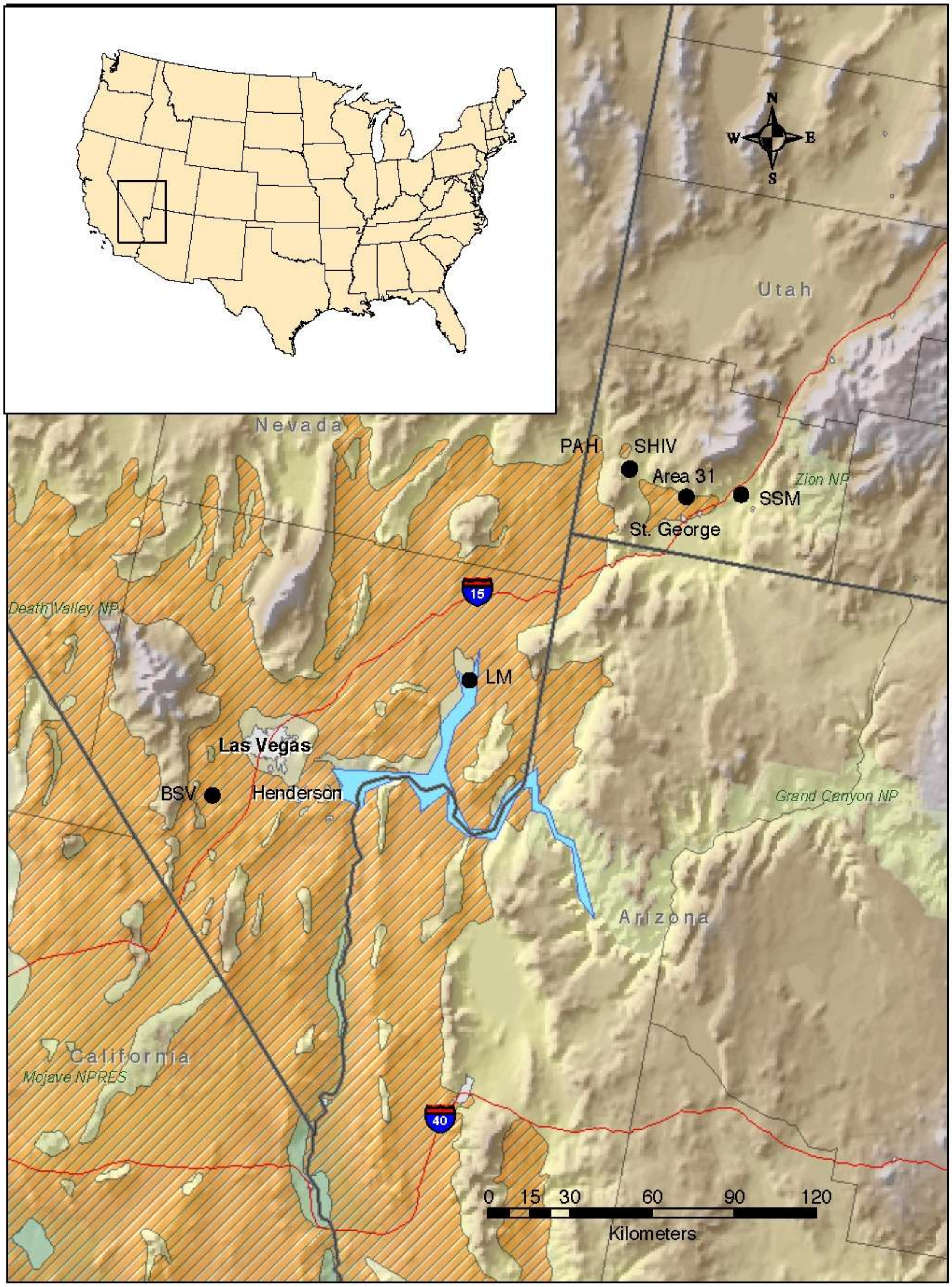
Fig. 7.

Area consumption for the Bird Spring Valley site is given by a 95% adaptive kernel analysis of the release points for all tortoises released in 1997 at Bird Spring Valley (solid black boundary). The blue boundary is the 95% kernel analysis including all points during the year for the same animals at the end of 1997. The black dashed boundary is the 95% kernel analysis for all points at the end of the 1998 season.

Fig. 8.

Area consumption for the Shivwits site is given by a 95% adaptive kernel analysis of the release points for all tortoises released in 1998 at Shivwits (black boundary). The blue boundary is the 95% kernel analysis including all points during the year for the same animals at the end of 1998. The black dashed boundary is the 95% kernel analysis for all points at the end of the 1999 season

Fig. 1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W
E
S
Utah
Nevada
PAH
SHIV
Area 31
SSM
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St. George
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Death Valley NP
LM
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BSV
Henderson
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Arizona
California
Mojave NPRES
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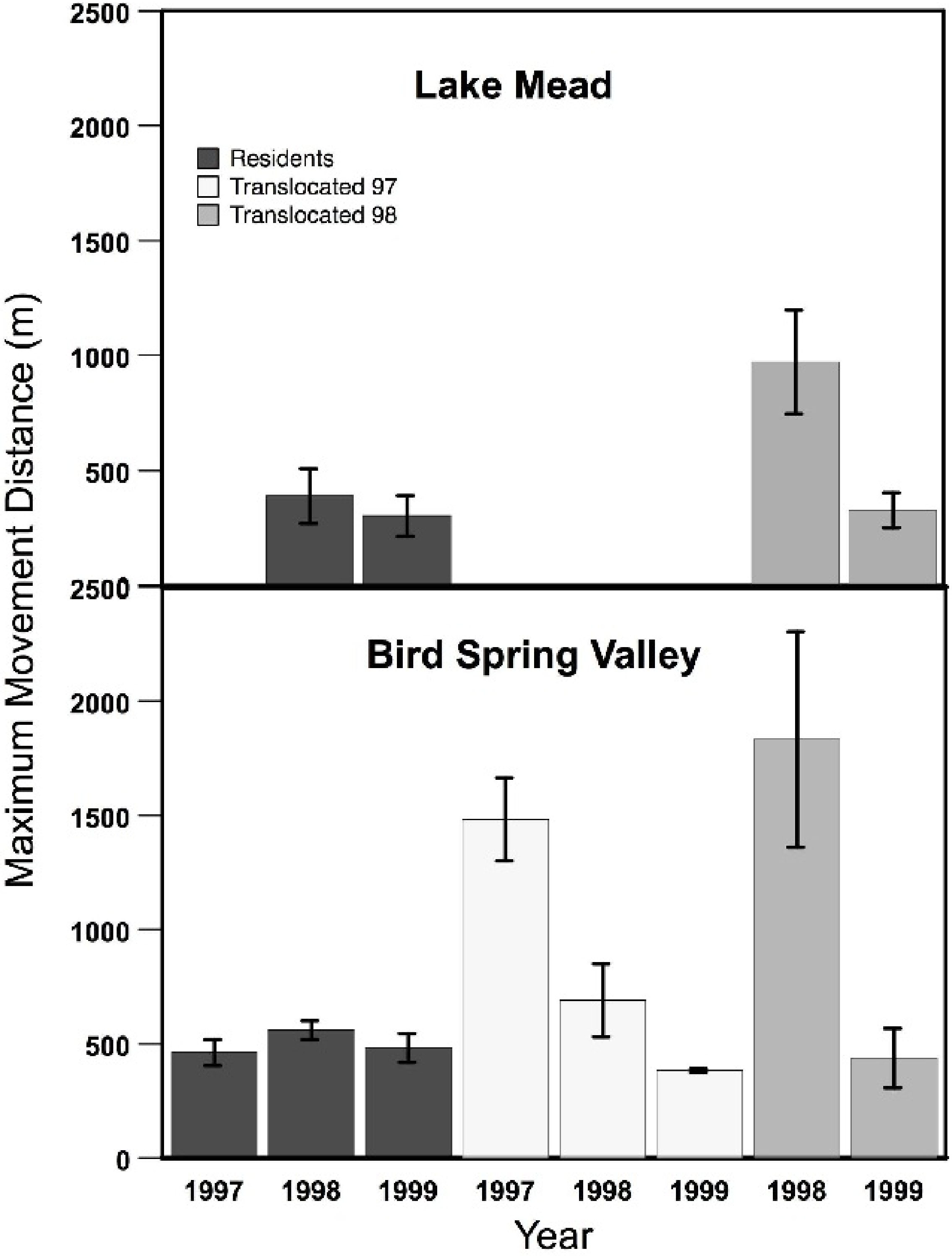
0
15
30
60
90
120
Kilometers

Fig. 2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Residents
Translocated 97
Translocated 98
Bird Spring Valley
Maximum Movement Distance (m)
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2000
1500
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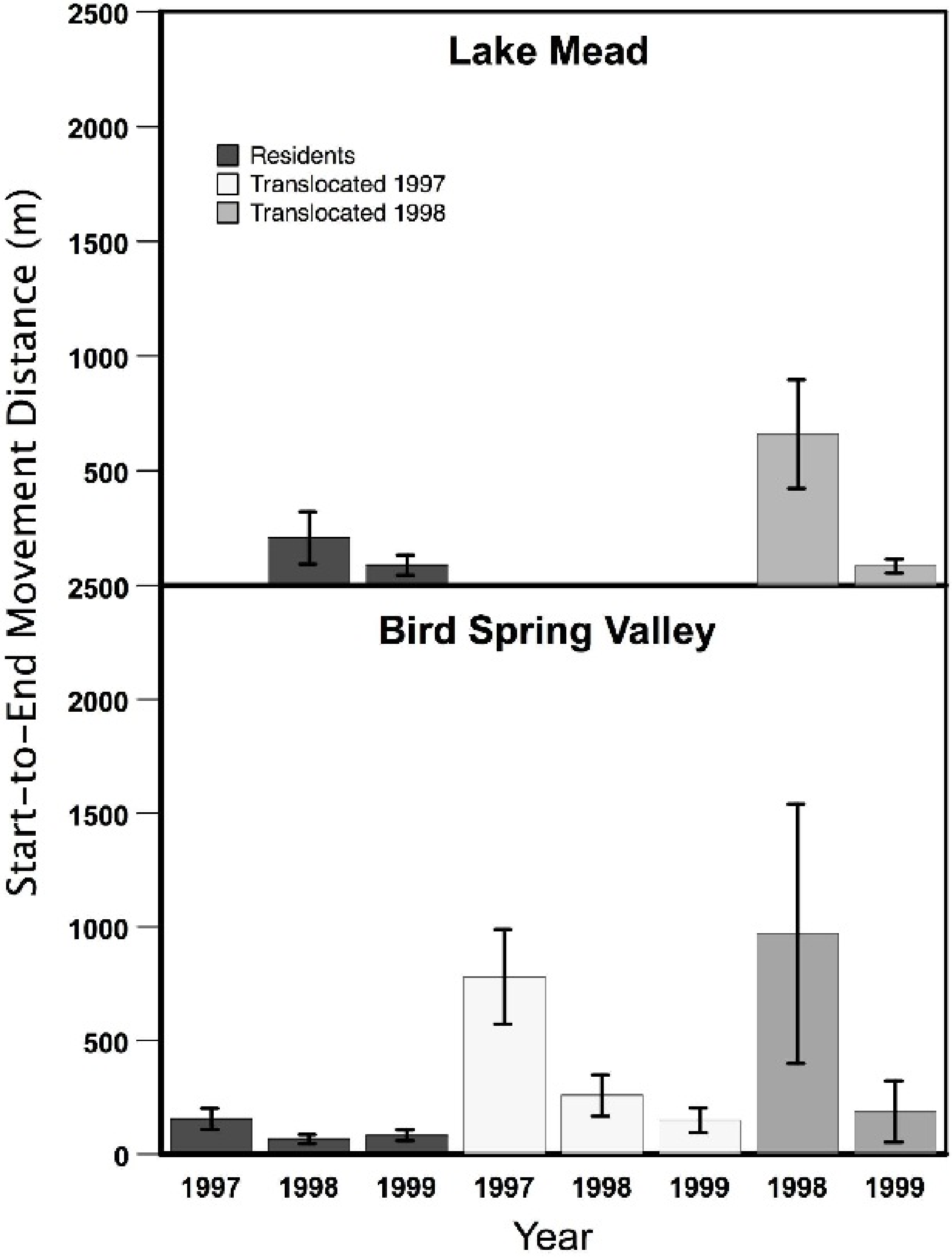
1998
1999
Year

Fig. 3


Lake Mead
Bird Spring Valley
Residents
Translocated 1997
Translocated 1998
Start-to-End Movement Distance (m)
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2000
1500
1000
500
0
1997
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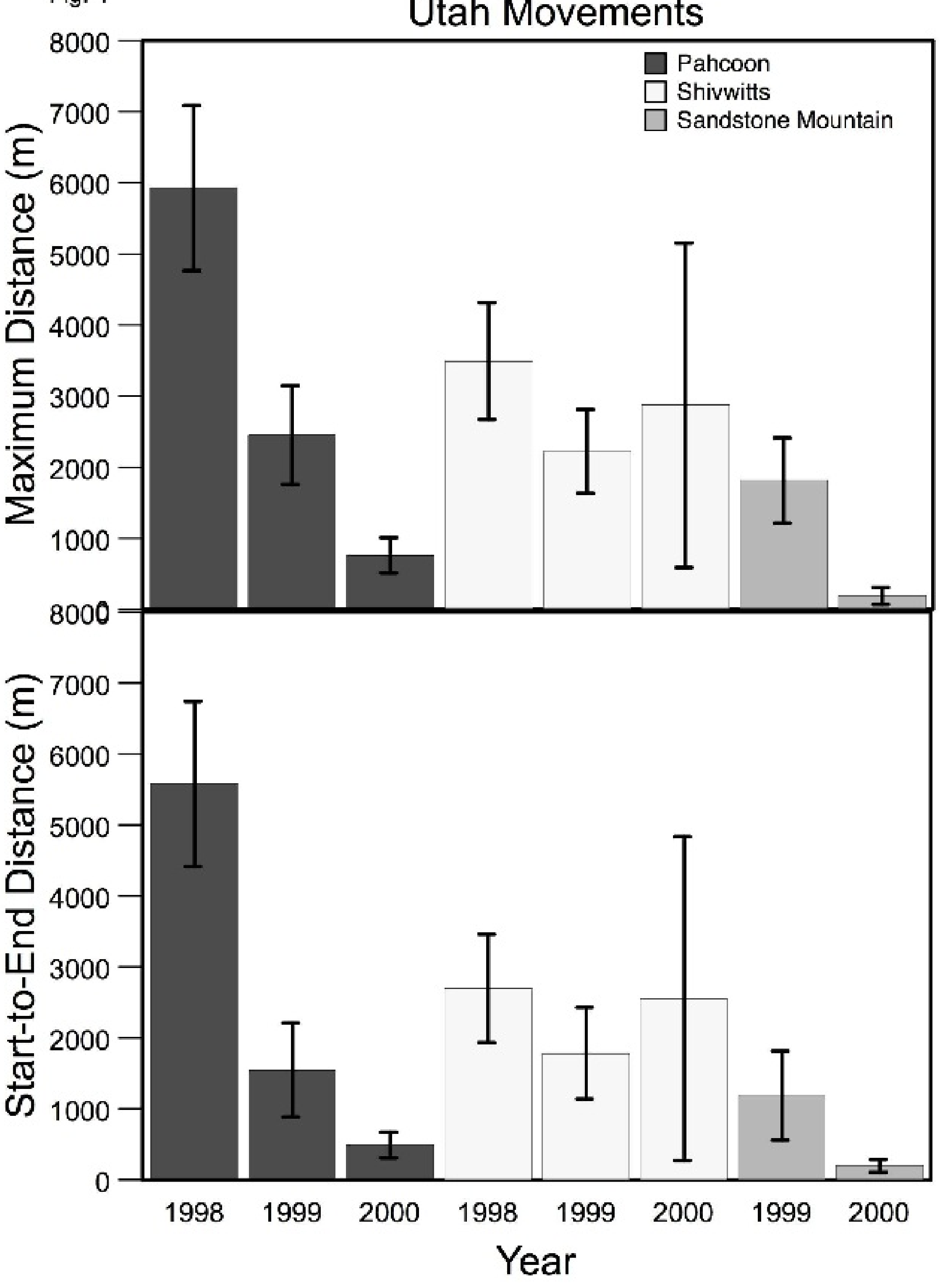
1999
1998
1999
Year

Fig. 4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Pahcoon
Shivwitts
Sandstone Mountain
Maximum Distance (m)
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7000
6000
5000
4000
3000
2000
1000
0
Start-to-End Distance (m)
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7000
6000
5000
4000
3000
2000
1000
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1998
1999
2000
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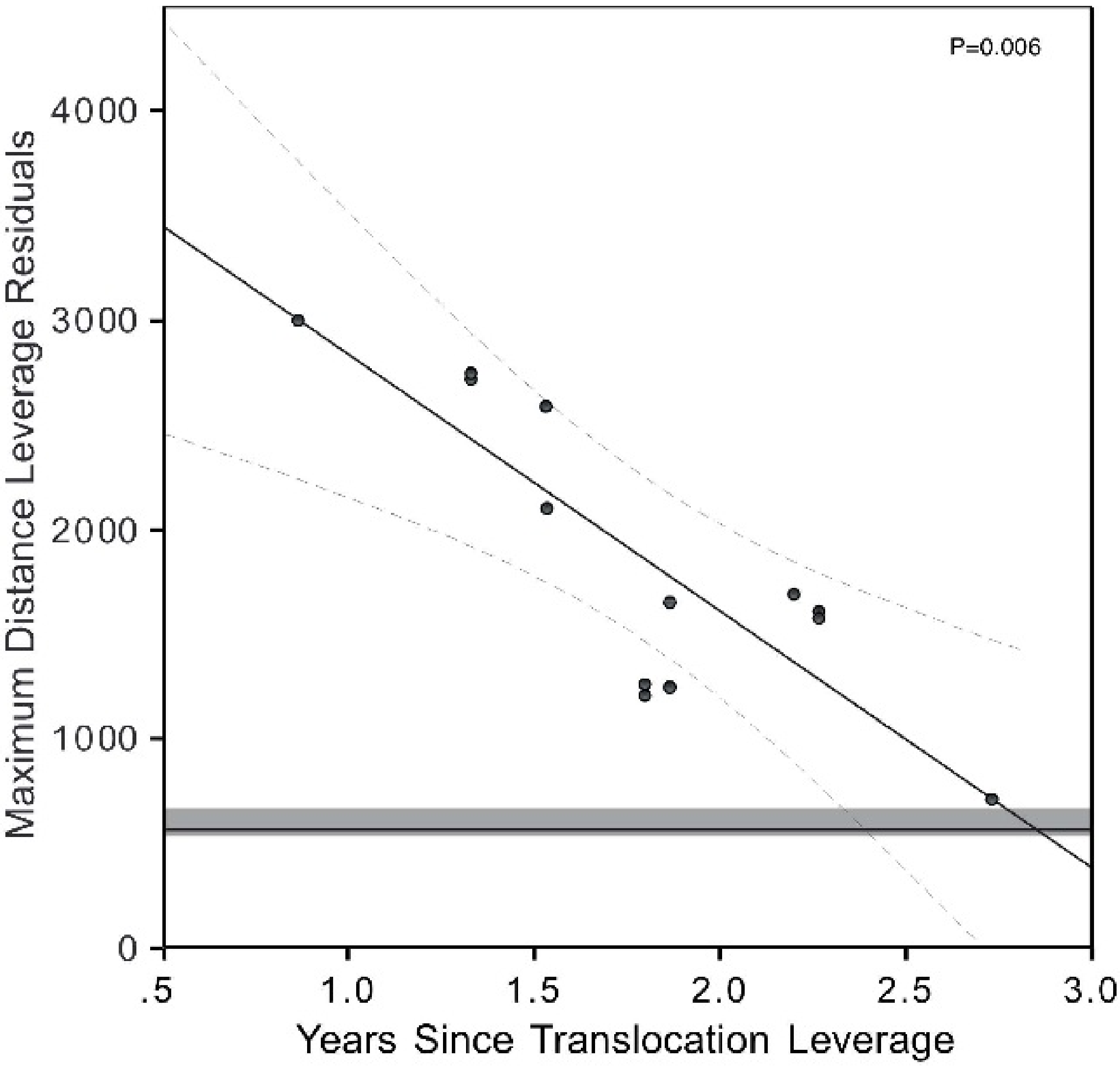
1999
2000
Year

Fig. 5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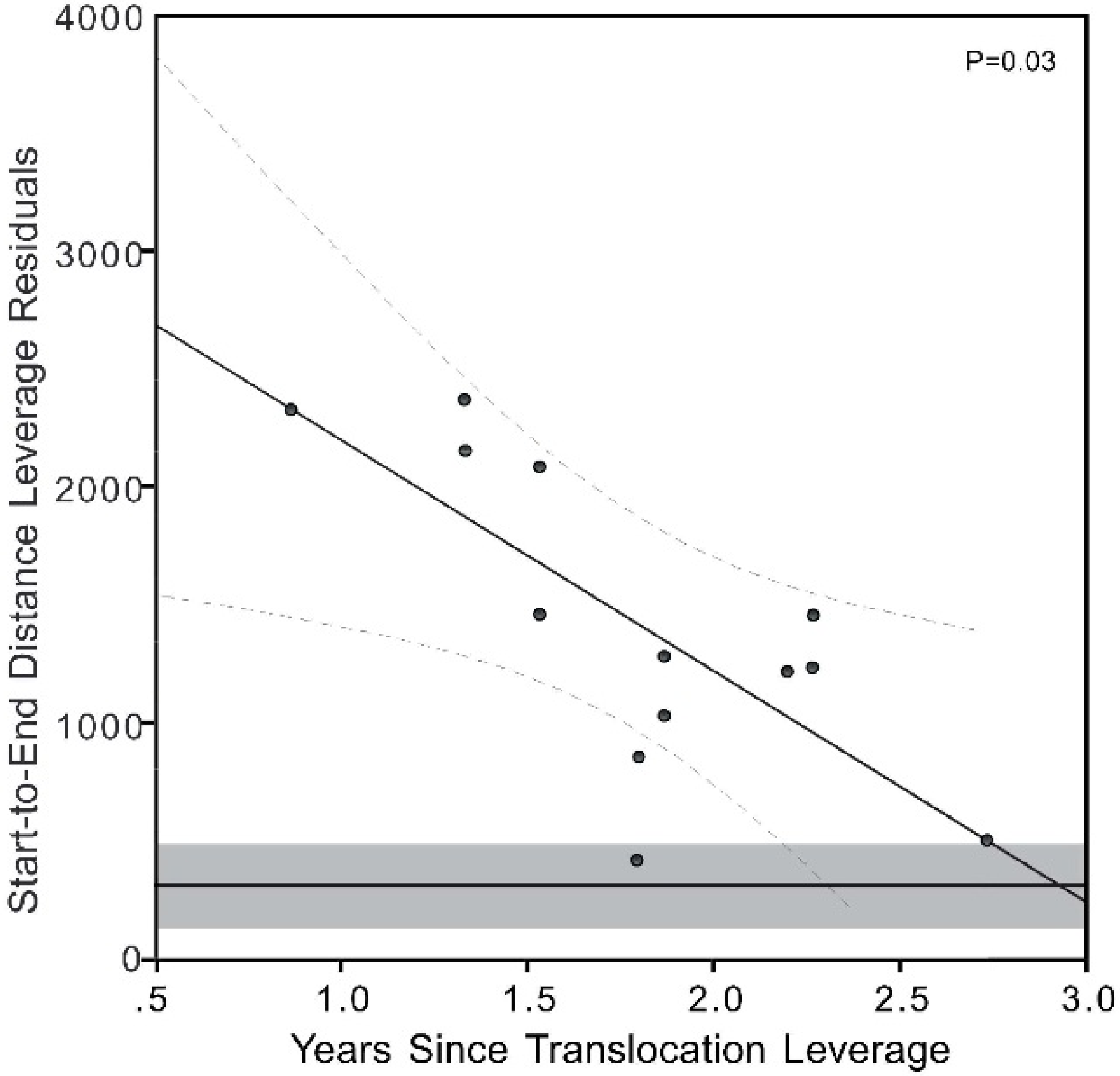
2.5
3.0
Years Since Translocation Leverage

Fig._6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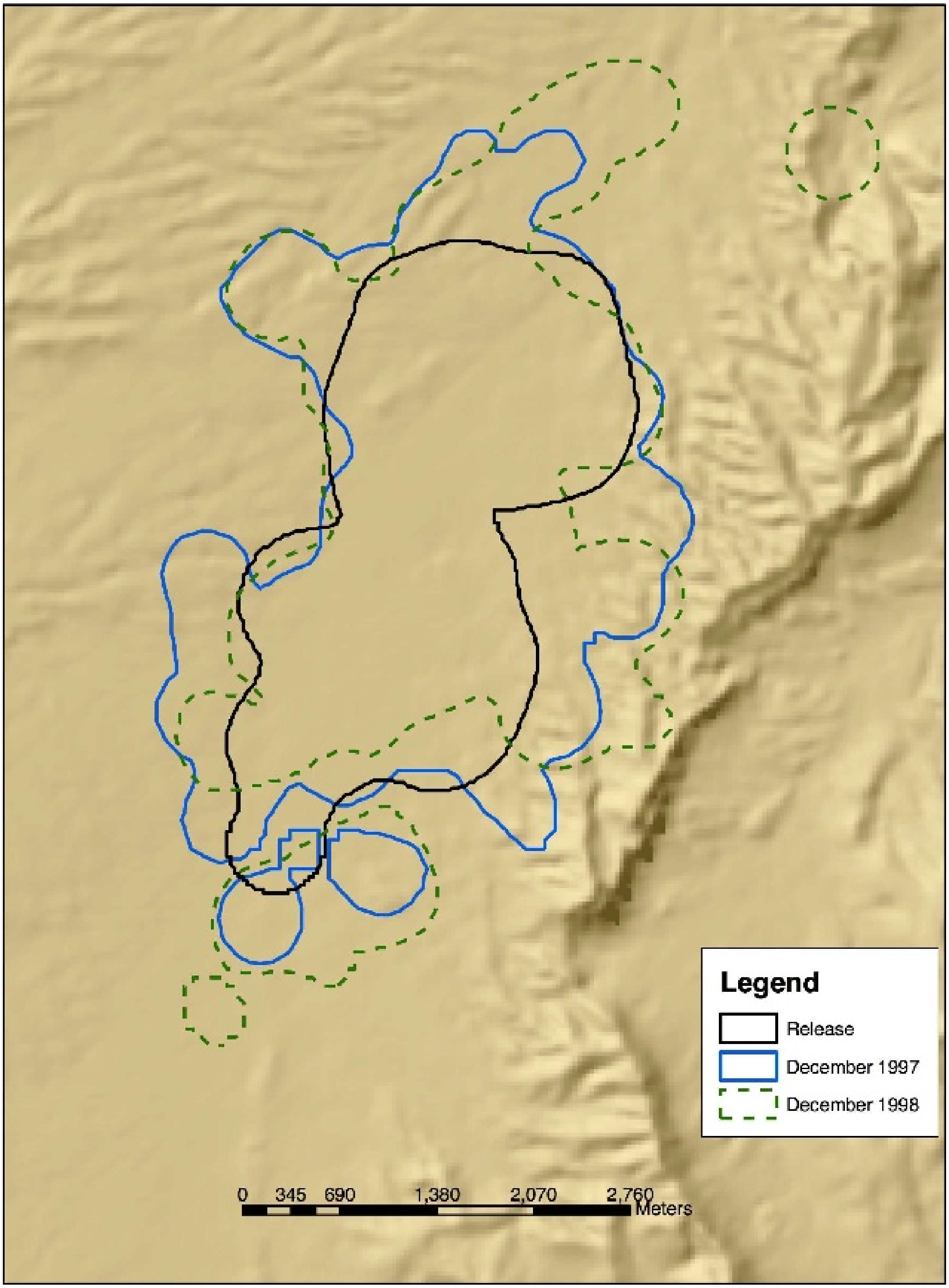
2.0
2.5
3.0
Years Since Translocation Leverage

Fig. 7


Legend
Release
December 1997
December 1998
0
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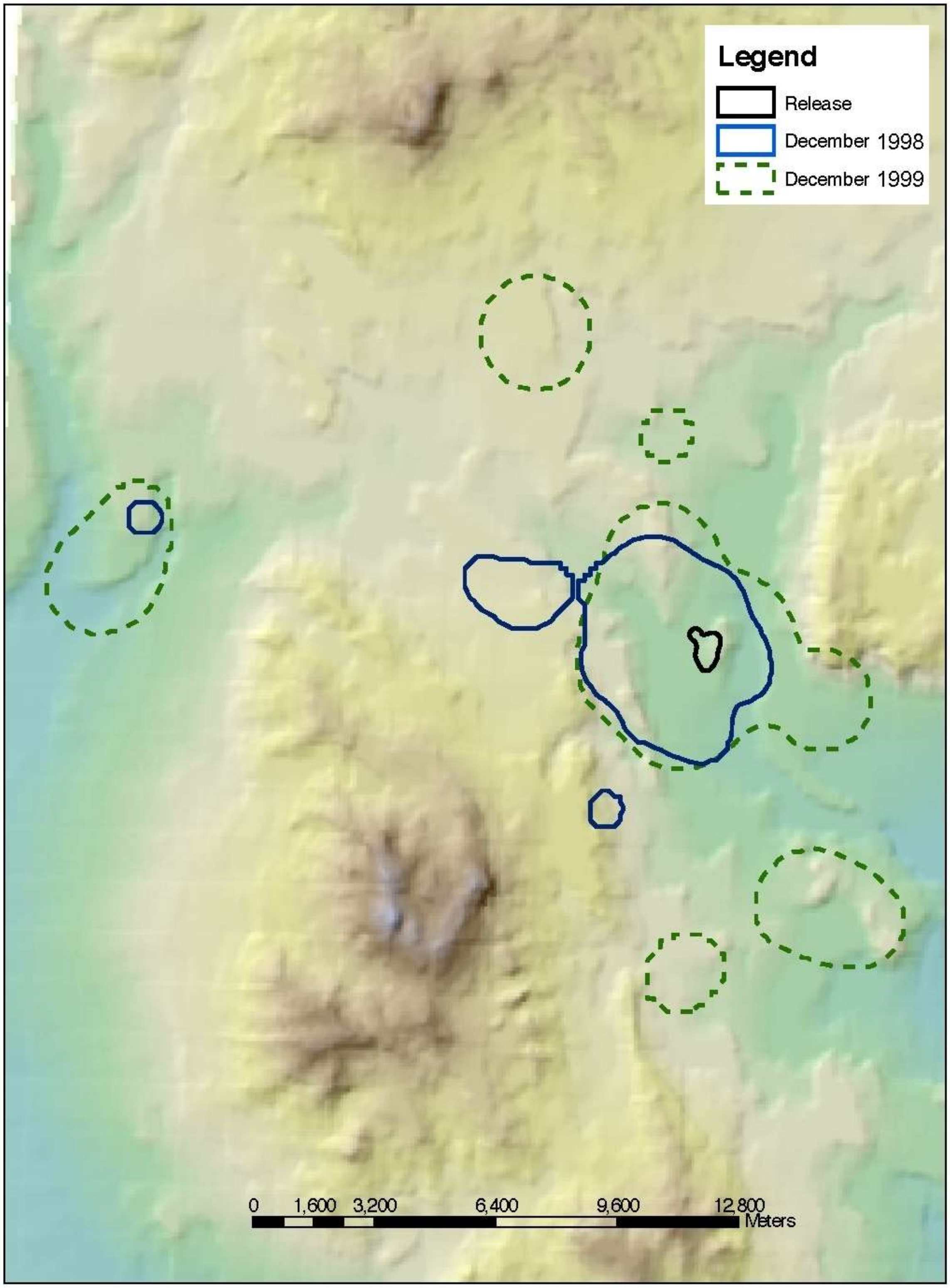
690
1,380
2,070
2,760
Meters

Fig. 8


Legend
Release
December 1998
December 1999
0
1,600
3,200
6,400
9,600
12,800
Meters

APPENDICES

APPENDIX 1.

Perennial plant code translations to species and common name, and the sites at which they occurred. The Pahcoon release site is given as PAH, and the transects sampled where tortoises were located at the end of the study are given as Pah B.

Species Code	Scientific Name	Common Name	Sites					
ACSP	*Acamptopappus spaerocepahlus*	Goldenhead		BSV				
AMDU	*Ambrosia dumosa*	White bursage	LM	BSV	SSM			Pah B
AMER	*Ambrosia eriocentra*	Wooly bursage		BSV				Pah B
ARFI	*Artemisia filifolia*	Sand sage			SSM	SHIV		Pah B
ARTR	*Artemisia tridentata*	Basin Big Sagebrush					PAH	Pah B
ATHY	*Atriplex hymenelytra*	Desert Holly	LM					
ATTR	*Atriplex truncata*	Wedge scale	LM					
BAMU	*Baileya multiradiata*	Wild marigold		BSV				
CELA	*Ceratoides lanata*	Winter Fat		BSV				
CHLI	*Chilopsis linearis*	Desert Willow						Pah B
CHOLLA	*Opuntia acanthocarpa/ Opuntia spinosior*	Cholla species			SSM			Pah B
CHNA	*Chrysothamnus nauseosus*	Rubber rabbitbrush		BSVB				
CHPA	*Chrysothamnus paniculatus*	Black Banded Rabbitbrush			SSM	SHIV		Pah B
CHSPP	*Chrysothamnus species*	Rabbitbrush species			SSM	SHIV	PAH	Pah B
CHVI	*Chrysothamnus viscidiflorus*	Sticky-leaved rabbitbrush		BSV				

Species Code	**Scientific Name**	**Common Name**	**Sites**					
COME	*Cowania mexicana*	Cliffrose			SSM		PAH	Pah B
CORA	*Coleogyne ramossisima*	Blackbruch		BSV	SSM	SHIV	PAH	
ECAN	*Echinocactus acanthodes*	Compass Barrel Cactus						Pah B
ECEN	*Echinocactus engelmanni*	Engelmann hedge-hog						Pah B
ENFA	*Encelia farinosa*	brittle bush				SHIV		
ENFR	*Encelia frutescens*	Rayless encelia		BSV				Pah B
EPCA	*Ephedra californica*	California Joint fir	LM	BSV				
EPNE	*Ephedra nevadensis*	Nevada joint fir	LM	BSV				
EPSPP	*Ephedra species*	Joint fir species			SSM	SHIV		Pah B
ERAN	*Eriodictyon angustifolium*	Narrow-leafed Yerba Santa						Pah B
ERFA	*Eriogonum fasciculatum*	California buckwheat		BSV		SHIV		Pah B
ERIN	*Eriogonum inflatum*	Desert trumpet		BSV				Pah B
ERTR	*Eriogonum trichopes*	Yellow trumpet		BSV				
ERWR	*Eriogonum wrightii*	Wrights eriogonum			SSM			
GRSP	*Grayia spinosa*	Spiny hop-sage		BSV				Pah B
GUSA	*Gutierriezia sarothrae*	Broom matchweed		BSV	SSM	SHIV	PAH	Pah B
HASP	*Haplopappus spinulosus*	Goldenweed		BSV				
HIRI	*Hilaria rigida*	Big galetta	LM	BSV	SSM			Pah B
HYSA	*Hymenoclia salsola*	Cheese-bush		BSV	SSM			Pah B
ISTE	*Isocoma tenuisecta*	Burro weed			SSM			
JUOS	*Juniperus osteosperma*	Utah juniper			SSM			
JUSC	*Juniperus scopulorum*	Rocky Mountain juniper				SHIV	PAH	Pah B

Species Code	Scientific Name	Common Name	Sites					
KOSP	*Koeberlinia spinosa*	Allthorn						Pah B
KRGR	*Krameria grayi*	White ratany		BSV				Pah B
KRPA	*Krameria parvifolia*	Little leaved ratany	LM	BSV	SSM			Pah B
KRSPP	*Krameria species*	Ratany speces			SSM			Pah B
LATR	*Larrea tridentata*	Creosote bush	LM	BSV	SSM			Pah B
LUEX	*Lupine excubitus*	Interior Bush Lupine				SHIV		
LUSP	*Lupinus sparsiflorus*	Coulter's lupine						Pah B
LYAN	*Lycium andersonii*	Narrow–leaved thornbush		BSV				
LYCO	*Lycium cooperi*	Peach-thorn		BSV				
LYSPP	*Lycium species*	Wolfberry species			SSM			
MASPP	*Malocothrix species*	e.g. Desert dandelion		BSV				
MESP	*Mendora spinescens*	Spiny monodora		BSV				
NADE	*Nada demissum*	Purple Mat	LM					
OPAC	*Opuntia acanthocarpa*	Deer horn cactus	LM		SSM			Pah B
OPBA	*Opuntia basilaris*	Beavertail Cactus		BSV				Pah B
OPEC	*Opuntia echinocarpa*	Thorny-fruited cactus		BSV				Pah B
OPER	*Opuntia erinacea*					SHIV		
OPPH	*Opuntia phaeacantha*	Desert prickly pear			SSM			Pah B
OPRA	*Opuntia ramossisima*	Pencil Cholla		BSV				
OPSPP	*Opuntia species*	Prickly pear species			SSM	SHIV		Pah B
ORHY	*Oryzopsus hymenoides*	Indian rice grass		BSV	SSM			Pah B
PASPP	*Parosela speices*	smoketree						Pah B

Species Code	Scientific Name	Common Name	Sites					
PIMO	*Pinus monphylla*					SHIV		Pah B
PRFA	*Prunus fasciculata*	Desert almond			SSM	SHIV	PAH	Pah B
PRSPP	*Prosopis species*	Mesquite species			SSM			Pah B
PSFR	*Psorothamnus fremontii*	Indigo Bush	LM	BSV	SSM			Pah B
QUTU	*Quercus turbinella*					SHIV		Pah B
RHTR	*Rhus trilobata*	Skunkbush sumac			SSM			
SADO	*Salvia dorri*	Purple desert sage		BSV				
SAMO	*Salvia mojavensis*	Mojave Sage		BSV b				
SAME	*Salazaria mexicana*	Bladder sage						Pah B
SPAM	*Sphaeralcea ambigua*	Desert mallow	LM	BSV	SSM			Pah B
SPCR	*Sporobolus cryptandrus*	Sand dropseed		BSV				
TARA	*Tamarix ramosissima*	Salt cedar	LM					
TESP	*Tetradymia spinosa*	Cotton Thorn	LM					
THMO	*Thamnosma montana*	Mojave desertrue						Pah B
UNK	*unknown*	unknown			SSM	SHIV	PAH	Pah B
VUOC	*Vulpia octoflora*	Sixweeks fescue		BSV				
XYTO	*Xylorhiza tortifolia*	Desert Aster		BSV				
YUBA	*Yucca baccata*	Banana Yucca						Pah B
YUBR	*Yucca brevifolia*	Joshua tree		BSV				Pah B
YUSC	*Yucca schidigera*	Mojave Yucca		BSV				
YUSPP	*Yucca species*	Yucca species			SSM			Pah B

Chapter 2. Hibernation in the Mojave Desert Tortoise: Hibernation Temperatures, Timing, and Environment

ABSTRACT

The purpose of this research was (1) to examine the onset, duration, and termination of hibernation over several years and a broad geographic area, (2) to record the temperatures experienced by tortoises during winter hibernation, and (3) evaluate hypotheses testing mechanisms underpinning the observed patterns. The timing of hibernation by desert tortoises differed among sites and years. Acute environmental cues did not appear to influence the timing of the hibernation period. Tortoises at the sites entered hibernation over as many as 44 days, emerged from hibernation over as many as 49 days**.** This range of variation in the timing of hibernation is greater than the duration of most of the mechanisms hypothesized to cue hibernation. There was a trend toward earlier initiation and a longer hibernation period at sites that were higher in elevation and generally cooler. The emergence date among the sites was generally similar. While the climate and the subsequent timing of hibernation differed among sites, the average temperatures experienced by tortoises while hibernating differed by only about five degrees from the coldest site to the warmest site. Thus, tortoises appear to choose hibernacula that have remarkably similar thermal characteristics.

INTRODUCTION

Desert tortoises (*Gopherus agassizii*) are distributed in desert and subtropical regions of the southwestern United States and northern Mexico (Germano et al. 1994). The northern extent of this distribution is a temperate zone where some environmental temperatures in winter can be inhospitable or even lethal to desert tortoises. Tortoises avoid cold temperatures in the winter by using underground cover sites (hibernacula), which generally consist of burrows (excavated in soil) or dens (natural rocky caves) (Burge 1977, Bulova 1994). Hibernacula generally have higher temperatures than the open environment during the winter, and provide substantial buffering from the daily temperature fluctuations present in the environment. Thus, hibernacula provide tortoises with protection from potentially lethal temperatures in winter.

Research on the hibernation of reptiles has focused on snakes (Drda 1968, Brown et al. 1974, Sexton and Hunt 1980, Costanzo 1986, Burger et al. 1988, Macartney et al. 1989, Weatherhead 1989, Graves and Duvall 1990), lizards (Garrick 1972, Etheridge et al. 1983) and aquatic turtles (Claussen et al. 1991), but few studies have dealt with tortoises (Vaughan 1984, Bailey et al. 1995, and Rautenstrauch et al. 1998). Nevertheless, understanding the timing of hibernation of desert tortoises could have important management implications for this sensitive species.

In the northeastern extent of their range, tortoises may hibernate for up to six continuous months (Woodbury and Hardy 1948, Bury et al. 1994). Little is known about the mechanisms cueing the onset and termination of hibernation behavior. Potential cues include reduced day length/photoperiod, cooler environmental temperatures, reduced forage availability and timing of precipitation events (Gregory 1982). Hibernation is thought to facilitate a reduction of metabolism during a time of the year with few resources. Tortoises, like other ectotherms, may be able to conserve energy by hibernating, as there is a concomitant reduction of metabolism with decreased body temperatures (Gregory 1982, Espinoza and Tracy 1997). Tortoises may further reduce their metabolism by entering a torpor-like state (Gregory 1982). This could allow tortoises to conserve energy during seasons with essentially no food resources. Literature reporting endogenous mechanisms cueing hibernation is largely unavailable, but observations of behaviors such as declining appetite, shelter-seeking behavior, and changing susceptibility to external cues suggest that the hibernation of some reptiles is possibly influenced by endogenous rhythms (Gregory 1982).

The purpose of this research was (1) to examine the onset, duration, and termination of hibernation over several years and a broad geographic area, (2) to record the temperatures experienced by tortoises during winter hibernation, and (3) evaluate hypotheses testing mechanisms underpinning the observed patterns.

MATERIALS AND METHODS

STUDY SITES

We studied hibernation in tortoises at four sites in the northeastern Mojave desert. The sites were located in the Mojave desert scrub biome (Turner 1982). The City Creek Site (CC) was located in Washington County north of St. George, Utah (37.1472 N 113.5868 W, Fig. 1), and ranged in elevation from 975 m to 1067 m, with highly variable topography: flat areas, dry washes up to 2 m deep, dunes, rocky cliffs and steep hills. The predominant substrate is red Navajo sandstone interspersed with ancient lava flows, sand dunes and cryptobiotic soils (Esque 1994). The Littlefield Site (LF) was located in Mohave County, north of Littlefield, Arizona (36.9252 N 113.9071 W, Fig. 1), and ranged in elevation from 576 m to 622 m. The topography was generally flat (2 to 5% slope), with numerous dry washes up to 3 m deep (Esque 1994). The substrate was shallow sandy/gravelly loam up to 0.6 m deep with an underlying calcium carbonate (caliche) hardpan layer. The Lake Mead site (LM) was located in Clark County, Nevada (36.4839 N; 114.3492 W, Fig. 1). The site was at the northern end (Overton arm) of the Lake Mead National Recreation Area, near Overton, NV. The site elevation ranged from lake level (approximately 325 m) to 597 m. The site consisted of the top and steep cliff sides of a mesa bordered on three sides by water. The soil consisted of coarse alluvium consolidated by calcium carbonate, interspersed with patches of windblown sand. The Bird Spring Valley site (BSV) was also in Clark County, Nevada (BSV 35.9727 N; 115.3363 W, Fig. 1). The valley was an extensive bajada ranging from 900 m to 1300 m in elevation and was of relatively even terrain with shallow arroyos lined by occasional caliche caves. The substrate was sandy/gravelly loam up to 0.75 m deep with an underlying hardpan layer composed of caliche . Mountainous peaks bordered Bird Spring Valley to both the east and west.

TORTOISE BODY TEMPERATURES

All experiments using animals were conducted according to IACUC guidelines (University of Nevada IACUC Protocols A95/96-19, A98/99-19, A98/99-29, and A95/96-28).

We used miniature data loggers (Stowaway #STEB16, Onset Computer Corporation, Pocasset, Ma) to collect body temperature data during hibernation of wild desert tortoises at the City Creek and Littlefield sites. The data loggers were 26.5 grams and came encased in a plastic rectangular housing (4.6 x 4.8 x 1.5 cm). The instruments were calibrated in water baths at temperatures over a range of 0 to 45 °C before, and again after placing them in the field. The dataloggers were programmed to record temperatures once per hour. For protection from the environment, the data loggers were wrapped in a layer of paper and covered with a layer of duct tape followed by a coating of epoxy (which served as weather-proofing). Each data logger was attached with 5-minute epoxy gel to a location on the carapace of a tortoise. The attachment location was chosen to reduce the restriction of movement of the animal within cover sites. On females, data loggers were placed on the anterior half of the carapace to avoid potential interference during copulation. Data loggers were placed on animals prior to the expected onset of hibernation and were removed within several weeks after emergence. The temperatures recorded by the data loggers at these two sites were the temperatures measured inside the plastic casing of the data loggers, not body temperatures of the tortoises. Nevertheless, the data from the loggers can be used to discern the timing of hibernation (see below), and temperatures of the loggers were likely similar to body temperatures while the animals were in hibernacula (Gregory 1982).

Body temperatures of tortoises at the Lake Mead and Bird Spring Valley sites were measured using StowAwayTM TidbiT^{TM} temperature data loggers (Onset Computer Corporation, Pocasset, Massachusetts), customized by Onset from their standard design (TBICU108, –20°C to +70°C). The data loggers were 25 mm in diameter, 14 mm thick and weighed approximately 15 g. The data loggers had a weather-resistant thermistor at the end of a 150 mm wire, which was affixed, using fast setting glue and silicone, between the tail and the carapace of the tortoise (Nussear et al. 2002). This location has been shown to approximate cloacal temperatures of desert tortoises (Nussear et al. 2002).

TIMING OF HIBERNATION

We recorded data on hibernating tortoises over the course of four winters (1995 - 1996, 1996 - 1997, 1997 - 1998 and 1998 - 1999) at the City Creek and Littlefield sites, and for one winter (1998 - 1999) at the Lake Mead and Bird Spring Valley sites. A summary of the number of tortoises studied at each site and year is given in Appendix 1.

The onset, duration, and termination of hibernation were interpreted from graphs of body temperatures by locating the date when the amplitude of the daily fluctuations became noticeably reduced (onset, Fig. 2a) or increased (termination, Fig. 2a). The accuracy of this interpretation was verified by weekly observations of the tortoises in the field. Temperatures of the data loggers at the City Creek and Littlefield study sites were clearly different when the tortoises were in and out of burrows (Fig. 2). We defined onset of hibernation as the Julian date after which a tortoise did not emerge from its hibernaculum for at least 14 days. Likewise, the termination of hibernation was defined as the Julian date when a tortoise emerged from the hibernaculum, without returning for at least 14 days. The "14-day" criterion allowed for a consistent quantification of the onset and termination dates for animals that had false onsets or brief emergences during hibernation. These criteria are similar to those used by Bailey et al. (1995). Some data loggers became overloaded with data and stopped recording temperatures before the tortoise emerged from hibernation. Thus, for some individuals durations of hibernation could not be calculated, although hibernation start dates were recorded.

We defined "average hibernation temperature" as the mean temperature of all measurements while an animal was hibernating. The "mid-hibernation temperature" was defined as the average temperature during the week of the winter solstice (i.e. week 51), and the "minimum temperature" as the lowest temperature experienced by the animal at any time during the hibernation period.

We compared Julian dates of onset, termination, and duration of hibernation, and the mean, minimum, and mid-hibernation temperatures using an Analysis of Variance (ANOVA) in JMP 5.0 (SAS Institute, 2003). Repeated measurements of animals were accounted for by using a nested, split-plot design with tortoises nested within site in order to allow for independent contrast analyses of the interaction term (SAS Pers. Comm.). Multiple comparisons to discern differences within significant effects were conducted using Tukey's-HSD.

Analysis of days before hibernation

To examine aspects of the behavior of tortoises prior to entering hibernation, we analyzed the number of hours that individuals at the Bird Spring Valley site spent at body temperatures above 30 ºC in the 30-day period prior to hibernation. We included the hours per day that operative temperatures at the same study site were above 30 ºC as a covariate. This analysis was conducted separately for each animal (N = 7).

Thermal Buffering Categories

Cover sites were classified by the degree of thermal buffering that they provided as interpreted by the daily and biweekly patterns in body temperature. The greatest buffering was represented by a pattern in which the body temperature was nearly constant, with difference of less than 1 ºC between the daily maximum and daily minimum temperatures. In addition, the average of the differences of absolute minimum and maximum temperatures for all successive 14 day periods throughout the hibernation period was < 1.5 ºC (Fig. 2a). Less buffering resulted in body temperatures that still retained differences of daily maximum and minimum temperatures of less than 1 ºC. However the body temperatures were influenced by local weather patterns when examined over longer time periods. In this category the average of the differences in the absolute maximum and absolute minimum temperatures for successive 14 day periods was greater than 1.5 ºC (Fig. 2b). The least buffering resulted in body temperatures that fluctuated greatly on a daily basis where the difference between the maximum and minimum daily temperature was more than 1 ºC (Fig. 2c).

Analyses of the use of hibernacula that resulted in the different thermal buffering categories were conducted for Littlefield and City Creek for the four years studied, and among all four sites for the winter of 1998-1999 using a contingency analysis in JMP 5.0 (SAS Institute, 2003).

METEOROLOGICAL DATA

Climate data for the study sites were obtained from: (1) City Creek - the St. George, Utah weather station, 4 km south of the CC site; (2) Littlefield - the Littlefield 1 NE station 10 km north of the LF site, (3) Lake Mead – from the Overton station, 1 km northwest of the site, and (4) Bird Spring Valley- from the Red Rock Canyon weather station 4 km northeast of the site (NOAA 1998). Soil temperatures during the winter of 1998 at Bird Spring Valley were measured at a central location at the site using a CR-10 weather station (Campbell Scientific, Logan Utah) and type K thermocouples (Omega Engineering, Stamford CN) at the surface, and buried 70 cm below the surface, just above the caliche layer.

RESULTS

CITY CREEK AND LITTLEFIELD

There was no overall difference for the average date of hibernation onset between tortoises at City Creek and Littlefield ($F_{1,32}$ = 3.26, P = 0.08). There were differences in the onset date among years. The average date of onset in the fall of 1995 (Nov. 3 ± 12d) was approximately nine days later than the average date of onset in the fall of 1996 (Oct. 25 ± 8 d)(Tukey's HSD Q = 2.72). The onset dates for all other years were statistically indistinguishable from one another. There were no site-by-year interactions of onset date ($F_{3,29}$ = 0.65, P = 0.59).

Tortoises at the City Creek and Littlefield sites spent a similar number of days in hibernation ranging from 106 to 182 days ($F_{1,23} = 2.22$, $P = 0.15$). The duration of hibernation varied among years. This can be attributed to a twenty-one day difference in duration of hibernation in the winters of 1997-1998 and 1998-1999 (154 ± 21 vs. 133 ± 21 days respectively, Tukey's HSD Q= 2.73). The durations of hibernation for all other years were statistically indistinguishable from one another. There was a significant year-by-site interaction for animals at Littlefield during the 1998-1999 season which had a shorter duration (134 ± 40 days) than the City Creek or Littlefield animals in the 1997-1998 season (154 ± 17, and 155 ± 25 days respectively)(Fig. 3)(Tukey's HSD Q = 3.27).

The ending date for hibernation in the spring did not differ between the two sites and ranged between February 11 to April 27 ($F_{1,23} = 0.07$, $P = 0.79$). There were significant differences in the termination date among years. In particular, the termination of hibernation (averaged for both sites) was earlier in the spring of 1997 (Mar. 15 ± 5 d), and in the spring of 1999 (Mar. 14 ± 17 d) than in the spring of 1996 (Mar. 25 ± 15 d) or 1998 (Apr. 1 ± 19 d) (Tukey's HSD Q = 2.72). There was no significant site-by-year interaction for termination date ($F_{3,29} = 2.76$, $P = 0.06$).

There were no differences in the average hibernation body temperature between City Creek and Littlefield ($F_{1,23} = 1.52$, $P = 0.23$; see Table 1.). There were differences among years ($F_{3,30} = 6.86$, $P = 0.0012$). The average hibernation body temperature of tortoises during the winter or 1996-1997 (12 ºC) was approximately two degrees cooler than either 1997-1998 (14 ºC) or 1995-1996 (14.2 ºC). There were no significant site-by-year interactions ($F_{3,30}$ = 1.325, p = 0.285). The mid-hibernation temperature did not differ between the two sites ($F_{1,23}$ = 1.89, P = 0.18). There were differences among years in that the animals' temperatures during the 51st week of 1998 (9.88 ºC) were significantly cooler than during the same week in 1995 (13.13 ºC). The average minimum temperature experienced did not differ for either site ($F_{1,23}$ = 0.1722, P = 0.68) or for any year ($F_{3,30}$ = 2.79, P = 0.058).

The degree to which tortoises were insulated from environmental variance in temperatures differed among sites for three of the four winters of our study (Table 2). In 1995, significantly more animals at City Creek were in hibernacula that provided medium buffering than at Littlefield, which had no animals in that category during that year. Tortoises at Littlefield were split equally between categories of high and low buffering, with two animals in each type of hibernaculum. Both sites had a similar distribution of hibernation patterns during the winter of 1996 (P = 0.87). The percent of animals in medium buffering hibernacula was 81.25 %, and that in low buffering hibernacula was 18.75% for both sites combined. During the winter of 1997, there was a different pattern of hibernaculum use between the two sites (P = 0.0003). All 16 animals at the City Creek site selected hibernacula that resulted in medium buffering patterns, and the 16 animals at Littlefield were nearly evenly divided among the three categories. The buffering categories during winter of 1998 differed between the sites (P = 0.009). All six of the animals monitored in 1998 at City Creek had medium buffering patterns, while the Littlefield animals were approximately evenly divided between medium and low levels of thermal buffering.

FOUR-SITE COMPARISONS

All four study sites were monitored in the winter of 1998 allowing comparison of regional differences in tortoise hibernation characteristics.

There were significant differences in the beginning of hibernation among sites ($F_{3,21}$ = 10.10, P = 0.003). Tortoises at Bird Spring Valley (onset date = Oct. 15 ± 15 d) entered hibernation earlier than tortoises either Lake Mead (Nov. 10 ± 7 d) or Littlefield (Nov. 11 ± 11 d). The onset date for tortoises at City Creek (Oct. 25 ± 6 d) did not differ significantly from the onset dates at the other sites (Fig. 4).

There were also significant differences in the duration of hibernation among sites ($F_{3,15}$ = 5.96, P < 0.007). The animals at Lake Mead (114 ± 18 days) and Littlefield (115 ± 14 days) hibernated for significantly fewer days than animals at City Creek (146 ± 13 days). Hibernation duration at Bird Spring Valley (131 ± 7.7 days) did not differ significantly from the other sites (Fig. 4).

The four study sites did not differ in termination date for hibernation ($F_{3,17}$ = 1.399, P = 0.278). The termination dates ranged in from February 11 to April 16 of 1999.

There was no influence of gender on the onset, duration, or termination of hibernation.

There were no differences among sites in the average hibernation temperatures ($F_{3,23} = 1.61$, $P = 0.21$), minimum temperatures ($F_{3,23} = 0.87$, $P = 0.76$), or mid hibernation temperatures ($F_{3,21} = 1.23$, $P = 0.32$)

Fifty-Seven % of the hibernacula provided medium buffering from thermal environments, while 37% had low buffering, and 5% had high levels of buffering. The distribution of animals in each of these patterns differed among sites. City Creek had a significantly greater proportion of animals with medium levels of buffering, which was in contrast to the Lake Mead site, which had more animals with low levels of buffering, and fewer with medium levels than at any other site. Littlefield and Bird Spring Valley had similar proportions of hibernacula that produced medium and low levels of buffering. There were very few animals with high thermal buffering patterns in their hibernation body temperatures. All of these animals were at the Littlefield site.

DAYS BEFORE HIBERNATION

The number of hours that operative temperature models were warmer than 30 ºC was positively correlated with the number of hours that tortoise body temperatures were warmer than 30 ºC for each of the seven tortoises. After taking the residuals of this first analysis and regressing them against the days prior to hibernation, six of the seven animals significantly decreased the number of hours per day that their body temperatures were above 30 ºC during the 30-day period prior to entering hibernation.

DISCUSSION

TIMING OF HIBERNATION

Onset

The timing of the onset of hibernation was fairly consistent between tortoises at City Creek and Littlefield among the four years of our study. While the onset dates for both sites combined were earlier in 1996 than in 1995, the onset dates for the other years were statistically indistinguishable (Fig. 3). Air temperatures at City Creek were cooler in 1996 than 1995. For example the average temperature at City Creek for October was cooler by 10 ºC (Fig. 5). However, similar temperature differences were present in other winters, yet they did not result in differences in the onset of hibernation. Ambient temperature data for all four years were not available for the Littlefield site.

In the winter of 1998 the date of onset of hibernation differed among the four study sites. Tortoises generally entered hibernation earlier at the sites with cooler temperatures. Tortoises entered hibernation earlier at the Bird Spring Valley site than at either Lake Mead or Littlefield. City Creek was the coolest site but had a narrow range of onset dates compared to the other sites during this year (Fig. 4). The City Creek site had colder mean air temperatures during the fall of 1998 than in the other three years of our study, and this may have cued animals to enter hibernation over a narrower period of time, as the range in hibernation dates at that site was narrower than in any other year (Fig. 3). Thus, under some circumstances climatic conditions may trigger more synchrony in the onset of hibernation, but in most sites and in most years, there was great variation in the date of onset. Therefore, we suggest that acute climactic conditions may be less influential to the timing of hibernation for this species than previously thought (e.g., see Woodbury 1948, Rautenstrauch et al. 1998), although extreme years may cause this timing to be more synchronized.

Decreases in air or ground temperature in the fall are the most frequently suggested cue for onset of hibernation (Gregory 1982). For example, tortoises began hibernating in Kern County, CA when surface temperatures fell below 20° C (Voigt 1972). Daily averages of the temperature of the soil surface at the Bird Spring Valley site fell below 20 ºC on September 27th in 1998, and the first tortoise entered hibernation three days later on September 30th. However, the last tortoise to enter hibernation at the site was on November 13th; at this time the temperature of the surface had fallen to approximately 12 ºC. Thus, while cooler soil temperatures may cue animals to begin entering hibernation, the animals' responses do not appear to be strongly coupled to this cue.

Other studies on hibernation in snakes (Viitanen 1967, Aleksiuk 1976, Sexton and Hunt 1980) suggest that reversals in the soil temperature gradient from surface to deep burrow temperature may cue the onset of, and emergence from, hibernation. Our data were consistent with this pattern also (Fig. 6), but again while animals did not enter hibernation until the average surface soil temperatures fell below deep soil temperatures, the onset of hibernation ranged over a 44-day period, suggesting that this cue has a very weak influence.

In general, the hypotheses to explain the onset of hibernation are not inconsistent with our data, yet none seem to be tightly coupled to the mechanisms cueing tortoises to enter hibernation. Among all of our sites and for all years of our study, there was great individual variation in the onset date of hibernation. We searched for temperature patterns for individuals in the days before entering hibernation. At Bird Spring Valley in 1998 we investigated the amount of time that animals had body temperatures above 30 ºC for each day during the 30 day period prior to their entry into hibernation. We chose 30 ºC because this temperature may have some biological relevance, for example, the digestion of plants by reptilian herbivores requires warm temperatures (Zimmerman and Tracy 1989, Espinoza and Tracy 1997). After controlling for the fact that the opportunity for selecting warmer temperatures was decreasing with the progression of fall, the majority of animals (6 of 7) showed a significant reduction in the amount of time during which they achieved high (30 ºC) body temperatures. This pattern may indicate that some individual physiological preparation precedes the onset of hibernation in the fall, for example the cessation of feeding, and clearance of digesta from the gut.

Duration

The duration of hibernation was approximately the same in City Creek and Littlefield over the four-year time period (Fig. 3). There was one winter in which the duration of hibernation by tortoises differed by twenty days from the other winters, but tortoises had a similar duration of hibernation for three of the four years at these two sites. The duration of hibernation differed among the four sites during the winter of 1998 - 1999 (Fig. 4), with tortoises at the warmer sites having shorter hibernation periods than those at cooler sites (Fig. 7).

Bailey et al. (1995) studied the hibernation of desert tortoises in the San Pedro River Valley, Arizona. The mean duration of hibernation at that site was 142 days (SE = 9.4). The duration measured at their site was similar to the mean duration of hibernation measured at City Creek (146 days) and Bird Spring Valley (132 days), but longer than the hibernation period at Littlefield or Lake Mead (approximately 115 days). The reported hibernation period for desert tortoises in Rock Valley, Nevada during the winter of 1996-1997 was 151 days (Nagy and Medica 1986). Over this time period, hibernating tortoises were reported to have lost very little body mass, and metabolic costs during hibernation were very low (Nagy and Medica 1986).

The dates on which tortoises emerged from hibernation were correlated with the ambient spring temperatures at City Creek and Littlefield (Fig. 5). As with the other measures of the timing of hibernation, the individual variation in the termination of hibernation within each site was great, varying by as much as 35 days**.** The average termination date did not differ among the four study sites during the winter of 1998, but that is because the range of days over which animals emerged from hibernation was great.

The increasing length of the photoperiod in the spring has been suggested as a possible exogenous cue that could trigger animals to emerge from hibernation (Gregory 1982). During the 35-day range over which individuals terminated hibernation in the spring, the photoperiod would have become approximately 1.5 hours longer. If photoperiod were an important cue for terminating hibernation, we would expect tighter correlation of the termination dates among individuals.

Differentials between air and surface temperatures in the fall and the spring have also been suggested as a cue for animals to begin or end hibernation (Sexton and Hunt 1980, Gregory 1982). However, to make such measurements, desert tortoises would be required to approach the substratum surface to “test“ the temperature, and our results indicate no such behavior. For example, the average daily hibernation temperatures of the tortoises at Bird Spring Valley (1998) remained very close to soil temperatures measured at 70 cm below the surface until the date when animals terminated hibernation. We observed that on approximately the first week of February, the average surface temperature began to rise regularly above that of the deep soil. However the animals did not begin to emerge from hibernation until approximately a month later. In addition, the animals at Littlefield that were in highly buffered hibernacula (e.g., see Fig. 2a and Table 2) had no variation in body temperature while hibernating. Thus, these animals were not apparently experiencing any external cues, and were not sampling the environment, yet they emerged from hibernation at about the same time as other animals.

Surface temperatures of the substratum have also been suggested as a cue that influences termination date. For example tortoises in the west Mojave reportedly did not emerge from hibernation until surface temperatures reached 20°C (Voigt 1972). Moreover *Terrapene carolina* and *T. ornata* in Missouri reportedly emerge from hibernation after five consecutive days of subsurface (10-20 cm) temperatures of 7° C or higher (Grobman 1990). We did not observe a relationship between surface temperatures and the termination of hibernation at our site.

TEMPERATURE AND THERMAL BUFFERING

Hibernation temperature was remarkably consistent among years and among sites. This suggests that, while there were large differences in the ambient temperatures at the four sites among years, the hibernacula chosen by the tortoises for hibernation were very similar in their thermal properties. The average hibernation temperatures were well above ambient temperatures for the corresponding times. It should be noted that tortoises choose one of the warmest microclimates in the environment for hibernation, which seems counter to the notion that animals should select colder temperatures to conserve energy when hibernating. While average air temperatures were similar among sites, the degree of daily fluctuation in hibernation temperatures differed greatly among the sites. Tortoises in sites that had colder climates sought shelters that were deeper, and therefore had more stable temperatures because they were more buffered from the environment (Woodbury and Hardy 1948). Some of the animals at the Littlefield site had body temperatures that had almost no fluctuation, not only on a daily basis, but also over the course of the winter. These animals selected hibernacula that consisted of very deep caves, which had very constant temperatures over time, similar to those reported by Woodbury and Hardy (1948). Interestingly, these caves were not used in all years for hibernation (Table 3).

The temperatures of reptile hibernacula have been described to range between 1 and 15 °C (Gregory 1982). Our data generally fall within this range, however, individuals may choose hibernacula that have temperatures above this range (Table 1). The mean minimum and maximum hibernation temperatures in our study were similar to those observed in the San Pedro Valley, Arizona (Bailey et al. 1995). The female tortoises in Arizona, however, had lower minimum temperatures than did males, while there were no apparent gender differences in hibernation temperatures of our study animals.

All of the hibernacula in our study provided some protective insulation from thermal extremes compared to surface temperatures, however, the relative amount of insulation depended on depth (distance from the site entrance) and/or overburden (depth of soil from the surface to the point where the tortoise resides) of the hibernacula. Similar patterns have been observed for turtles (Bailey et al. 1995, Woodbury and Hardy 1948, Huot-Daubremont et al. 1996, Grobman 1990), snakes (Brown et al. 1974, Sexton and Hunt 1980, Costanzo 1986, Weatherhead 1989, Claussen et al. 1991) and lizards (Etheridge et al. 1983).

HOURS ABOVE 30 C

Six of seven animals in our study showed significantly decreasing amounts of time spent at high body temperatures as the tortoises approached hibernation after controlling for the effects of decreasing amounts of time that operative temperature models were at high body temperatures. This may indicate the presence of some physiological process of preparing for hibernation. Alternatively this could indicate that there is great thermal heterogeneity at different microsites in the field, and that tortoises experience different thermal environments.

Thyroxine (a thyroid-produced hormone) is related to periods of high activity, and correspondingly high selected body temperatures. Whether thyroxine influences temperature selection or whether temperature selection influences thyroxine levels is presently unknown (Rostal pers. comm.). Thyroxine levels in desert tortoises vary over the course of a year (Kohel et al. 2000). The lowest levels of thyroxine occur in October, immediately preceding hibernation

(Kohel et al. 2000). Thyroxine increases in January to the highest levels for the year by the month of April (Kohel et al. 2000). Other hormones such as plasma testosterone have been measured throughout the year for desert tortoises, but none of the annual patterns coincide with that of Thyroxine (e.g., Rostal et. Al 1994).

If thyroxine influences temperature selection in this species, then it is conceivable that hormonal levels may provide a previously unexplored mechanism that could influence the timing of hibernation. It may be possible then that increasing levels of this (or another) hormone trigger the termination of hibernation in the spring. The plausibility of this possible mechanism warrants further investigation, but could better explain the individual variation in the onset, duration, and termination of hibernation in this species than mechanisms involving environmental cues.

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TABLES

TABLE 1.

Tortoise body temperatures during hibernation for the winter of 1998 - 1999. Mean temperature is defined as the mean temperatures of all individuals from the initiation to the termination of hibernation. The minimum temperature is the average lowest temperature experienced by animals at each site during the hibernation period. The mid-hibernation temperature is the mean temperature for individuals at each site during week 51 of the year. The study sites are abbreviated as follows: City Creek (CC), Littlefield (LF), Bird Spring Valley (BSV), and Lake Mead (LM).

Year / Site	**Mean Temperature (ºC) ± SD**	**Minimum Temperature (ºC) ± SD**	**Mid-hibernation Average (ºC) ± SD**
1995			
CC	12.2 ± 1.1	8.2 ± 2.3	10.3 ± 2.4
LF	16.0 ± 3.8	9.7 ± 6.0	16.3 ± 6.4
1996			
CC	11.4 ± 1.5	6.5 ± 2.4	10.2 ± 1.4
LF	12.1 ± 1.5	7.9 ± 3.4	11.3 ± 2.2
1997			
CC	13.4 ± 2.0	9.3 ± 2.2	10.7 ± 3.2
LF	14.9 ± 4.4	10.1 ± 5.4	12.7 ± 6.3
1998			
BSV	14.7 ± 3.3	9.4 ± 4.6	10.0 ± 3.5
CC	11.9 ± 3.1	8.1 ± 3.4	8.9 ± 3.9
LF	12.8 ± 4.9	8.3 ± 6.6	11.4 ± 6.1
LM	15.2 ± 1.9	9.9 ± 4.29	12.7 ± 2.5

TABLE 2.

The number of animals in each temperature buffering category for the hibernacula selected by animals at the City Creek and Littlefield sites for the four winters (1995-1998). The site and year for each row are given in the first column. Probability values are those given for the Likelihood ratio, or Pearsons (depending on suspect values due to low values) Chi-Square test testing for a difference among categories and/or sites. The study sites are abbreviated as follows: City Creek (CC), Littlefield (LF).

Year / Site	**High (N)**	**Medium (N)**	**Low (N)**	**P**
1995				
CC	0	7	2	0.02
LF	2	0	2	
1996				
CC	0	8	2	0.87
LF	2	0	2	
1997				
CC	0	16	0	0.0003
LF	4	7	5	
1998				
CC	0	6	0	0.03
LF	0	4	5	

TABLE 3.

The number of animals in each temperature buffering category for the hibernacula selected by animals at all four sites for the winter of 1998. The site is given in the first column. The post-hoc cell contributions for significance are given in parentheses in each cell. Post-hoc cell contributions with an absolute value of >1.96 indicate a significant divergence from the expected ratio. The study sites are abbreviated as follows: City Creek (CC), Littlefield (LF), Bird Spring Valley (BSV), and Lake Mead (LM).

Site	**High** **N (Cell contrib)**	**Medium** **N (Cell contrib)**	**Low** **N (Cell contrib)**
CC	**0** (-1.784)	**13** (4.602)	**4** (-3.856)
BSV	**0** (-1.373)	**13** (-.335)	**11** (1.003)
LF	**6** (4.397)	**12** (-1.305)	**8** (-0.775)
LM	**0** (-1.224)	**4** (-3.731)	**16** (4.409)

FIGURES

FIG. 1.

The study sites are indicated by the black circles on the map of the southwestern United States. The site southwest of Las Vegas, Nevada was Bird Spring Valley. The Lake Mead site on the northern end of Lake Mead. The site in extreme northwest Arizona was Littlefield and City Creek is located in southwestern Utah.

FIG. 2.

Three examples of tortoise body temperatures prior to, during and following hibernation. Data are presented as the daily minimum (filled circles) and maximum (unfilled circles) temperatures (ºC). Panel A is an example of a high buffering in the body temperature pattern, in which daily variation in temperature was less than one degree Celsius, and there was no evidence of the influence of local fluctuations in climate on tortoise hibernation temperature. Panel B demonstrates a medium level of temperature buffering during hibernation, in which daily variation in animal temperature is less than one degree Celsius, but the animal's temperature was influenced by changes in local climate. Panel C is an example of a low temperature buffering, in which animal temperatures fluctuated by greater than one degree Celsius on a daily basis.

Fig. 3.

Onset, duration, and termination of hibernation at the City Creek and Littlefield sites for the four winters from 1995 through 1998. The four winters at Littlefield are in the top half of the figure, City Creek is given in the bottom half. Years are sorted from bottom to top in each panel and listed as the year in which each hibernation period began. The distance between the onset and termination dates is the duration of hibernation. The median onset and termination dates for each site are shown as a filled circle. The box surrounding the filled circle depicts the 25th and 75th quartile. The range of values for each measure is given by the dotted lines ("whiskers") outside of each box, and possible outliers are given by the open circles outside the box.

Fig. 4.

Onset, duration, and termination of hibernation at the City Creek, Littlefield. Lake Mead and Bird Spring Valley sites for the winter of 1998 - 1999. The distance between the onset and termination dates is representative of the duration of hibernation. The median onset and termination dates for each site and are shown as a filled circle. The box surrounding the filled circle depicts the 25th and 75th quartile. The range of values for each measure is given by the dotted lines ("whiskers") outside of each box, and possible outliers are given by the open circles outside the box.

Fig. 5.

Average monthly temperature of the air for the four-year observation period at the City Creek site. Data were obtained from the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html) for St. George Utah. This weather station was located 3.2 km from the City Creek field site. Data for Littlefield were similar for 1997 - 1999, but were unavailable for 1995 – 1996.

Fig. 6.

Hibernation and soil temperatures at the Bird Spring Valley site for the winter of 1998 - 1999. Soil temperatures were recorded for the surface (line with unfilled circles), and 70 cm below the surface (line with filled circles), and are expressed as daily averages. Tortoise body temperatures (line with unfilled squares) are expressed as daily averages of animals that were in hibernation for that day, error bars represent the 95% confidence interval for that mean. The number of animals in hibernation increased from October 1st to November 13th as individuals at the study site entered hibernation and decreased in a similar fashion in the spring. Therefore the number of animals contributing to the average temperature ranges from one to six. Periods in which only one animal is represented were October 1st, and from March 11th to March 19th. The gray vertical bars represent the range of time over which animals were either entering or exiting hibernation. Because the some of the tortoise data loggers overloaded with data before the termination of hibernation, radio telemetry observations were used to extend the estimate of the range of termination dates.

Fig. 7.

Average monthly temperature for the four sites during the winter of 1998 - 1999. Data were obtained from the National Climatic Data Center (http://www.ncdc.noaa.gov/oa/ncdc.html). All weather stations were the nearest available to the site. And were as follows: City Cree - Saint George, Lake Mead - Overton, Littlefield - Mesquite, Bird Spring Valley - Red Rock). Data for Bird Spring Valley were not available for the month of January.

Fig. 1

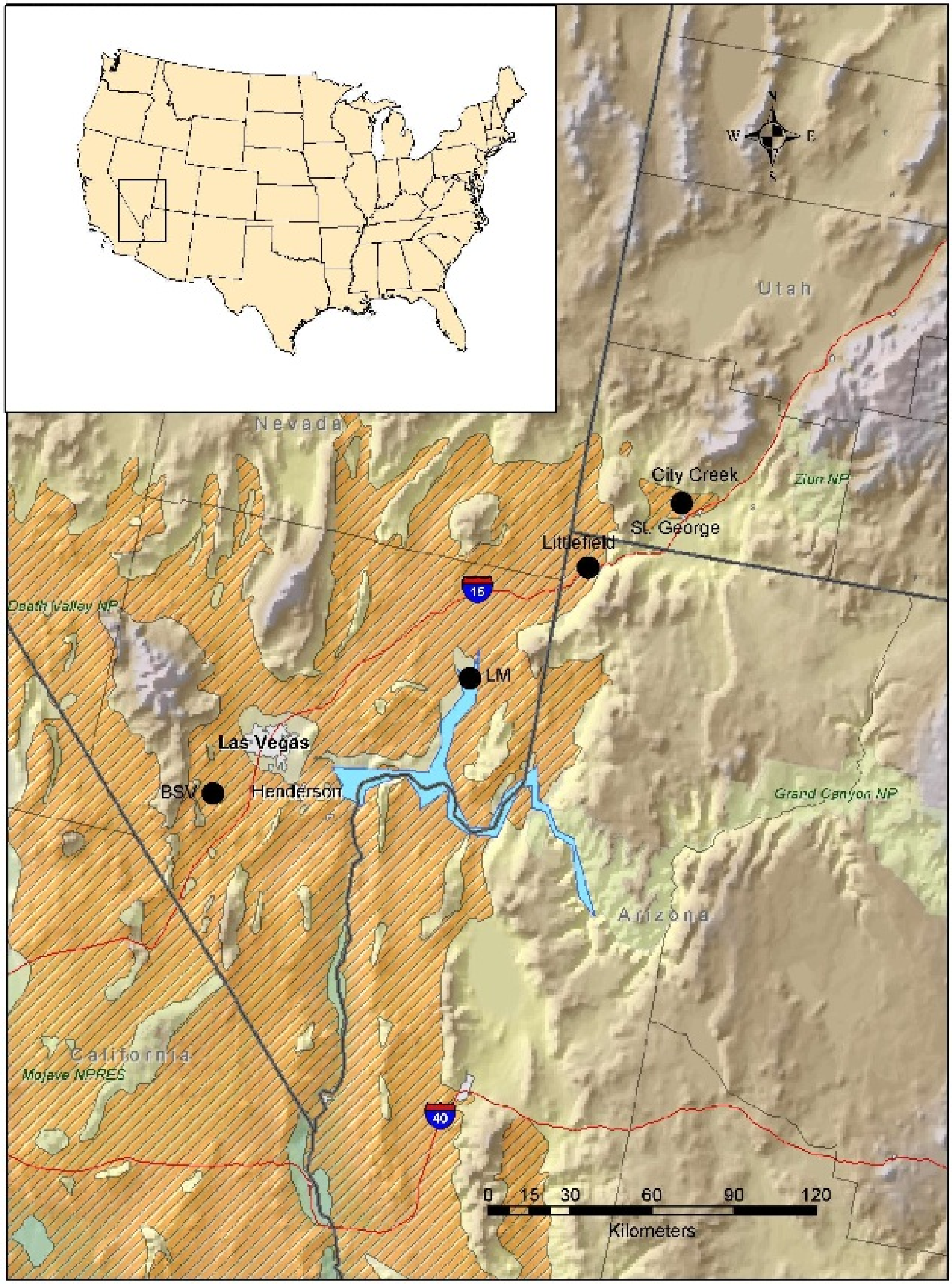

N
W
E
S
Utah
Nevada
City Creek
St. George
Zion NP
Littlefield
15
Death Valley NP
LM
Las Vegas
BSV
Henderson
Grand Canyon NP
Arizona
California
Mojave NPRES
40
0
15
30
60
90
120
Kilometers

Fig. 2

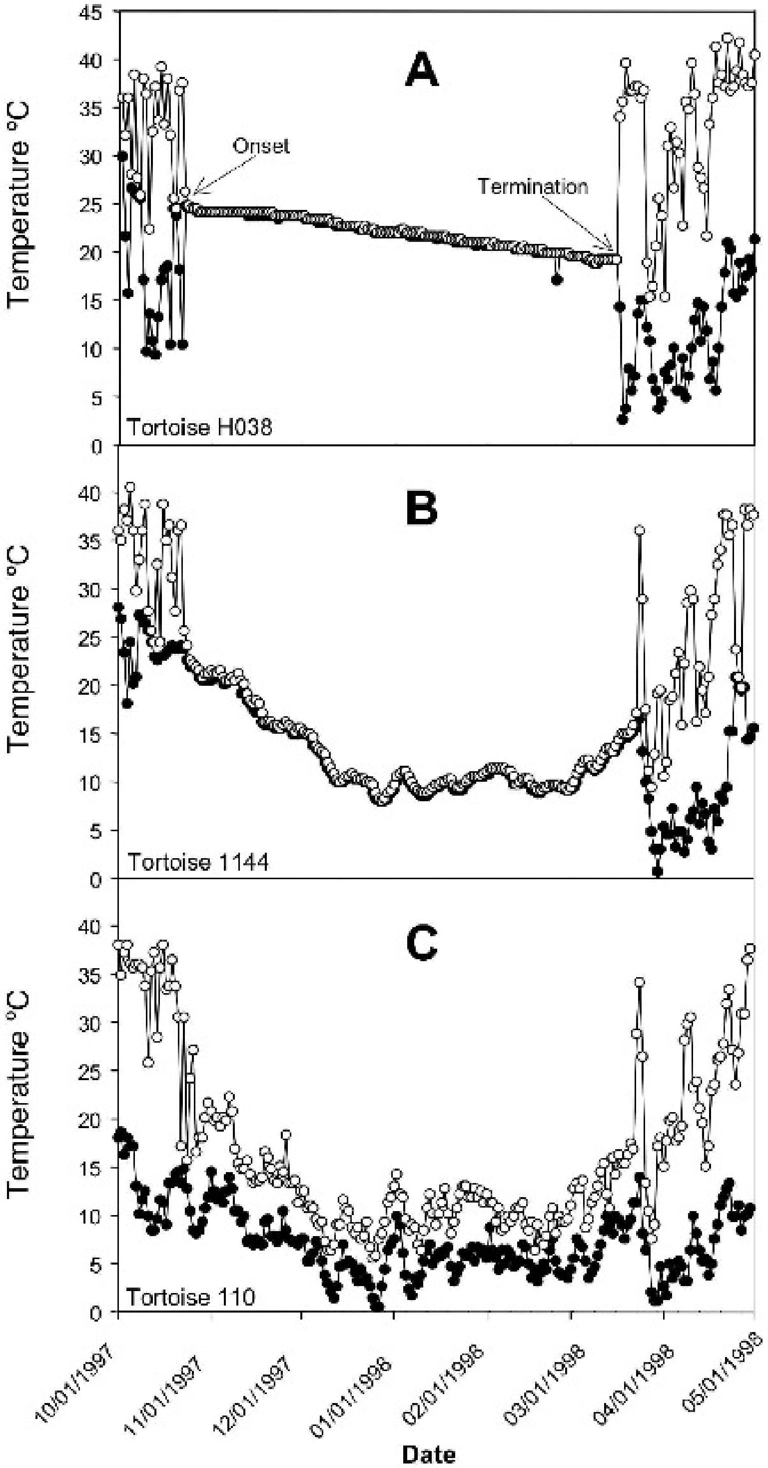

A
B
C
Onset
Termination
Tortoise H038
Tortoise 1144
Tortoise 110
Temperature °C
0
5
10
15
20
25
30
35
40
45
10/01/1997
11/01/1997
12/01/1997
01/01/1998
02/01/1998
03/01/1998
04/01/1998
05/01/1998
Date

Fig. 3

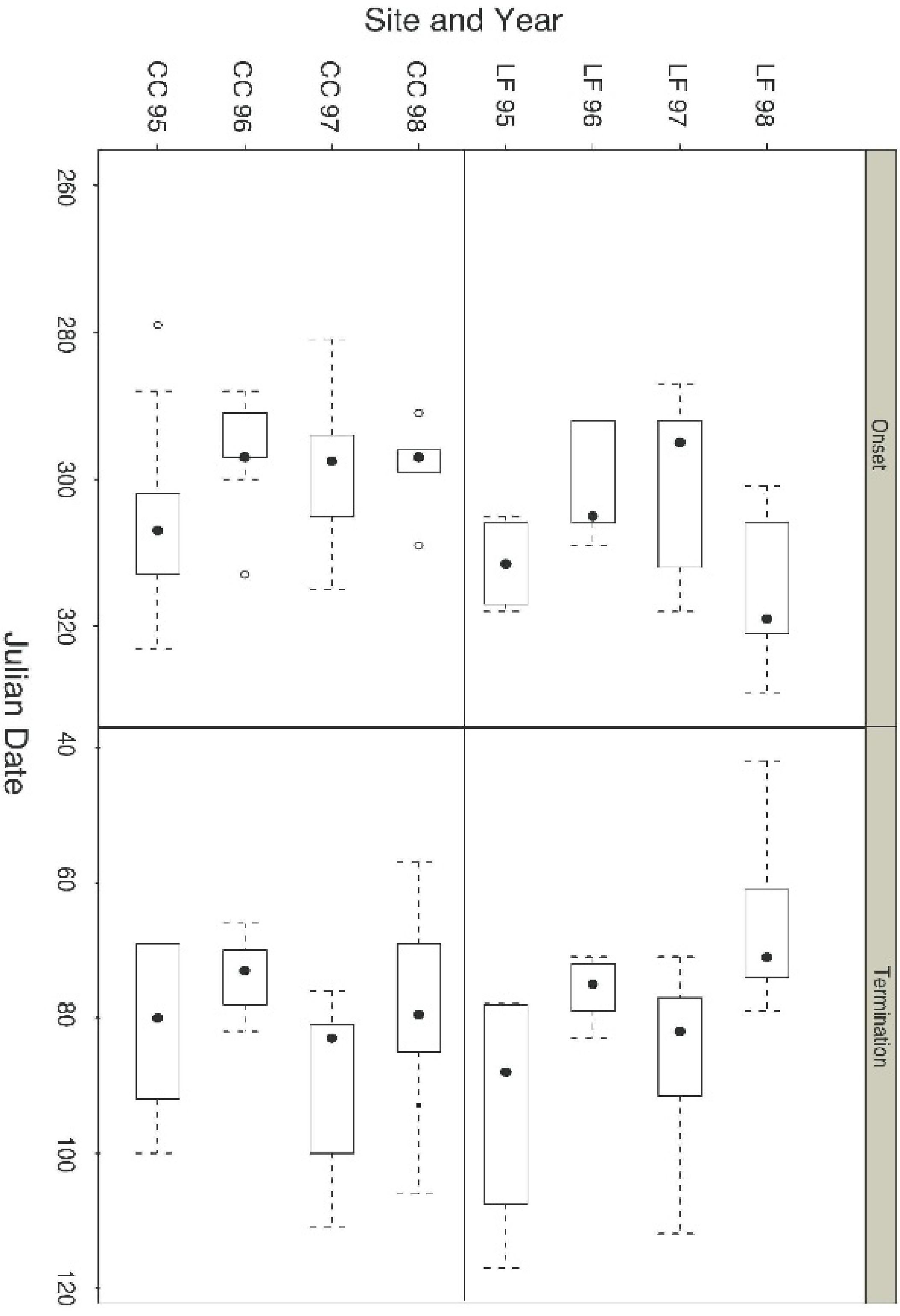

Site and Year
LF 98
LF 97
LF 96
LF 95
CC 98
CC 97
CC 96
CC 95
Onset
Termination
260
280
300
320
40
60
80
100
120
Julian Date

Fig. 4

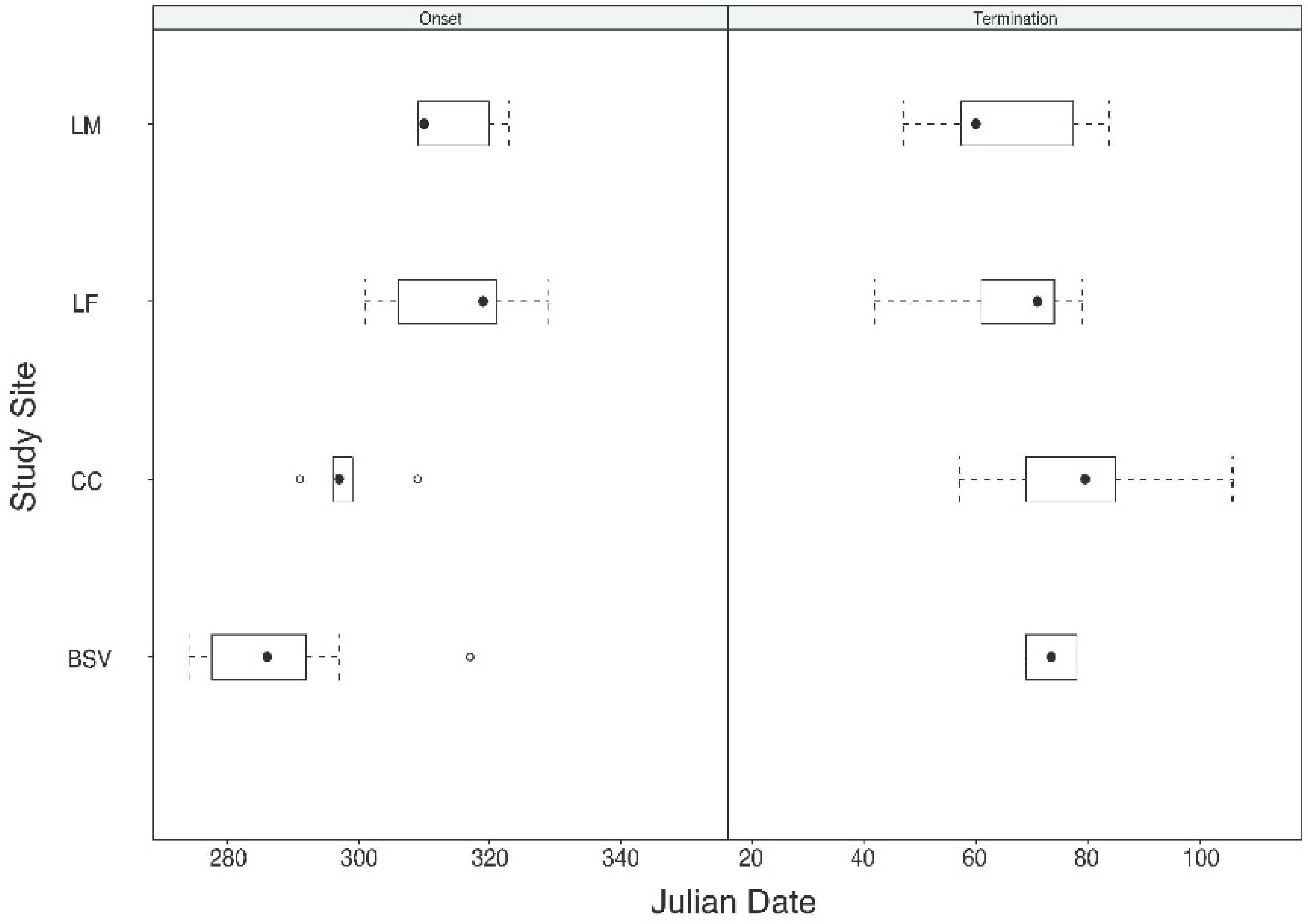

Onset
Termination
LM
LF
CC
BSV
Study Site
280
300
320
340
20
40
60
80
100
Julian Date

Fig. 5

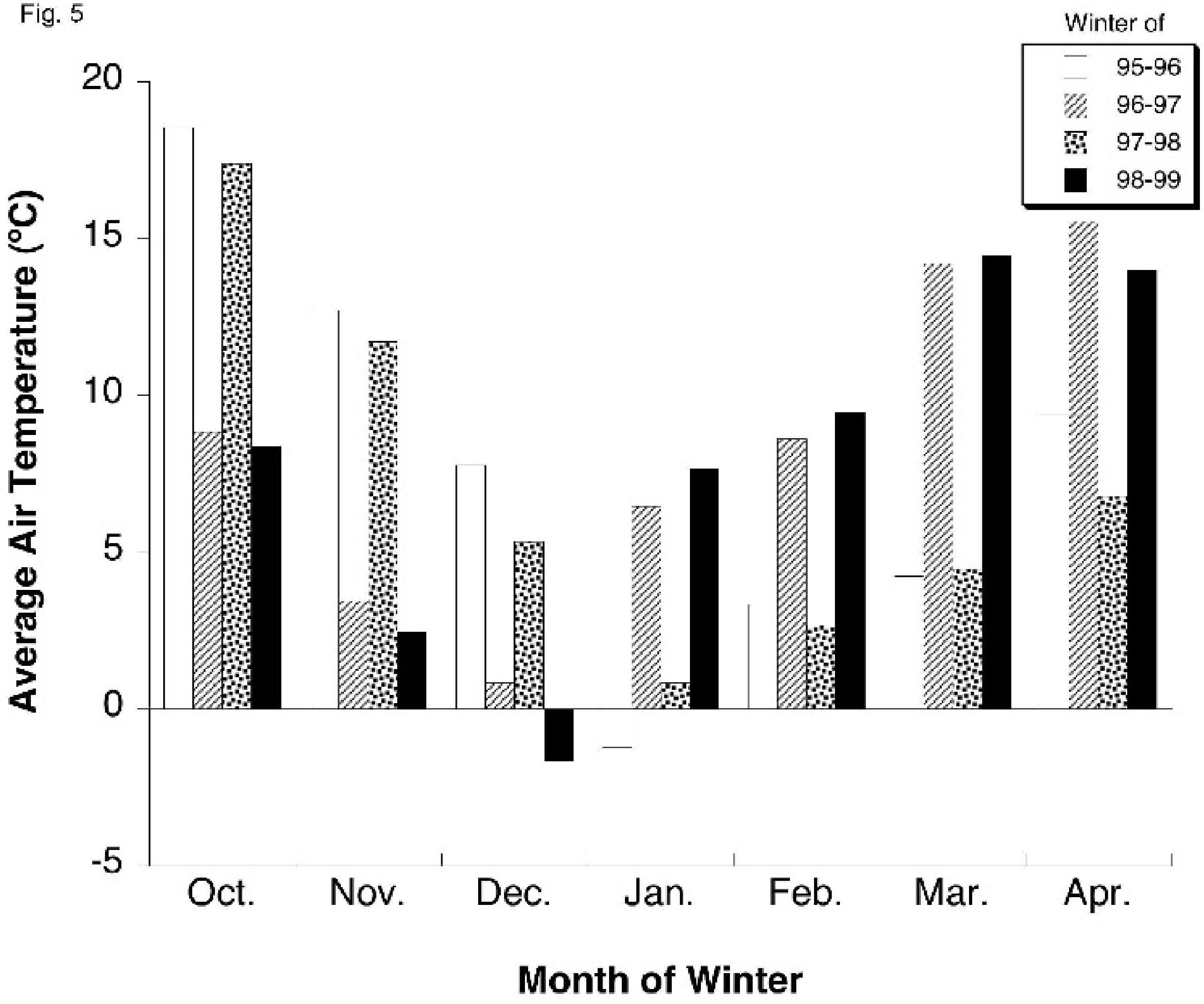

Winter of
95-96
96-97
97-98
98-99
Average Air Temperature (°C)
20
15
10
5
0
-5
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
Month of Winter

Fig. 6

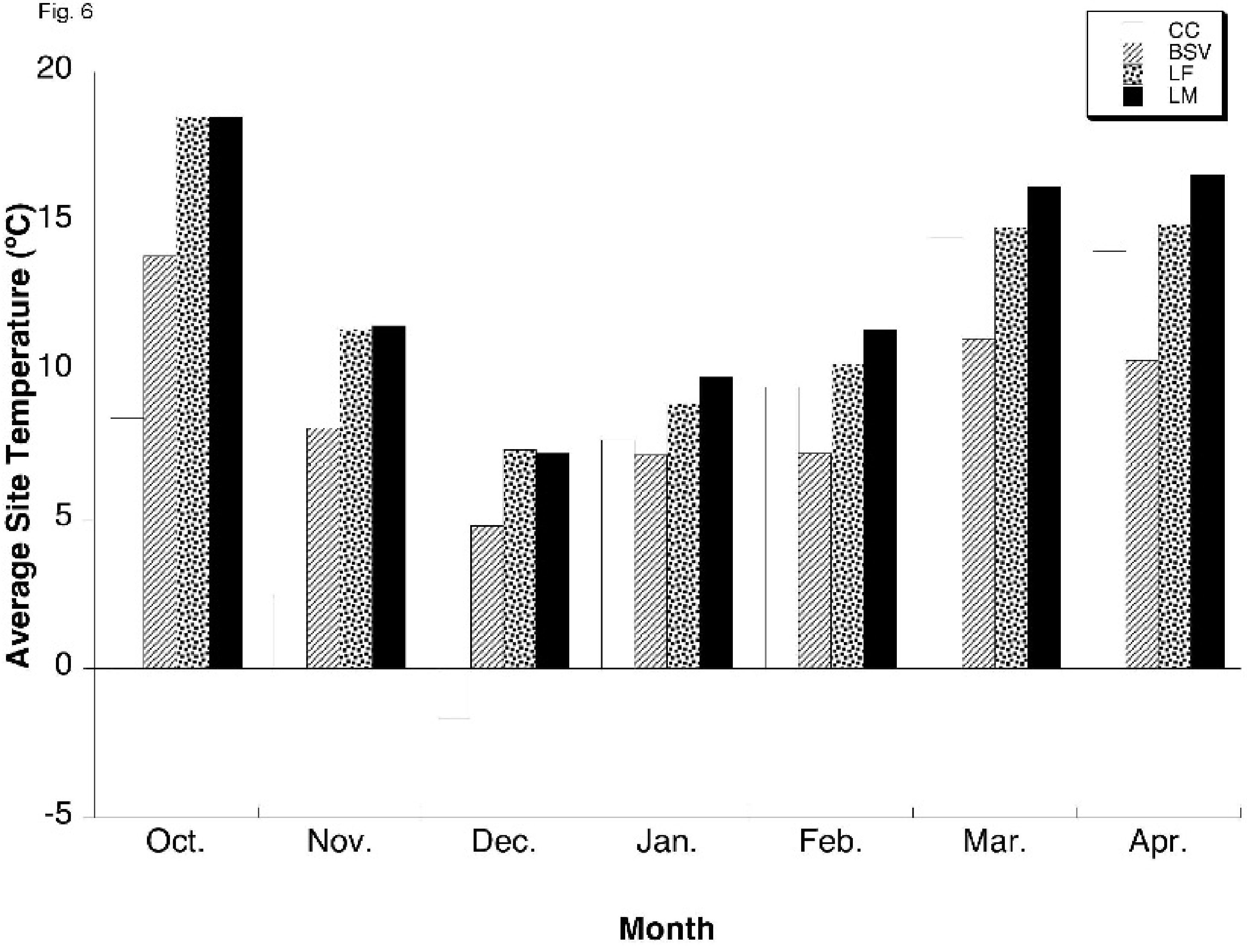
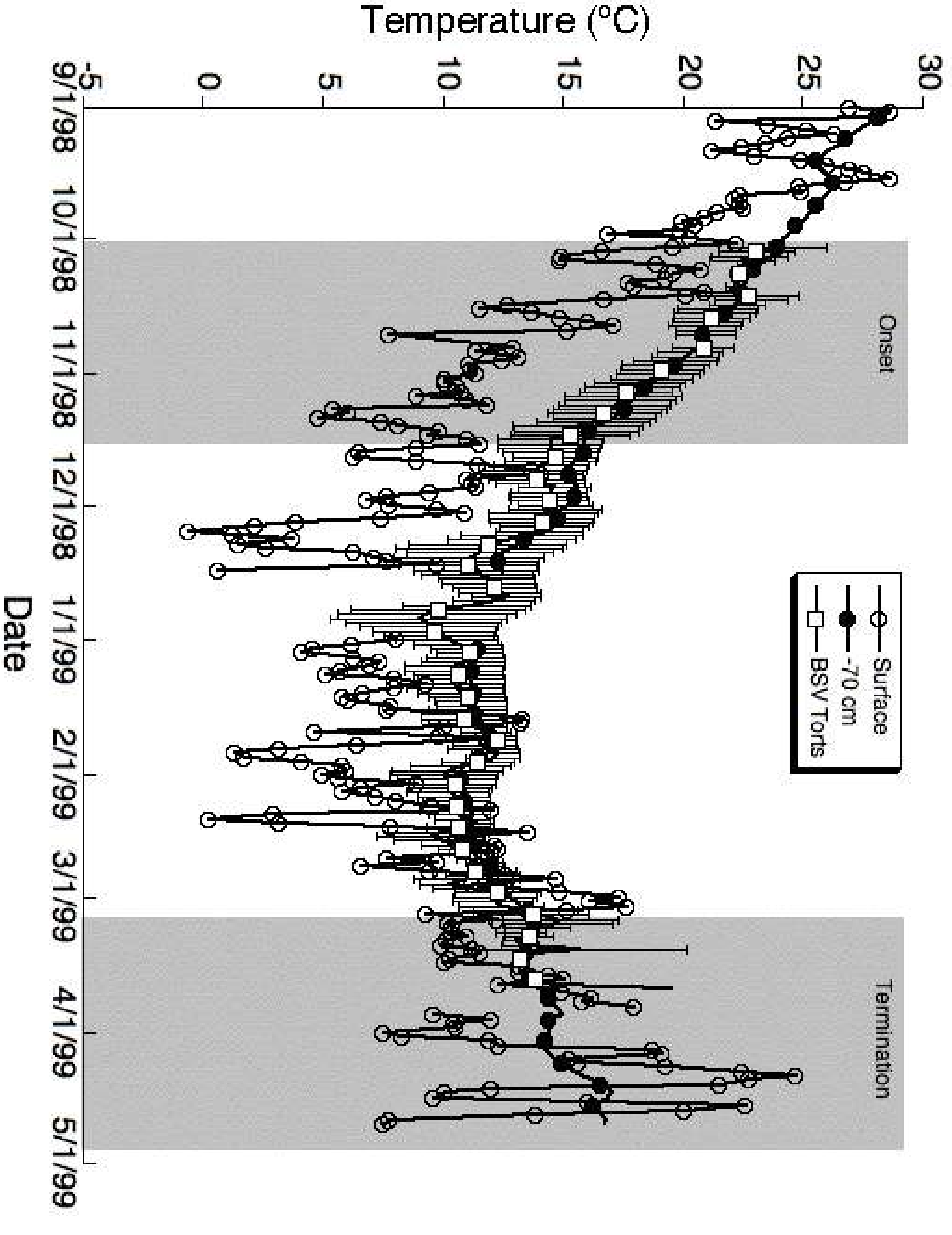

Average Site Temperature (°C)
20
15
10
5
0
-5
Oct.
Nov.
Dec.
Jan.
Feb.
Mar.
Apr.
Month
CC
BSV
LF
LM

Fig. 7


Temperature (°C)
30
25
20
15
10
5
0
-5
Date
9/1/98
10/1/98
11/1/98
12/1/98
1/1/99
2/1/99
3/1/99
4/1/99
5/1/99
Onset
Termination
Surface
-70 cm
BSV Torts

APPENDICES

APPENDIX 1. SAMPLE SIZES

The number of animals studied at each site, and the number contributing to the data for onset dates, duration and termination dates. Not all animals were measured in all years, and not all animals in a single year contributed to the determination of the timing of onset, duration, and termination of hibernation due to equipment difficulties.

Site	***Year***	***Onset (N)***	***Duration (N)***	***Termination (N)***	***Total (N)***
CC	1995-1996	9	9	9	9
CC	1996-1997	9	9	10	10
CC	1997-1998	10	9	9	10
CC	1998-1999	6	6	6	6
LF	1995-1996	4	4	4	4
LF	1996-1997	6	6	6	6
LF	1997-1998	11	11	11	11
LF	1998-1999	5	5	5	5
BSV	1998-1999	7	2	2	7
LM	1998-1999	7	6	8	9

Chapter 3. The relationship between the absorptance of the carapace and the thermal biology of desert tortoises

ABSTRACT

Shell color of Individual desert tortoises can be variable, and differences in shell color can affect the tortoise's absorptance of solar radiation. Differences in absorptance result in different amounts of radiant energy absorbed by the animal's carapace, which should, in turn, influence the energy balance, body temperature, metabolic rate, and behavior of the animal. To understand this mechanism of energy exchange and the resulting influence on tortoise thermal biology and behavior, we manipulated absorptance to solar radiation of desert tortoises by painting their carapaces with paints that had either high or low absorptance to solar radiation. This caused the tortoises to have absorptances above and well below that of natural coloration. Animals were placed in outdoor enclosures with identical thermal environments, and we compared the amount of activity time with the amount of time spent in burrows, the partitioning of activity time, maximum body temperatures, and rates of heating among animals with altered absorptance to that of naturally colored animals. Neither treatment group differed in the amount of time they were active, nor did they heat or cool at different rates. Tortoises in all of the treatment groups had similar body temperatures. These results suggest that tortoises likely have physiological and

behavioral mechanisms to regulate heat exchange with the environment so as to hold body temperatures within tolerable limits irrespective of carapace coloration or absorptivity.

INTRODUCTION

The biophysical properties of an organism affect its heat exchange and thermal biology. One property, the absorptance to solar radiation, has been studied in several reptiles and has been shown to influence heating rates and temperatures achieved in lab and field studies (Cole 1943, Pearson 1977, Gibson and Falls 1979). An animal's absorptance to solar radiation can vary within an individual, among individuals, and among populations (Hutchinson and Larimer 1960, Norris 1967, Gibson and Falls 1979, Christian et al. 1996, De Jong et al. 1996, Forsman 1997, Qualls and Shine 1998, Nussear et al. 2000). While absorptance is fairly well understood in lizards especially, little has been done to examine the importance of animal absorptance to the thermal biology of turtles and tortoises (Voigt 1972, Bartholomew 1982, Cooper and Greenberg 1992).

Desert tortoises can exhibit very different pigmentation that is fixed for any given ontogenetic stage (Berry et al. 2002). Absorptance to solar radiation does not necessarily correlate with the visual appearance of the animal as the visible wavelengths account for only about half of the incident solar energy (Christian et al. 1996, Nussear et al. 2000). However, these differences in pigmentation suggest concordant differences in the amount of solar energy that can be absorbed.

In this study, the absorptance of the carapaces of desert tortoises (*Gopherus agassizii*) was altered to high (95%) and low (20%) levels, relative to their natural levels (85%) using tempera paints. Two experiments were conducted, one in which animals were allowed to behave and thermoregulate freely in outdoor enclosures, and another in which animals were immobilized and forced to warm up under the same conditions. Our hypothesis for the freely thermoregulating animals was that, relative to naturally colored animals, the tortoises with a higher level of absorptance would heat more quickly, and thus achieve higher body temperatures than naturally colored animals, and as a result would have less time during the day when body temperatures were tolerable for activity. This effect could result in either less activity time per day, or if daily activity times were of similar duration the activity would be broken into shorter bouts of activity mixed with periods of cooling in the burrow. We hypothesized that the animals in the low absorptance treatment group would heat at slower rates than naturally colored animals, and as a result would take longer times to achieve maximum body temperatures. This could result in longer time available for activity during the day, or the capacity to be active for longer periods at a time.

Because there were no differences among the treatment groups of tortoises that were allowed to thermoregulate behaviorally the second experiment was conducted explicitly to test the influence of the paints on heating rates of animals under the same thermal conditions. In this experiment, tortoises were not allowed to thermoregulate behaviorally.

MATERIALS AND METHODS

ANIMALS AND DATALOGGERS

All experiments using animals were conducted according to IACUC guidelines (University of Nevada IACUC Protocol #A00-01-25).

Ten desert tortoises (*Gopherus agassizii*) from a captive laboratory population were used in the behavioral thermoregulation portion of this study. The animals were all males ranging in carapace length from 225 to 274 mm (mean = 256 mm SD = 16 mm). Each tortoise was fitted with a datalogger (Hobotemp Model # H08-006-04, Onset Computer Corp. Pocasset MA) that recorded its body temperature as measured above the tail (Nussear et al. 2002) and the voltage produced by a flexible solar panel (3.8 x 5 cm, Single cell 0-50 ma, Iowa Thin Film Technology, Bane IA) affixed to the central vertebral scute with velcro. The solar panel was calibrated to correspond with the incident solar radiation by using a 2 ohm resistor bridged across the positive and negative terminals of the panel. The tortoises were assigned randomly to ten outdoor enclosures and to either the control or the treatment group.

Outdoor Enclosures

Each enclosure was 2.4 m by 4.9 m in area and was fenced with poultry netting on all sides, as well as the floor to prevent tortoises from escaping the pens, or digging underneath the pen walls. The pens were aligned adjacent to one another, and therefore a 0.61 m tall section of plywood was installed extending upward from the ground to prevent tortoises in adjacent pens from interacting through the poultry wire. Each pen contained an artificial burrow constructed from a 0.3 m diameter piece of PVC that was cut to 1.83 m in length. At the bottom end of the artificial burrow, a box was constructed from plywood that allowed the tortoises to turn around within the burrow. These boxes had a hinged roof that allowed access to the animals when downloading the dataloggers. Both the PVC tube and the burrow box were covered with approximately 10 cm of soil to reduce the effect of the outside environment on burrow temperature.

Environment

One of the outdoor enclosures with an identical burrow system was instrumented with a weather station which recorded environmental and operative temperatures (Zimmerman 1994) in several locations in the pen. Operative temperatures were measured using cast aluminum T_e models in the following locations: a) deep in the burrow, b) at the mouth of the burrow, c) in full sunlight , and d) in full shade.

We also measured the amount of solar radiation using a thermal pile pyranometer (Kipp and Zonen CM5, Delft, Netherlands), and wind speed with cup anemometer (Campbell Scientific model number 03101, Logan Utah). In addition, an air temperature profile was measured with shielded thermocouples (Christian and Tracy 1985) at several heights including the surface (0 cm, 1cm, 4cm, 15 cm , 21 cm), and one air temperature deep in the burrow.

ABSORPTANCE AND EMISSIVITY MEASUREMENTS

We measured the absorptance to solar radiation of desert tortoises and paint samples over the range of 180 to 2600 nm using a spectrophotometer with a reflecting sphere attachment (Model 5420, Beckman Inc., Fullerton, CA). Squares of cardboard were coated with samples of the tempera paints used on tortoises, and reflectances of the paint samples were measured. Reflectance was converted to absorptance using Absorptance = 1 – Reflectance (This calculation assumes that energy loss due to transmission was negligible). The absorptance curve was integrated in relation to a clear day solar radiation curve to give absorptance as a fraction of the percent of incident solar radiation (Nussear et al. 2000). Absorptances of the white and black tempera paints were 20% and 95% respectively.

The reflectance of the carapace for the ten desert tortoises used in the outdoor enclosure experiments were also measured on the same instrument. As tortoise coloration differs on different parts of the carapace, several sample reflectances were taken on each tortoise. Two straight lines were run across the carapace and five random points along each line were sampled for absorptance.

Absorptance values were integrated against a clear day solar incident radiation curve to calculate percent of the incident solar radiation absorbed (Nussear et al. 2000). The average absorptance for the 10 tortoises was 85%, with a standard error of 2%.

Emissivity was measured at several places on the carapace for two tortoises. Emissivity was measured using an infrared camera (Inframetrix Model 600, Inframetrix Wakefield, MA). Flat black paint (Krylon #1602) was used as a standard for comparison. Emissivity of the tortoise carapace was 0.96, which was the same as the standard for all samples taken.

Experimental Design

The ten tortoises were placed individually in separate enclosures (described above) for a seven day acclimation period, followed by a 44 day experimental period beginning on 25 July and ending on 8 September, 2001. The experiment consisted of three phases, and each phase was separated by one day during which animals were painted. (1) Control Phase - For the first all ten tortoises remained naturally colored (average absorptance to solar radiation = 85%). (2) – White phase - on day 12 the carapaces of five tortoises were painted with white tempera paint which had an absorptance to solar radiation of 20% (BestTemp White # 5060, Certified Color Corp., Santa Ana, CA). They remained painted with the white paint for an 18 day period. (3) Black phase – after being painted white for 18 days the tortoises in the treatment group were painted with black paint which had an absorptance of 95% (BestTemp Black # 5000). Tortoises were then monitored for an additional 13 days before the study was concluded.

Data from the dataloggers attached to the tortoises recorded body temperatures and the voltage generated by the solar panel at 10 minute intervals during the experiment. Presence of a voltage (above the baseline) generated by the solar panel was used as an indication that an animal was out of its burrow. We used the body temperature and solar panel measurements to calculate A) the total amount of time that animals were active during each day, B) the daily average of the duration of activity bouts, C) the number of activity bouts per day, and D) the maximum body temperature for each day of the experiment.

Each of the response variables were analyzed using a repeated measures ANOVA for each phase of the experiment. Days on which the treatment tortoises were painted were not included in the analyses. Data for some animals on some days were unavailable due to equipment failure, therefore univariate repeated measures were calculated. The significance tests reported use the Univariate Greenhouse-Geiser estimations for degrees of freedom, and corrections of the F statistics for sphericity to correct for sphericity of the error variance where appropriate.

Heating Rates

To measure heating rates of naturally colored animals and those painted with the high and low absorptance paints all animals were allowed to warm under the same environmental conditions. Eighteen tortoises (mean mass = 1847 g, SD = 548 g) were randomly assigned to one of three coloration groups. (1) Naturally colored animals, (2) animals painted with the white (20% absorptive) paint, and (3) animals painted with the black (95% absorptive) paint. Each tortoise was placed on the top of a cylinder (0.1 m diameter, 0.18 m high) to inhibit their ability to move. A 24 ga thermocouple was affixed to a position above the tail (as in Nussear et al. 2002) to record body temperatures while the animals were exposed to direct sunlight. The experiment was conducted between two greenhouses to minimize wind, thus minimizing the contribution of convection to heat exchange during the experiment.

Three operative temperature models were also placed on the top of cylinders, and were painted 1) with a paint that mimicked natural coloration (Krylon #1904) (Zimmerman 1994), as well as the 2) high (95%) and 3) low (20%) absorptance paints used on the live animals. The amount of incident solar radiation was measured with the same pyranometer as used in the exclosures. All data were recorded using a CR10X Datalogger, equipped with an AM416 Multiplexor (Campbell Scientific, Logan UT).

The animals were shaded while the thermocouples were attached. When all of the animals were set up on cylinders and thermocouples placed, the shade was removed and the animals were exposed to the solar environment, with an average incident radiation of 825 W/m^2 (SD = 6 W/m^2). The animals were allowed to warm up in this environment for 22 minutes, before the experiment was halted because some of the animals showed signs of thermal stress. Heating rates (ºC/min) were calculated for each animal. The heating rates were analyzed using an ANOVA, using treatment group as a factor and body mass as a covariate. Heating-rate comparisons between the treatment groups and each color of model were conducted using one sample t tests (Statview v 5.01, SAS Institute 1998).

RESULTS

DAILY ACTIVITY TIME

There was no significant difference in daily activity time between the two groups of animals during the control phase of the experiment ($F_{1,4}$ = 0.22, P = 0.66). There were significant differences in the amount of time that animals were active ($F_{3,12}$ = 3.28, P = 0.06) among days, and there was no significant treatment group by time interaction ($F_{3,12}$ = 0.77, P = 0.66).

There was no difference in the number of hours of daily activity for white tortoises, compared to the naturally colored animals ($F_{1,5}$ = 0.006, P = 0.94, Fig. 1). Also, there were significant differences in the amount of time that animals were active on any given day ($F_{3,18}$ = 4.52, P = 0.01), however there was no group by time interaction ($F_{3,18}$ = 1.31, P = 0.31).

There was no difference in daily activity time of black tortoises with respect to naturally colored tortoises ($F_{1,5}$ = 0.36, P = 0.58; Fig. 1). There were no significant differences in the time active among days for this part of the experiment ($F_{3,17} = 1.18$, $P = 0.35$), and there was no treatment group by time interaction ($F_{3,17} = 1.08$, $P = 0.39$).

A simple linear regression of the 24-h average of air temperature on the amount of time (hours per day) that animals were active (both treatment groups pooled) yielded a significant negative relationship with animals decreasing activity as air temperature increased ($F_{1,40} = 54.15$, $P < 0.0001$, Fig. 2).

LENGTH OF ACTIVITY BOUTS

Before any tortoises were painted (during the "control phase") there was no difference in the length of time that tortoises spent out of burrows per activity bout ($F_{1,4} = 0.13$, $P = 0.73$). There were differences in the length of activity bouts among days ($F_{3,11} = 3.72$, $P = 0.05$), but there was no time by group interaction ($F_{3,11} = 3.16$, $P = 0.07$).

When the treatment animals were painted white there were no differences in the length of activity bouts between the white tortoises and the naturally colored tortoises ($F_{1,6} = 1.13$, $P = 0.33$, Fig. 3). There was also no significant difference in the average length of activity bouts on different days ($F_{4,21} = 2.47$, $P = 0.08$), and there was no time by group interaction ($F_{4,21} = 0.74$, $P = 0.56$).

When the treatment animals were painted black there was no difference in the average length of activity bouts compared to the naturally colored tortoises ($F_{1,6} = 0.64$, $P = 0.45$, Fig. 3). There were no differences in the length of activity bouts on different days in this segment of the experiment ($F_{3,20}$ = 0.69, P = 0.58), and there was no treatment by time interaction ($F_{3,20}$ = 0.48, P = 0.71).

NUMBER OF ACTIVITY BOUTS

Before tortoises were painted (during the “control phase”) there were no differences in the number of activity bouts per day between the treatment and control groups of animals ($F_{1,4}$ = 0.30, P = 0.61). There were no differences in the number of bouts among days ($F_{3,13}$ = 0.86, P = 0.49), and there was no time by group interaction ($F_{3,13}$ = 0.35, P = 0.8)

When the treatment animals were painted white, there was no difference in the number of daily activity bouts between treatment groups ($F_{1,6}$ = 0.58, P = 0.50, Fig. 4). There were differences in the number of bouts among days ($F_{4,23}$ = 4.31, P = 0.001), however there was no treatment by time interaction ($F_{4,23}$ = 0.75, P = 0.56).

When the treatment animals were painted black, there were no differences between the treatment and control groups in the number of activity bouts per day ($F_{1,6}$ = 1.05, P = 0.34, Fig. 4). There were differences in the number of bouts among days ($F_{4,26}$ = 1.21, P = 0.02), however there was no time by treatment interaction ($F_{4,26}$ = 1.21, P = 0.33).

MAXIMUM BODY TEMPERATURE

Before tortoises were painted (during the “control phase”) the maximum body temperatures reached by animals did not differ between the two groups ($F_{1,5}$ = 0.22, P = 0.89). There was no difference in the maximum temperatures among different days ($F_{3,13}$ = 1.64, P = 0.27), and there was no time by group interaction ($F_{3,13}$ = 0.62, P = 0.60).

After the animals were painted white there was no difference between the maximum temperatures achieved by animals in the two groups ($F_{1,7}$ = 0.47, P = 0.52, Fig. 5). The tortoises had different maximum temperatures among the days of the experiment ($F_{4,25}$ = 2.79, P = 0.05), however there was no time by treatment interaction ($F_{4,25}$ = 0.66, P = 0.61).

When the animals were painted black, there was no difference in the maximum temperatures achieved by the two groups of tortoises ($F_{1,6}$ = 2.69, P = 0.15, Fig. 5). There was no significant time effect ($F_{2,15}$ = 2.7, P = 0.09), and no significant time by treatment interaction ($F_{2,15}$ = 0.55, P = 0.62).

HEATING RATES

There was no statistical difference in the heating rates among the three groups of animals ($F_{5,12}$ = 0.49, P = 0.78), and the average rate of heating was 0.15 ºC/min (SD = 0.07). Body mass was not a significant covariate in the model ($F_{2,15}$ = 0.61, P = 0.55).

The operative temperature models painted with paints having different absorptances heated at different rates (Fig. 6). The operative temperature models heated at the following rates: White 0.11 ºC/min; Natural 0.26 ºC/min; Black 0.36 ºC/min. The heating rates for the three treatment groups of tortoises were: White 0.14 ± 0.06 ºC/min; Natural 0.15 ± 0.07 ºC/min; Black 0.17 ± 0.09 ºC/min. The heating rates were not statistically different from that of the white model (White t = -1.97 df = 5, P = 0.11, Natural t = -1.23, df = 5, P = 0.27, Black t = -0.53, df = 5, P = 0.62). The heating rates of the live animals for each of the treatments were slower than the naturally colored model (White t = -5.198, df = 5, P = 0.004, Natural t = -3.85, df = 5, P = 0.01, Black t = -2.6, df = 5, P = 0.05). In addition the heating rates of the live animals for each of the treatments were slower than the black model (White t = -8.023, df = 5, P = 0.0005, Natural t = -6.144, df = 5, P = 0.002, Black t = -4.42, df = 5, P = 0.007).

DISCUSSION

Experimental manipulation of the absorptance of the carapaces of desert tortoises did not affect daily activity time, the partitioning of activity time, or maximum body temperatures when tortoises were unrestricted in outdoor enclosures. In addition, tortoises with different carapace absorptances that were placed in the same environment, but not allowed to thermoregulate behaviorally, did not heat at different rates. These results indicate that tortoises have some unknown means to alter heat exchange in relation to different rates of radiant energy absorption.

The relationship between animal coloration, and its effects on thermal biology, has been shown in several reptiles (in both lab and field conditions), to affect body temperatures and heating rates (Cole 1943, Pearson 1977, Gibson and Falls 1979). Thus, absorptance to solar radiation ultimately can influence the time that animals can remain active in the habitat on a given day or season (Pearson 1977, Christian et al. 1983, Christian et al. 1985, Grant 1990, Cooper and Greenberg 1992).

Most literature on the biophysical properties of reptiles has discussed the contribution of the animal's absorptance to the energy balance of the organism (Norris 1967, Porter and Gates 1969, Tracy 1982, Bakken 1992). While Norris (1967) cautions that the effect of the absorptance on temperature change may be lessened for animals of larger body size (but see Porter and Tracy 1983), the mathematical and physical models typically used for the calculation (or measurement) of operative temperature are influenced significantly by the absorptance of the animal to solar radiation (Porter and Gates 1969, Tracy 1982, Grant and Dunham 1988, Bakken 1992, Christian et al. 1996, Campbell and Norman 1998).

When the lizard *Liolaemus multiformus* was painted with black and silver paints, lizards painted with black paint came to higher temperatures than did naturally colored animals, and lizards painted with silver paint came to lower temperatures than either the naturally colored or the black lizards (Pearson 1977). However, the differences in equilibrium temperatures after the hour long heating experiment were only 1.5 to 2.5 ºC, and no statistical test of this difference was reported. Additionally, the heating rates of the three color groups of animals were reported to be similar. Pearson (1977) suggested that there existed a trade-off in energy balance between the increased reflectance of the silver paint absorbing less energy, and a reduced emissitivity of the paint, resulting in less thermal energy being emitting from the animal, thus minimizing the net effect of the paint. This conclusion has been shown to be based on faulty interpretation of the physics of heat exchange (Tracy 1979, Nussear et al. 2000).

Differences in emissivity among the treatment groups probably did not influence our results. Our animals had an emissivity of 0.96, which is common for living organisms. While the tempera paints may have a different emissivity, it is unlikely to have been of significance, as most paints have an emissivity of about 0.9 (Mills 1999). In fact, black tempera paint is frequently used as a standard in thermal imaging studies (Zickel 1997, Maldague 1999).

While well described in lizards and snakes, the importance of absorptance to the thermal biology of turtles and tortoises has not been well demonstrated (Boyer 1965, Hailey and Loveridge 1998). In this study, altering the absorptance of solar radiation at the animals' surface did not result in changes in daily activity time (Fig. 1), or in activity time (Fig. 3, and 4). Animals also came to the same maximal temperatures (Fig. 5). While the coloration of tortoises did not change the activity times during the day, animals had different amounts of activity among days. Activity time correlated negatively with many measurements of the environment that indicated how warm the day was in general. Among the best predictors of activity time was the 24-hour average of air temperature for each day. In general, the longest daily activity times were on days with the coolest daily average air temperature (Fig. 2).

Tortoises with different absorptances did not have different rates of heating in the same thermal environment when behavioral thermoregulation was abrogated. However there may have been physiological changes that affected heating rates, including changes in blood flow to the appendages (Voigt 1975, Turner and Tracy 1983, Dzialowski and O'Connor 1999) and/or changes in heart rate (Voigt 1975, Naegle 1976). For example, surface blood flow for two species of turtles measured using the ^{113}Xenon-clearance technique showed that blood turnover under the skin of the limbs was at least four times faster than under the carapace, and was unrelated to heart rate (Weathers and White 1971). While heart rate generally increases when heating in turtles and tortoises (Voigt 1975, Naegle 1976), it may not be a strong indication of the blood flow and its associated heat exchange at the interior surface of the carapace (Weathers and White 1971).

Previous studies of thermoregulation of desert tortoises noted that the surface of the carapace could be 8 to10 ºC warmer than internal body temperatures when animals were undergoing temperature change (McGinnis

1971, Voigt 1972). These differences were present even after one hour of bodily heating. During this time, the carapace temperature frequently exceeded lethal body temperatures for the desert tortoises. During cooling, carapace temperatures were cooler than body temperatures, allowing the animals to retain “preferred” body temperatures for greater periods of time (e.g. up to 17 hours; (Voigt 1972).

Our results strongly suggest that the carapace can provide significant insulation from solar radiation as suggested by earlier studies (Boyer 1965, McGinnis 1971). Additionally, our results suggest that the color differences that naturally occur in the carapaces of desert tortoises probably have little significance to the thermal biology of the animal. However, the carapace itself, perhaps in combination with other physiological mechanisms such as alterations of blood flow, appears to be significant to the thermal biology of the tortoise, offering protection via shielding tortoises from intense solar radiation (McGinnis 1971, Bartholomew 1982). Nevertheless, we demonstrate the absence of the predicted correlation between absorptance and heating rates. This leads us to conclude that operative temperature models generally used for ectothermic reptiles (Tracy 1982) may be inadequate for turtles and tortoises, and that other physiological mechanisms are important to heat exchange in these organisms. Therefore, we suggest further research on effects of the thermal properties of the carapace and its interaction with blood flow on the rates of heat exchange in these organisms.

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FIGURES

FIG. 1.

Length of activity time (hours per day) for painted and naturally colored tortoises in the two treatment phases of the experiment. The left half of the plot shows the period during which the treatment animals were painted white, and the right half shows the period when they were painted black. The boxes show the upper and lower quartiles (box boundaries), the median (horizontal line), mean (diamond) and the range of the data (whiskers). In addition, the average daily values for each group are shown for each box as open circles.

Fig. 2.

Average daily activity time (hours per day) as a function of average air temperature (ºC) for each day of the experiment. As the treatment groups did not differ in daily activity time data for both groups were combined.

Fig. 3.

Average length of individual activity bouts (minutes per bout) for the two groups of tortoises (painted and naturally colored). The left half of the plot shows the period that the treatment animals were painted white, and the right half shows the period that they were painted black. The boxes show the upper and lower quartiles (Box boundaries), the median (horizontal line), mean (diamond) and the range of the data (whiskers). In addition the average daily values for each group are shown for each box as open circles.

Fig. 4.

Average number of individual activity bouts per day for the two groups of tortoises (painted and naturally colored). The left half of the plot shows the period that the treatment animals were painted white, and the right half shows the period that they were painted black. The boxes show the upper and lower quartiles (box boundaries), the median (horizontal line), mean (diamond) and the range of the data (whiskers). In addition the average daily values for each group are shown for each box as open circles.

Fig. 5.

Average maximum body temperature (ºC) for the two groups of tortoises (painted and naturally colored). The left half of the plot shows the period that the treatment animals were painted white, and the right half shows the period that they were painted black. The boxes show the upper and lower quartiles (box boundaries), the median (horizontal line), mean (diamond) and the range of the data (whiskers). In addition the average daily values for each group are shown for each box as open circles.

Fig. 6.

Degrees heated by tortoises over time for the three treatment groups during the controlled heating experiment. Degrees heated (ºC) from time 0 is displayed on the ordinate, and time elapsed (min) is given on the abscissa. The three groups of tortoises are represented by circles, error bars are 95% confidence limits for the mean at each minute. The three operative temperature models are given by the squares connected with lines. No error bars are given for operative temperature models as only one of each color was used.

Fig. 1

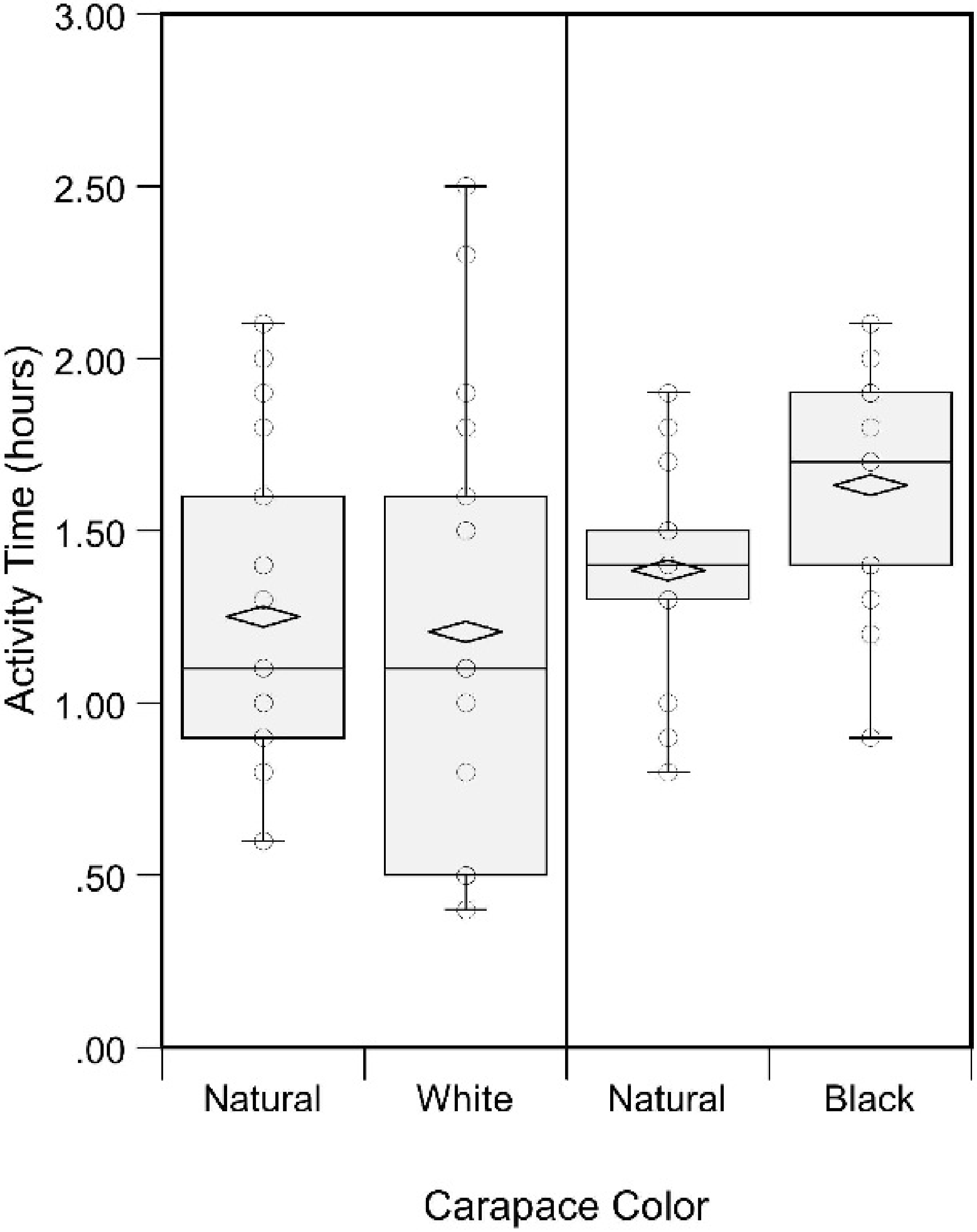

3.00
2.50
2.00
1.50
1.00
.50
.00
Activity Time (hours)
Natural
White
Natural
Black
Carapace Color

Fig. 2

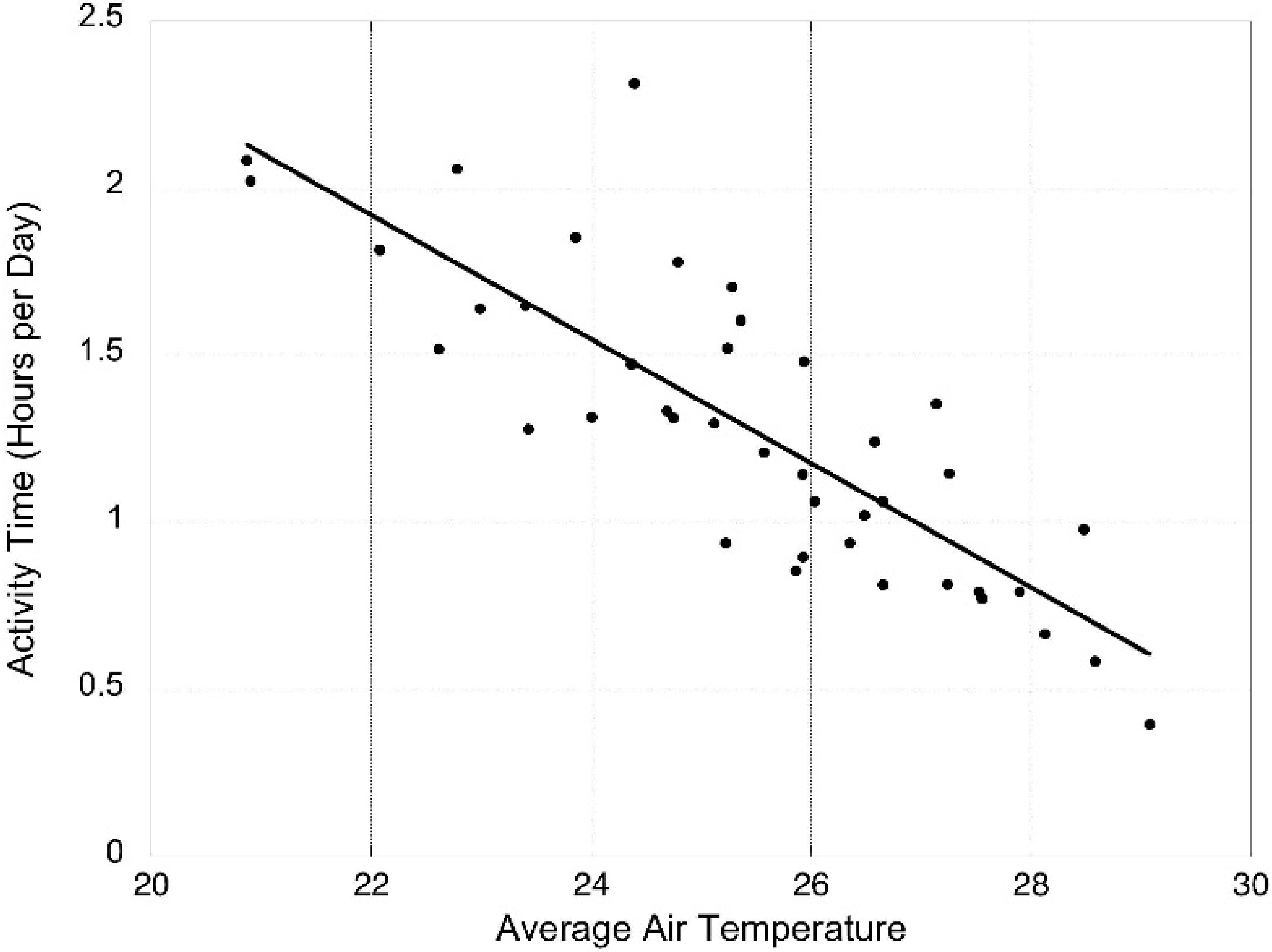

Activity Time (Hours per Day)
2.5
2
1.5
1
0.5
0
20
22
24
26
28
30
Average Air Temperature

Fig. 3

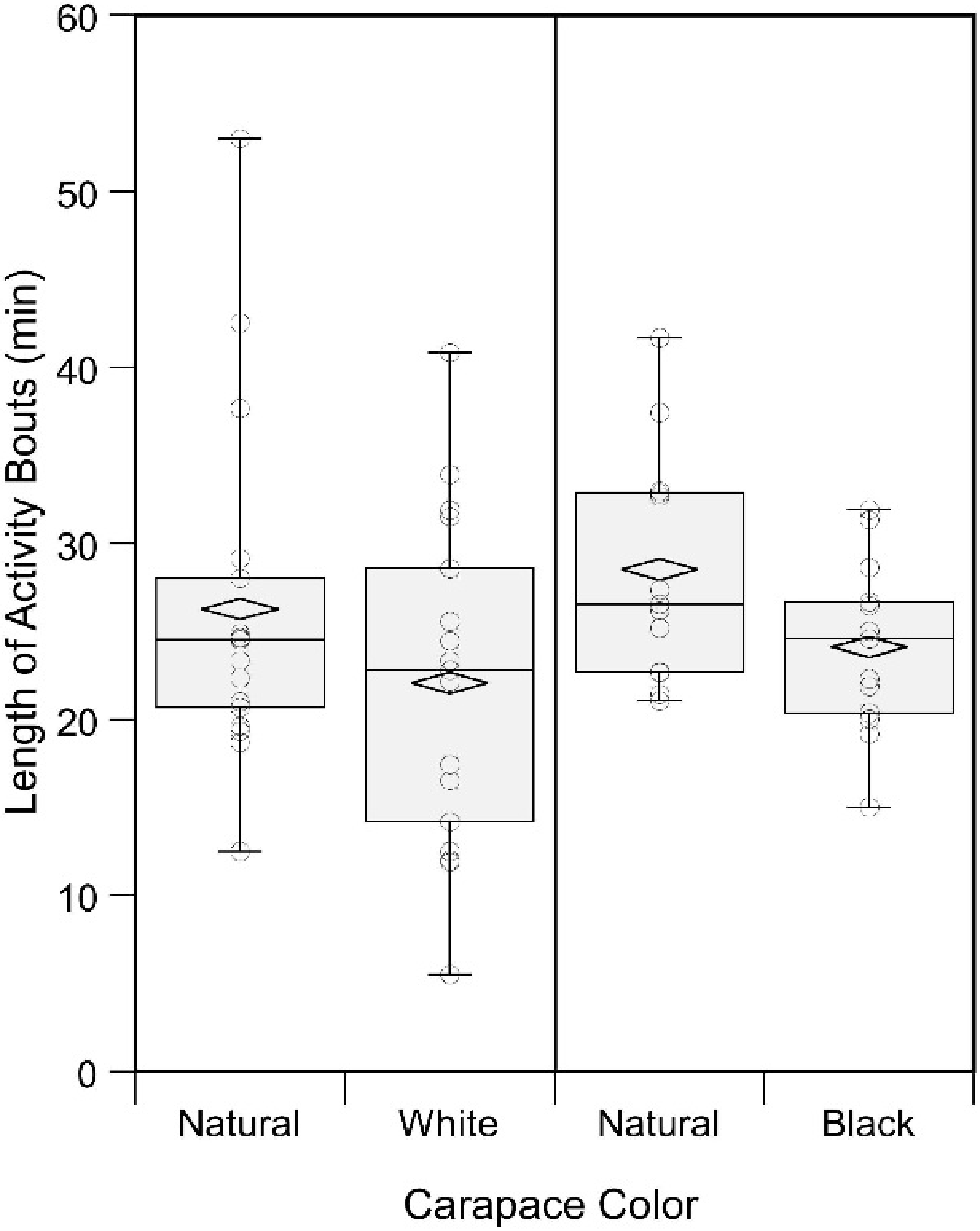

60
50
40
30
20
10
0
Length of Activity Bouts (min)
Natural
White
Natural
Black
Carapace Color

Fig. 4

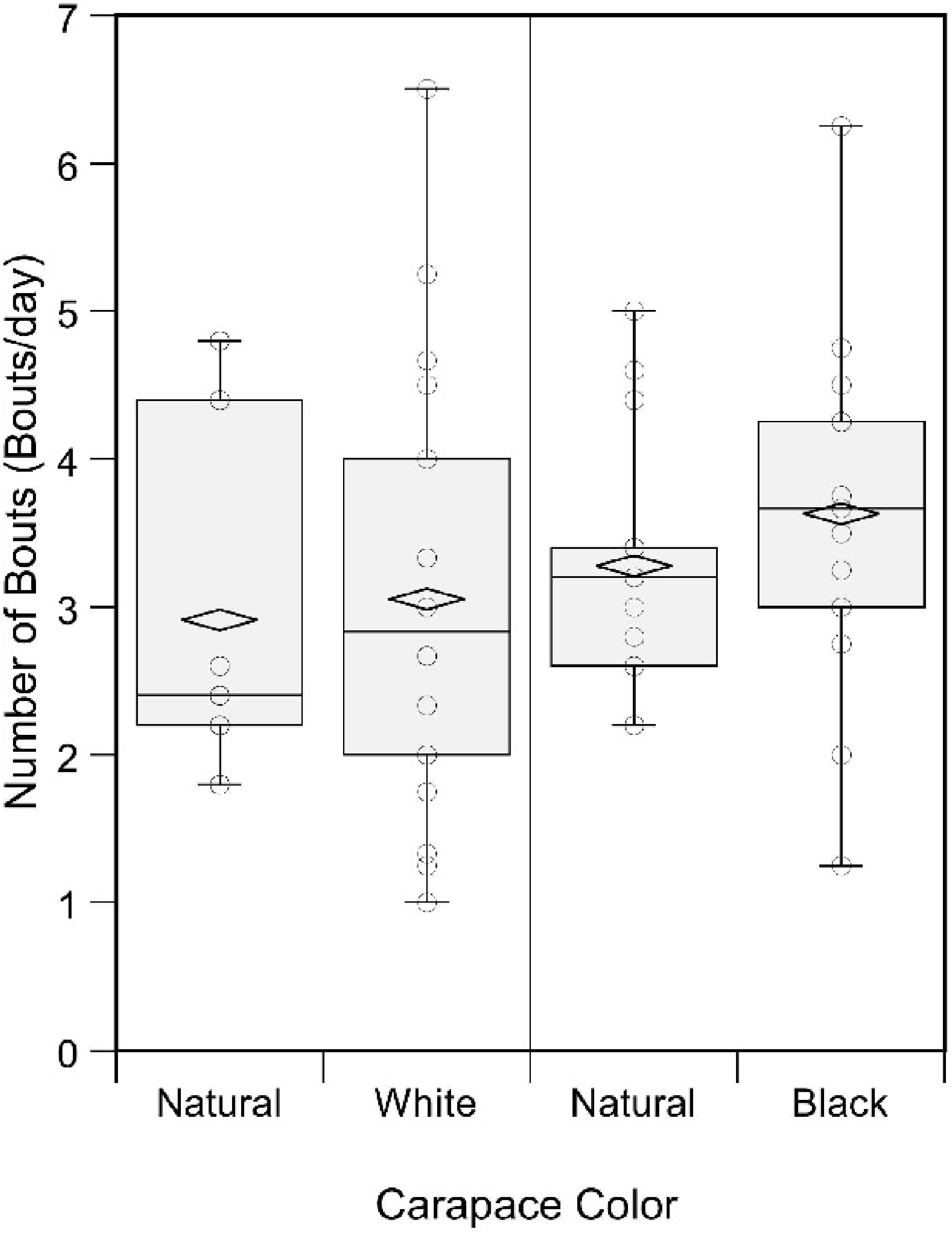

7
6
5
4
3
2
1
0
Number of Bouts (Bouts/day)
Natural
White
Natural
Black
Carapace Color

Fig. 5

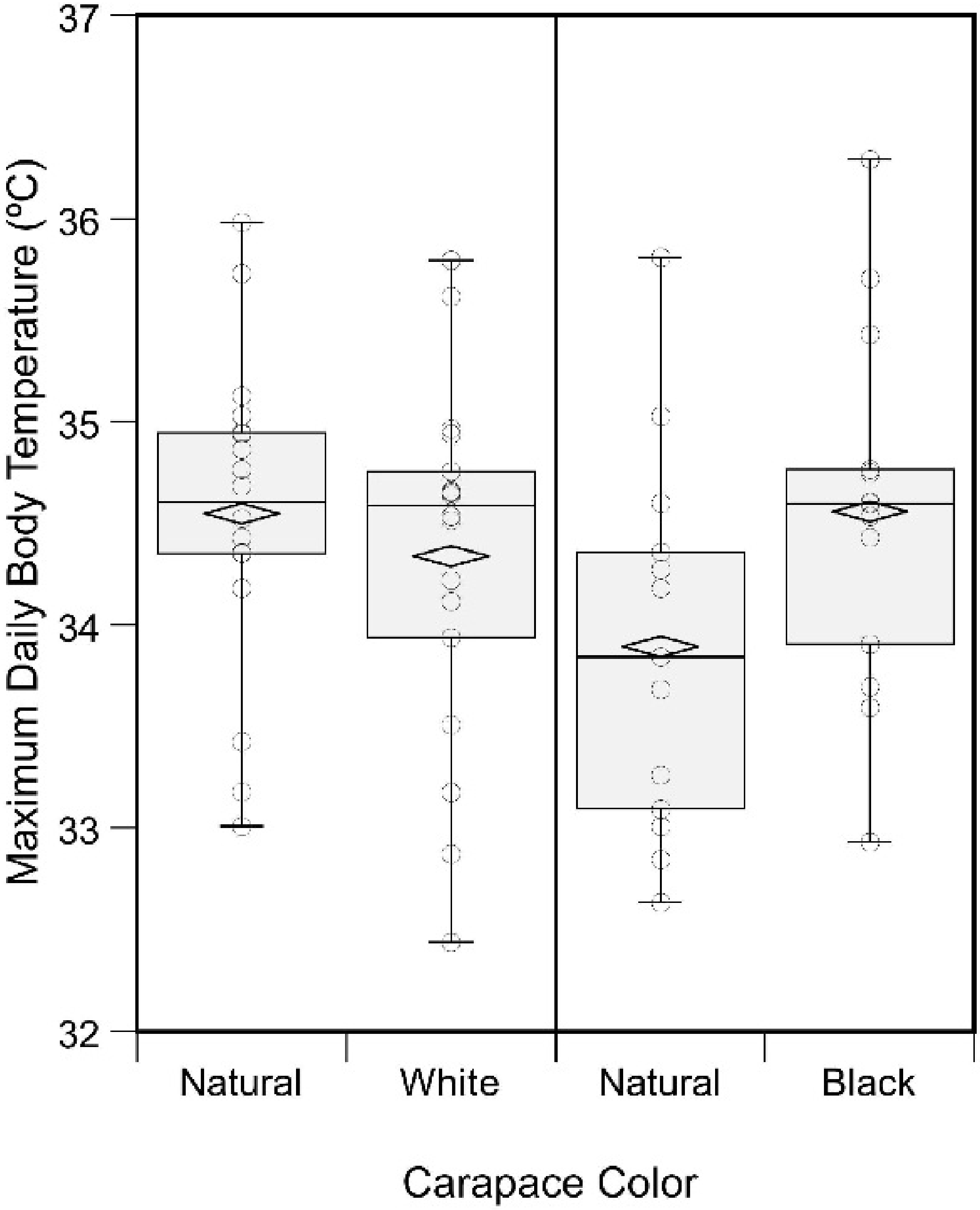
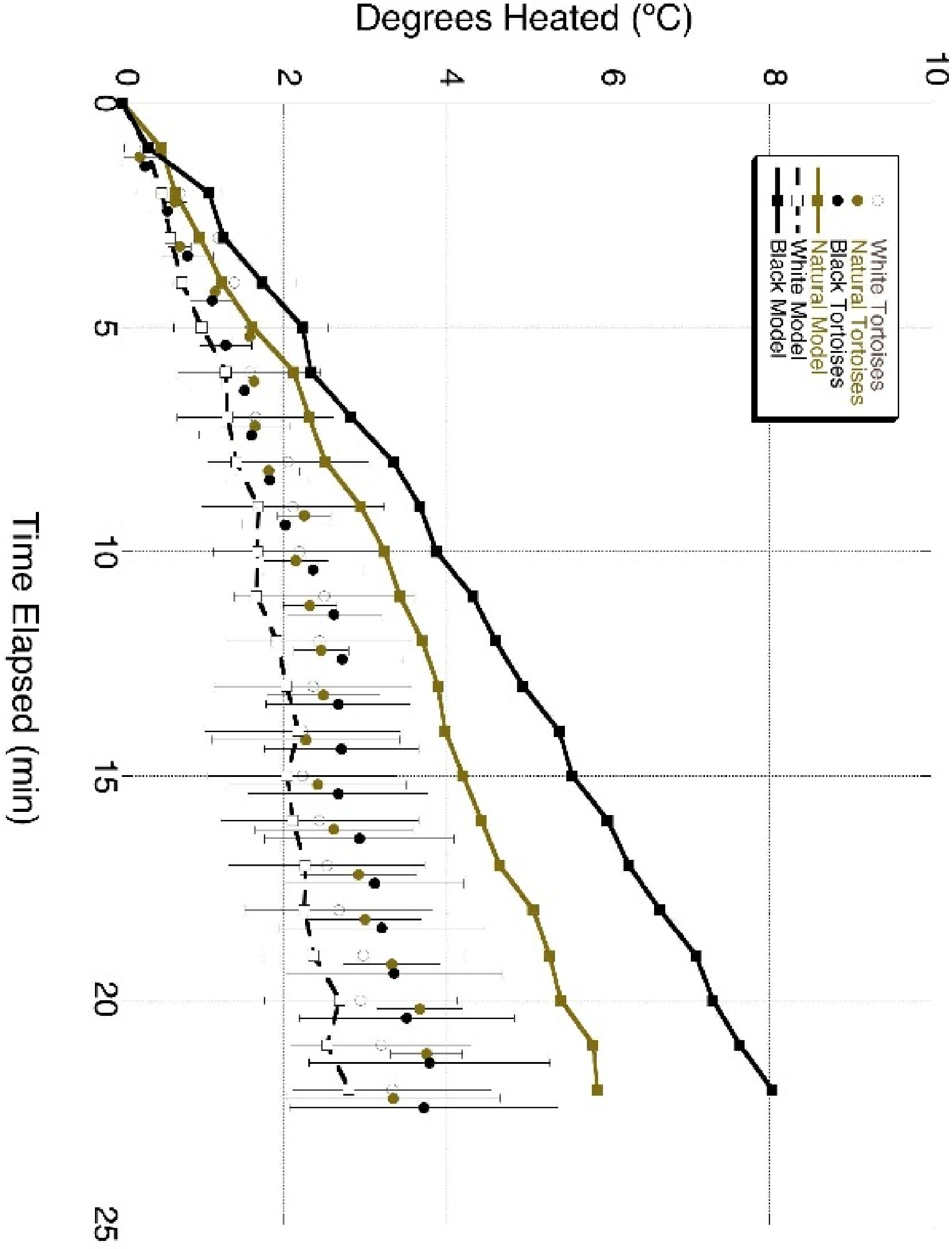

37
36
35
34
33
32
Maximum Daily Body Temperature (ºC)
Natural
White
Natural
Black
Carapace Color

Fig. 6


Degrees Heated (°C)
0
2
4
6
8
10
Time Elapsed (min)
0
5
10
15
20
25
○ White Tortoises
● Natural Tortoises
● Black Tortoises
Natural Model
White Model
Black Model

Chapter 4. Can modeling of desert tortoise activity improve population monitoring for desert tortoises?

ABSTRACT

The federally-listed desert tortoise is currently the focus of a large, multi-state monitoring program that uses Distance Sampling to estimate population densities from surveys collected using transects. A critical assumption of this technique is that **all** animals very close to the transect line are observed. Because desert tortoises spend large proportions of the year in underground burrows, this assumption cannot be met. Therefore, the standard transect technique requires a correction factor that accounts for the proportion of animals active and available to be counted (g_0). This correction factor (g_0) is currently estimated from daily censuses of small populations of tortoises (6 – 12 individuals). Collecting these data is costly, and the estimate of g_0 obtained lacks precision due to the small sample sizes used. We used data from a very large experimental population to model the proportion of animals active as a function of the biophysical attributes of the environment. Inputs to the model included environmental temperatures, operative temperatures, rainfall, and solar radiation. Modeling activity did not improve the precision of estimates of availability (g_0) over inferences from the small experimental populations. We assessed the repeatability of tortoise activity by determining the extent to which activity on any given day predicted activity on the subsequent days, given similar environmental

conditions. Tortoise behavior was correlated on consecutive days, however there was very little explained variance in the relationship between the proportion of animals active on consecutive days, indicating that behavior was not repeatable.

INTRODUCTION

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

Beginning in the 1970s, desert tortoise densities were estimated for several dozen permanent study plots (PSPs) (most commonly 1 mi^2 in area, but some were larger plots) located throughout the Mojave desert (Berry 1984). Density on the plots was generally estimated using capture recapture methods based on two thirty-day surveys of the plots. While there are long-term tortoise density data available from these study plots, the methods used to select and analyze the plot data violated many of the statistical assumptions of capture-recapture estimators (Bury and Corn 1995). In addition, the plots were not randomly placed and were of insufficient numbers within the management units designated by the 1994 Recovery Plan to be representative of those areas. Density estimates from the permanent study plots frequently had high variances because relatively few animals were found on the plots in some years (Berry 1984, Freilich et al, 2000). Indeed, sampling on several of the study plots was discontinued due to low numbers of tortoises encountered. Thus, PSPs were not recommended in the Recovery Plan as the method of choice to be used for long-term monitoring of desert tortoise population densities.

Range-wide monitoring of population size was initiated in 1996, using stratified random transects in all 14 Desert Wildlife Management Areas (DWMAs) contained in the six Recovery Units (Fig. 1; U. S. Fish and Wildlife Service 1994, Anderson et al. 2001). Estimates of tortoise population density within DWMAs have been calculated from the observations of tortoises along transects using “distance sampling” calculations (Anderson et al. 2001, Buckland et al. 2001). This equation is:

$$D=\frac{n}{(l \times w \times P_a} \qquad \text{EQ. 1)}$$

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

Desert tortoises spend much of the year in burrows even during the active season (Woodbury and Hardy 1948, Marlow 1979, Nagy and Medica 1986, Bulova 1994), and only the proportion of the tortoise population that is above ground is usually sampled. This can lead to a violation of a critical assumption of the distance sampling technique, namely, that all animals on the line are found (Anderson et al. 2001, Buckland et al. 2001). Above ground availability (g_0) is currently estimated by monitoring the proportion of radio telemetered animals (N = 6 - 12) that are visible to observers at several sites within the desert tortoise recovery units (Anderson et al. 2001).

The goal of this study was to explore the error induced by estimating g_0 from observations of small focal populations and to explore the extent to which using a new approach (modeling) to estimate g_0 using a suite of environmental conditions was possible.

MATERIALS AND METHODS

POWER ANALYSIS

An analysis was conducted to estimate the statistical power to detect growth in populations at different growth rates and with different degrees of error in the density estimates. The power analysis was conducted using computer simulations (Link and Hatfield 1990) of population growth for populations with a constant average growth rate for a 25 year period. The simulated growth rates ranged from 1 to 5% annual growth in increments of 1% (Hatfield et al. 1996). The coefficients of variation for the density estimates ranged from 5% to 100% in increments of five percent for each subsequent analysis (Fig. 2).

Each simulated population started with 1000 individuals. The populations were simulated to grow at a specified average population growth randomly modified according to a specified coefficient of variation. Thus a population of N_{t+1} at time (t+1) is calculated as a product of the population a year prior (N_t) multiplied by λ randomly varying according to a normal distribution of variation, with a specified coefficient of variation.

$$N_{t+1}=N_t\times f(\lambda,C \qquad \text{EQ. 2}$$

Each simulated population was allowed to grow for 25 years and the annual population sizes were regressed against time. One thousand simulations of population growth with each set of population parameters (λ and CV) were simulated to determine the proportion of regressions that were statistically significant – this is power (Hatfield et al. 1996).

SOURCE OF DATA FOR CALCULATING G_0

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

Approximately 150 adult desert tortoises at one site were tracked weekly over a three year period (1997 - 1999) using hand held radio telemetry receivers (e.g., Telonics TR-2, Mesa AZ). Radio transmitters (AVM models G3, SB2, or SB2-RL) were attached to each tortoise in a manner similar to that described in Boarman et al. (1998). The body of the transmitter was attached with epoxy to the first costal scute, usually on the left side of the animal, to provide the best positioning of the antenna. The antenna was then affixed (with epoxy) to the center of each costal scute from front to rear, wrapping around the back of the animal and continuing forward on the opposite side. Silicone caulk was used to secure the antenna in the scute margins to allow for growth of the animals (Boarman et al. 1998). All tortoises were numbered with a paper tag covered with clear epoxy, and notched on the marginal scutes by creating a small groove using a triangular file (Cagle 1939).

When tortoises were located the date, time, and the microhabitat of the animals were recorded. Microhabitats were categorized as in the open, under vegetation, in a pallet (a shallow shelter that does not completely cover the tortoise, Bulova 1994), or in a burrow (Fig. 3). Microhabitat data were further reduced to indicate whether an animal was above ground (i.e. under vegetation or in the open), or below ground (i.e., in a burrow or a pallet) to estimate the proportion of animals above ground (i.e., available to be sampled; g_0) from the microhabitat data as a function of year, season, week, and time of day (Fig. 4).

ENVIRONMENT

A weather station recorded environmental and operative temperatures (T_e) (Bakken et al. 1985) at a central location on the study site. Operative temperatures were measured using cast aluminum operative temperature models of both juvenile (CL = 80 mm), and adult sized (CL = 240 mm) tortoises in full sun, and in shaded microhabitats (Zimmerman 1994) . The amount of solar radiation (W/m^2) was measured using a pyranometer (Li-Cor model number LI-200SA, Lincoln, Nebraska USA). Wind speed (m/s) was measured at a height of 1 m from the surface with a cup anemometer (Campbell Scientific model number 03101, Logan Utah). Air temperatures were measured at 10 cm, 20 cm, and 40 cm above the ground with shielded thermocouples (Christian and Tracy 1985). Soil temperatures were measured at the surface, 10 cm, 20cm, and 70 cm below the surface. All thermocouples were 24 ga. type k (Omega Engineering, Stamford CN). Data were recored using a CR-10 X datalogger with an AM416 multiplexer (Campbell Scientific, Logan Utah).

AVERAGE AND VARIANCE OF G_0 WITH SAMPLE SIZE.

To determine the average error possible in estimates of the proportion of tortoises that were above ground and available to be censused, the microhabitat locations of 376 observations of tortoises from May 24, 1999 to June 18, 1999 were scored as either above ground (1), or below ground (0). Incremental samples ranging from 3 to 150 observations were drawn randomly from the full dataset of 376 locations, and the average and standard deviation of the location scores were calculated. The mean and standard deviation for each sample size was repeated for 100 random draws (with replacement) of observations at each sample size (Fig. 5).

A power function was fitted to the curve created by the standard deviations of the measurements ($y = 0.5479 * x^{-0.5678}$), and the first derivative of the fitted function ($dy/dx = 0.0311 * x^{-1.5678}$) was used to display the number of samples at which there was relatively little change in the reduction of the standard deviation as sample sizes increased (Fig. 5).

MODEL OF G_0

We used an Artificial Neural Network (ANN) to model daily tortoise activity (g_0) as a function of 18 site-specific environmental variables recorded with the weather station described above (Fig. 6), including daily values of maximum solar radiation, rainfall, average wind speed, and minimum, maximum, and average temperatures of air, soil, and operative temperature (T_e) models (Bakken et al.

1985). The model was constructed from 334 days of input using 65% of the data for training, 25% for cross-validation, and 10% for testing the network. Specifically, the neural network was a back-propagating network consisting of one hidden layer of four processing elements and one hidden layer, using Tan-h transfer functions, with a momentum-learning-rate of 0.7 per epoch (Principe et al. 1999). Weight decay was enabled to allow model inputs to drop out of the model if they did not contribute to the prediction of g_0. The network was constructed using NeuroSolutions for Excel (Version 4.2, Neuro Dimension Inc., Gainesville FL).

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

REPEATABILITY OF G_0

To assess the repeatability of tortoise activity across time, consecutive pairs of days were chosen from three years so that the difference in the maximum operative temperature between the first and second day was not greater than 5 ºC. The average number of tortoises active on the first and second days were then regressed against one another to give an indication of the repeatability of percent activity for the tortoise population on similar days, expressed as Pearson's correlation coefficient (r).

RESULTS

POWER ANALYSIS

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

MICROHABITAT USE

The proportions of animals that were found in underground microhabitats over the three year study period ranged from 60 to 75% (Fig. 3). In addition, the numbers of animals in different microhabitats differed among years ($\chi^2 = 324.317$, df = 6, $P < 0.0001$).

Tortoises used burrows more than the other three microhabitats (Fig. 3). The proportion of animals active varied annually, seasonally, weekly, and even over the course of a day (Fig. 4). For example, high levels of spring activity in April and May of 1998, were not as great in either 1997 or 1999. The period of activity in the fall of 1997 (~ October), was qualitatively higher than that seen in either of the other two years. Activity varies as a function of time of day, but this variation was not consistent throughout the season, or among years. For example, the variation in the proportion of animals active during spring in 1997 was greater than that for 1998.

AVERAGE AND VARIANCE OF G_0 WITH SAMPLE SIZE

Sample size had a large influence on the precision of the estimates of g_0 (Fig. 5). An average of 100 estimates of the proportion of animals active was very similar to the average of the population of 150 tortoises, However, as would be expected, the variance of the estimates was greater for smaller sample sizes. The reduction in the variance of the estimates of activity was not linearly related to the number of samples. A power function was fitted to the curve created by the standard deviations of the means with an explained variance of 97%. The rate of change of standard deviation (where the first derivative of the power function fit to the standard deviations approached 0) indicates that at least 20 to 30 animals should be sampled to minimize the variance in g_0 estimates. Samples in excess of 30 did little to reduce the variance in the standard deviation around the mean. The sample size required to achieve a coefficient of variation in the estimate of g_0 (let alone other sources of variation implicit in the sampling technique) of less than 12% (see power analysis above) was approximately 87 to 100 animals. This implies that focal populations may never be of sufficient size to precisely estimate g_0.

NEURAL NETWORK MODEL

The neural network model of tortoise activity yielded a significantly correlated estimate of modeled g_0 and measured g_0 ($F_{1,82} = 58.3$, $P < 0.0001$), but explained only 42% of the variance in g_0 (Fig. 6). This level of explained variance corresponded to a CV of ~44%, which was far greater than the 12% CV that would be required to detect a 1% growth rate in tortoise populations over a 25 year period. The inputs to the model which were most influential were the maximum daily temperature of the large T_e model , the surface temperature in a shaded microhabitat, and the daily average of the large T_e model in the sunny microhabitat (Table 1).

REPEATABILITY

The proportions of tortoises active on the first versus the second consecutive day were significantly correlated. However, this correlation explained only 29% of the variance ($r = 0.54$; Fig. 7). Thus, while tortoises avoid lethal extremes in the environment (Zimmerman et al. 1994), they may not be equally active on days with hospitable conditions, suggesting that the daily activity of adult tortoises on average is not tightly coupled to the environment.

DISCUSSION

The recovery plan for desert tortoises lists several criteria that must be satisfied for desert tortoise populations to be delisted. The foremost criterion requires that there be a statistically significant upward or level trend in population size over a 25 year period (U. S. Fish and Wildlife Service 1994). The maximum reasonable population growth rate for tortoise populations has been estimated to be approximately 1% per year under ideal reproductive conditions (U. S. Fish and Wildlife Service 1994). The power analysis herein indicates that to detect a trend over a 25 year time period with a 1% annual growth rate, the coefficient of variation about the density estimates would have to be 12% or less.

Current estimates of population density from range-wide transect sampling for desert tortoises for the years 2001 through 2003 have coefficients of variation that range from 9.5 to 56.2%, depending on the year and area sampled (Medica pers comm.). With this magnitude of variation tortoise populations would have to increase at rates of at least 4% per year to detect an upward trend in a 25 year period with sufficient power (Cohen 1988). Alarmingly, tortoise populations could decline up to 4% per year, and still not be distinguishable from populations with no statistical trend at all. Small differences in the estimate as a result of the variance of g_0 can cause large differences in the density estimates of tortoises. Clearly more precision in the population density estimates is necessary to make sound decisions regarding the recovery and conservation of this species, as the error present in the current sampling method is exceedingly high (Gerrodette 1987, Taylor and Gerrodette 1993, Freilich et al. 2004).

The difficulties of sampling desert tortoises for population densities largely result from the fossorial lifestyle of the species (Freilich et al. 2004). Tortoises spend much of the year in underground burrows (Fig. 2, and 3) (Woodbury and Hardy 1948, Marlow 1979, Nagy and Medica 1986, Bulova 1994), and the patterns of tortoise activity vary annually, seasonally, and daily (Fig. 4)(Freilich et al. 2000, Anderson et al. 2001), yet none of this variance is accounted for in current estimates of g_0, which is critical because an improperly calculated g_0 will impart significant error to density estimates. Both of the modifiers to the density estimation equation (P_a and g_0) are influenced by tortoise activity and the mechanisms determining these patterns (EQ. 1). The precision of the detectability estimate (P_a) calculated by distance sampling is largely influenced by the numbers of animals encountered on the transect. A sample must comprise at least 60 - 80 animals to estimate P_a with adequate precision (Buckland et al. 2001). To achieve sample sizes of 60-80 tortoises, animals in burrows have been included in the samples. However, statistically the animals in burrows are treated in the same way as animals on the surface. Specifically, the different probability of detecting burrows as a function of distance from the line, and the detectability of tortoises in those burrows have not been evaluated. Additionally**,** the proportion of animals above ground, which should equal g_0 in the strictest sense is influenced by the sample size of focal populations (Fig. 5), and by the times of year that tortoises are sampled (Fig. 4).

Some years may have so few tortoises active that the numbers of animals encountered on transects will be low, and the precision about the estimate of P_a will be low (e.g. Fig. 4, 1999). Other years may have high variability in the proportion of animals active as a function of the week of the year, or time of day during the sampling period (e.g. Fig. 4, spring of 1997). If this inherent lack of precision in the estimation of the availability of animals to be sampled is unquantified, the error, will be unrealized and will be incorporated into the estimates of tortoise density in unknown magnitudes.

Focal observations of 8 - 10 tortoises per site are currently used to infer g_0 during the sampling period. If focal populations are used, the number of animals included in the sample is important to the precision and accuracy of the g_0 estimate. Monte Carlo simulations of g_0 measured from a radio-telemetered population of approximately 150 animals indicate that the sampling error associated with samples of eight to twelve animals (the number of focal animals used in many of the focal sites) may lead to errors in the estimation of g_0 as high as 50% (Fig. 5). This level of error results in density estimates that can vary by as much as 100%. Additionally, even if the sample sizes are increased to twenty or thirty animals, the variance in the estimates of g_0 resulting from “snap shot” monitoring of focal animals remains as high as 25 % (in this analysis). Indeed, a population of approximately 100 tortoises would be required to achieve a coefficient of variation for g_0 alone that was 12% (Fig. 5). Thus, precise estimates of g_0 may require large focal groups that would be prohibitively costly, and may not reduce the error in the estimation of g_0 sufficiently to increase the precision of annual density estimates to acceptable levels.

We modeled tortoise activity as one possible approach to create a more cost effective and precise means of estimating g_0. Artificial neural networks are capable of resolving complex interactions of many variables, and for this reason they are beginning to be used widely for ecological modeling (Lek and Guegan 1999). ANN models can be resolved to reveal the most informative parameters contributing to the model to give insight into what must be measured in the field, and what data are not informative (Olden and Jackson 2002). Neural network models are currently being applied toward predicting the abundance of animals in a population as a function of meteorological parameters (Lusk et al. 2001), and we adopted a similar approach toward modeling tortoise activity.

We modeled the proportions of animals active on a given day as a function of several environmental variables related to the biophysical environment of desert tortoises (Zimmerman 1994, Hillard 1996) (Fig. 6). This model had a high level of variance around the mean predictions. In fact, the amount of variation explained by our model is roughly equivalent to that expected using focal populations to estimate g_0. Thus, our initial model does not create an improvement over using focal animals to estimate g_0.

To test the precision with which it is possible to model g_0, we examined the repeatability of activity estimates, under similar environmental conditions, of the proportion of tortoises that were active on consecutive days (Fig. 7). Despite similar environmental conditions, the proportion of tortoises active on consecutive days was only weakly correlated (Fig. 7). This indicates that the behavior of tortoises is not especially predictable based upon environmental variables alone. This may place limitations on our ability ever to model tortoise activity.

SUMMARY

- Estimates of desert tortoise densities are needed for a key delisting criterion important to management of this federally listed species, but current density estimates have such high variability that the detection of subtle trends in population sizes is difficult (or impossible).
- Tortoises spend much of the year in underground burrows, and this makes estimating the density of tortoises very difficult.
- Tortoise activity varies greatly across many time scales.
- Estimates of tortoise activity influence population density estimates, and currently lack precision
- Modeling of tortoise activity as a function of environmental conditions also lacks precision
- Tortoise activity is not tightly correlated on days with similar environmental conditions
- It may not be possible to estimate tortoise activity precisely using modeling activity.

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TABLES

TABLE 1.

Sensitivity analyses of the input variables to the results of the Artificial Neural Network. Air and Soil temperatures are expressed in centimeters above or below the surface. The sensitivity analysis consisted of running the model with each input value set at one standard deviation above and below its mean, and measuring how much the output varied. The influence on g_0 is the standard deviation of each output divided by the standard deviation of each input.

Inputs to Model	**Influence on g_0**
Max of Large Te in Shade	0.027
Max of Surface Temp in Shade	0.024
Average of Large Te in Sun	0.021
Average of Tair (20 cm)in Shade	0.017
Max of Small Te Model in Sun	0.016
Average of Small Te Model in Sun	0.014
Average Soil Temp (-30cm) in Sun	0.013
Min of Small Te Model in Shade	0.013
Average of Large Te model in Shade	0.009
Average of Soil Temp (-10 cm) in Sun	0.007
Average of Small Te model in Shade	0.006
Average soil temp (-70cm) in Sun	0.005
Min of Small Te model in Sun	0.005
Max of Large Te model in Sun	0.003
Max of Surface temp in Sun	0.002
Average of Tair (40 cm) in Sun	0.002
Average of Wind Speed (m/s)	0.001
Average of Tair (40 cm) in Shade	0.001

Figures

Fig. 1.

Map of transects surveyed during the 2001 season. The cream colored background indicates the distributional range of desert tortoises as given in (Germano et al. 1994), The filled triangles indicate transect locations. The black outlined boundaries are the DWMAs designated in the 1994 Recovery Plan.

Fig. 2.

Power to detect growth different trends in annualized population growth rates as a function of the coefficient of variation of the density estimates. The coefficient of variation is given on the abscissa, and the power to detect growth is given on the ordinate. The curves on the graph represent the power to detect different population growth rates.

Fig. 3.

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

Fig. 4.

The proportion of animals active for each hour of the day calculated from daily tracking of 150 tortoises at Bird Spring Valley, Nevada. The proportion of tortoises active is denoted by the color, where blue colors indicate low levels of activity, and red denotes high levels of activity.

Fig. 5.

Variance in g_0 as a function of the number of tortoises sampled. The mean activity for each 1000 random draws is given by the dots, and the error bars are one SD of the mean value. The first derivative of the function fitted to the standard deviations is given as the solid line that originates below 0 on the y axis.

Fig. 6.

Measured vs. modeled g_0 for Bird Spring Valley, Nevada for 1997 to 1999 using an artificial neural network model. The proportion of animals active that was measured is given on the abscissa, and the modeled proportion of animals active is given on the ordinate.

Fig. 7.

Repeatability of g_0 on consecutive days with similar environmental conditions. Animal activity on the first of two consecutive days is given on the abscissa, and activity of animals on the second day is given on the ordinate.

Fig. 1

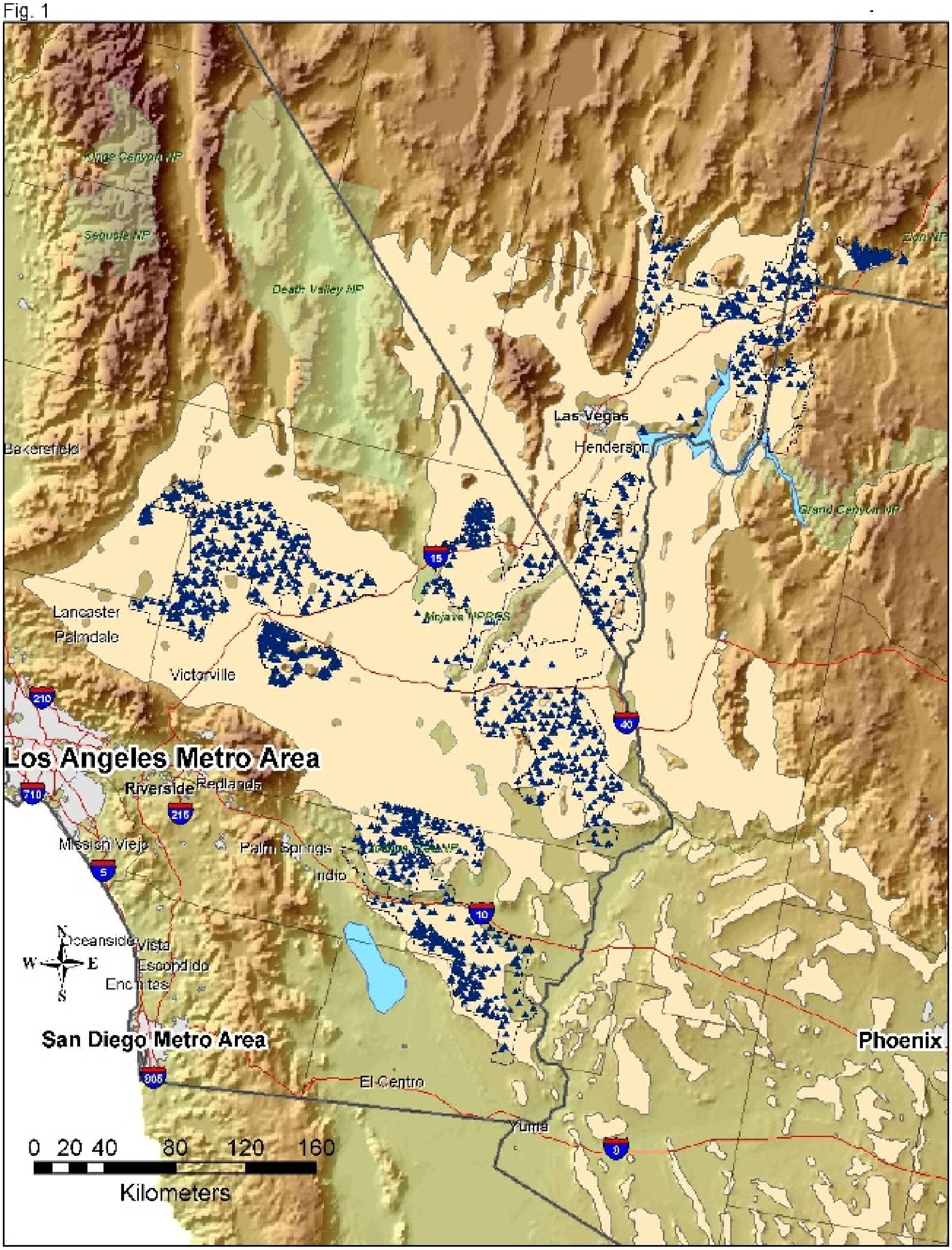

Kings Canyon NP
Sequoia NP
Death Valley NP
Zion NP
Las Vegas
Henderson
Bakersfield
Grand Canyon NP
15
Mojave NPRES
Lancaster
Palmdale
Victorville
210
40
Los Angeles Metro Area
710
Riverside
Redlands
215
Mission Viejo
Palm Springs
Joshua Tree NP
Indio
5
10
N
W
E
S
Oceanside
Vista
Escondido
Encinitas
San Diego Metro Area
Phoenix
805
El Centro
Yuma
8
0
20
40
80
120
160
Kilometers

Fig. 2

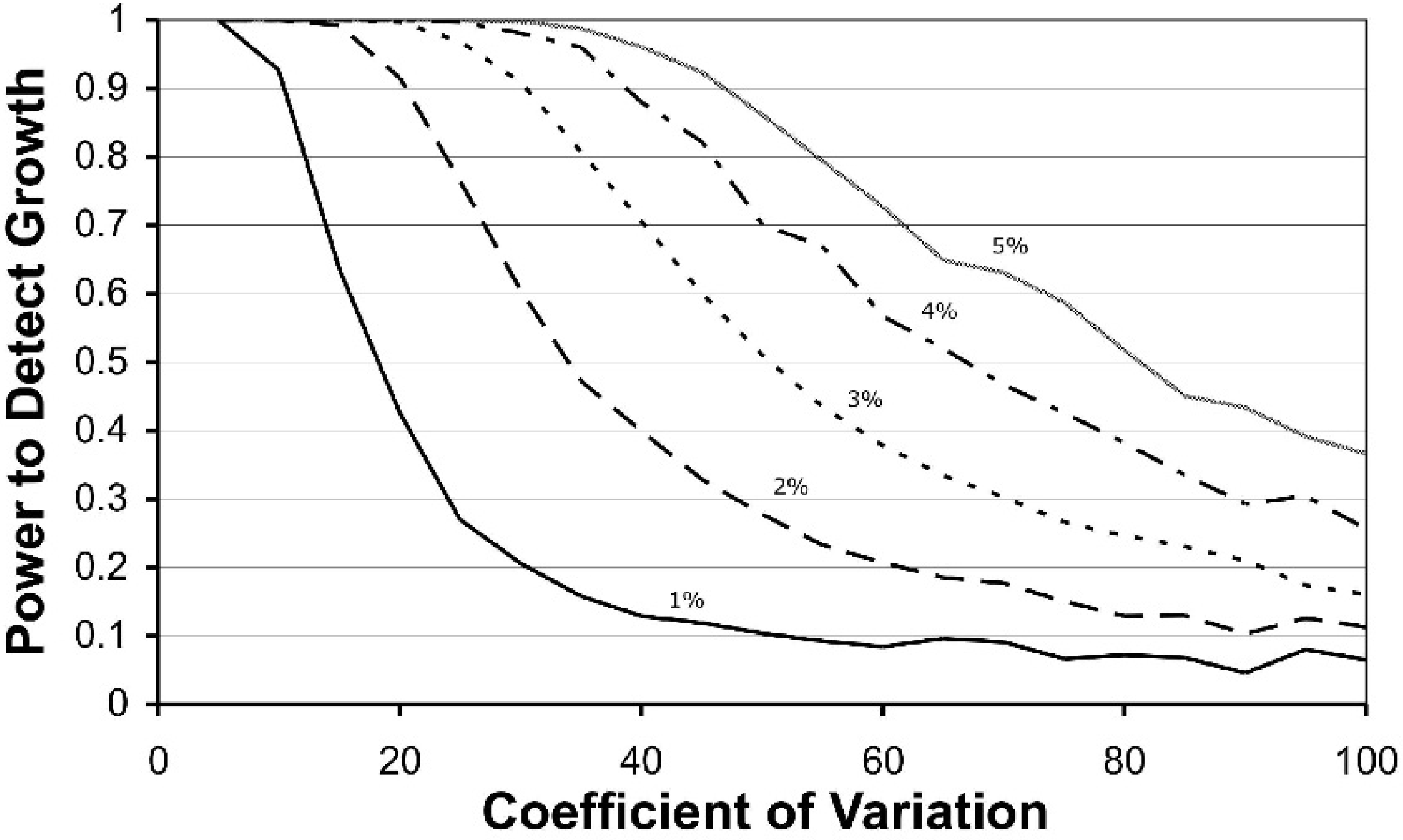

Power to Detect Growth
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
5%
4%
3%
2%
1%
0
20
40
60
80
100
Coefficient of Variation

Fig. 3

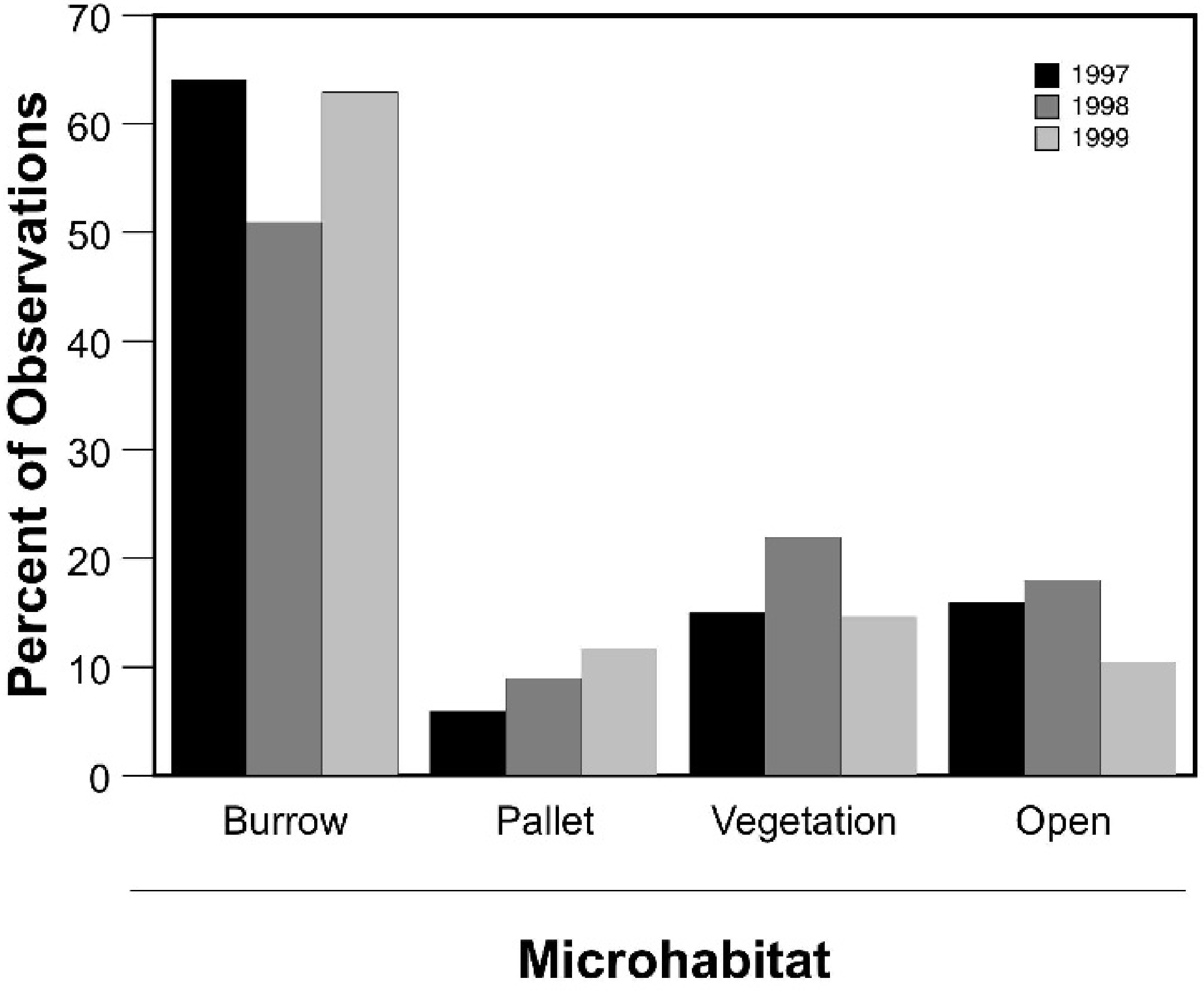

70
60
50
40
30
20
10
0
Percent of Observations
■ 1997
■ 1998
□ 1999
Burrow
Pallet
Vegetation
Open
Microhabitat

Fig. 4

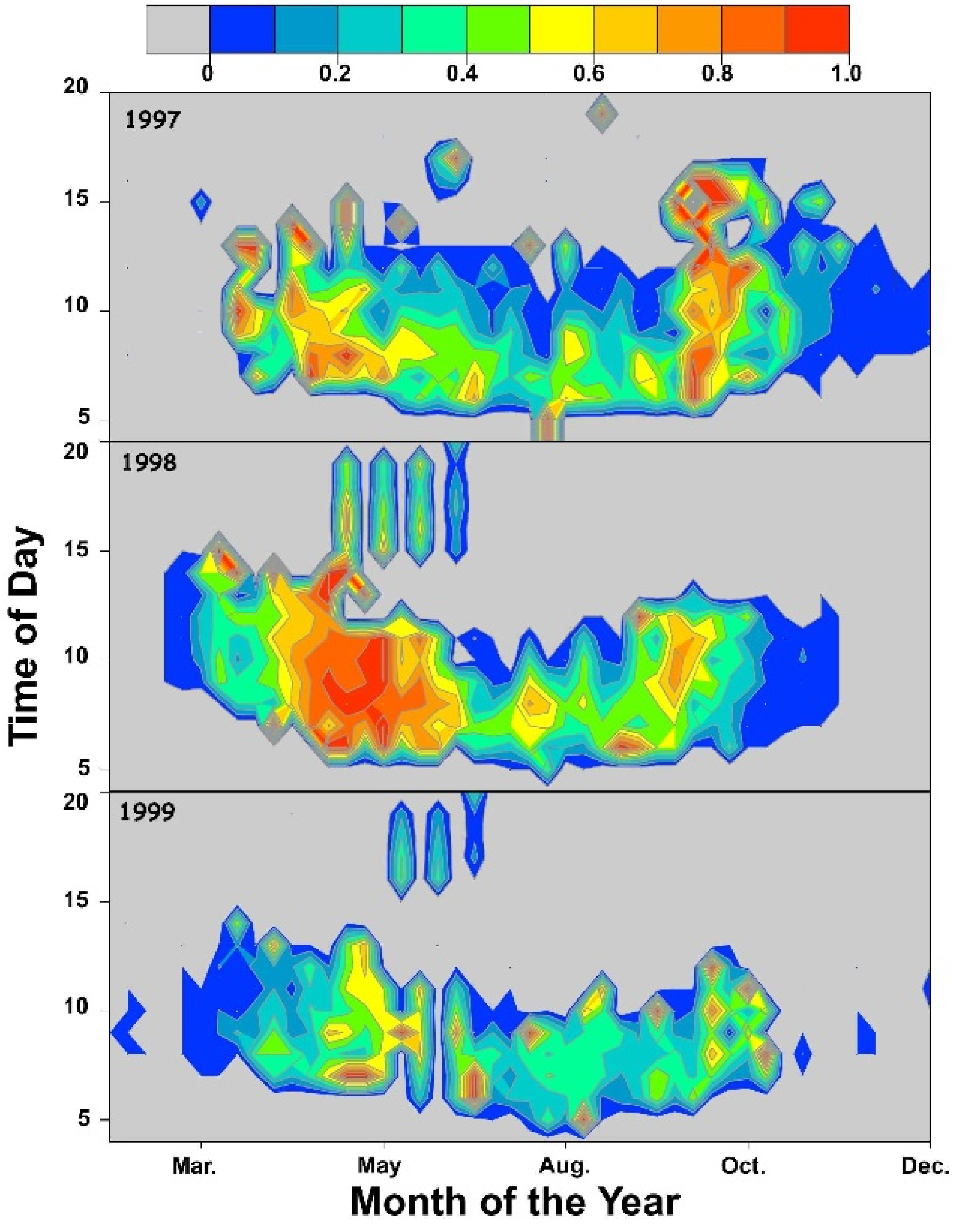

0
0.2
0.4
0.6
0.8
1.0
1997
1998
1999
20
15
10
5
Time of Day
Mar.
May
Aug.
Oct.
Dec.
Month of the Year

Fig. 5

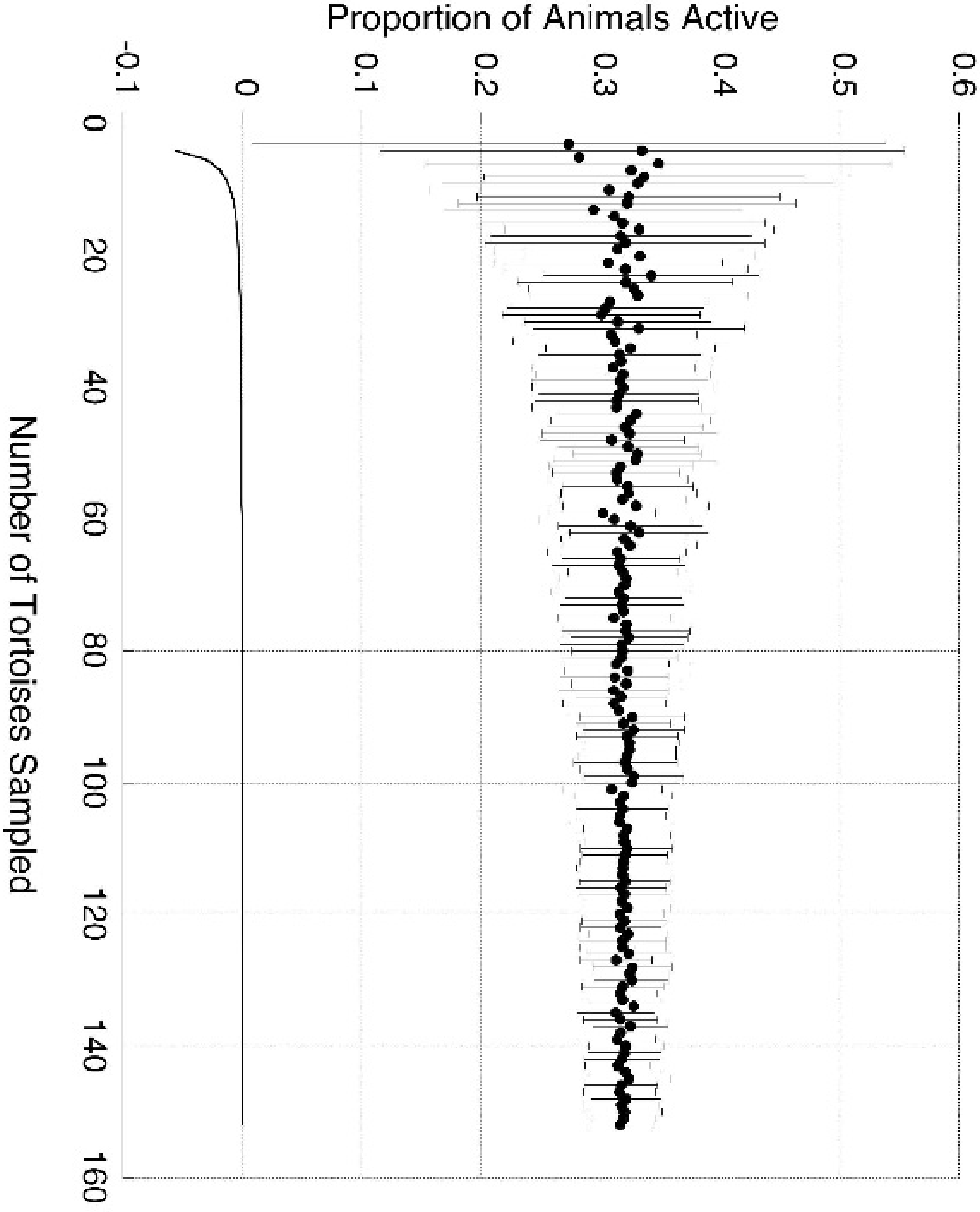

Proportion of Animals Active
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
0
20
40
60
80
100
120
140
160
Number of Tortoises Sampled

Fig. 6

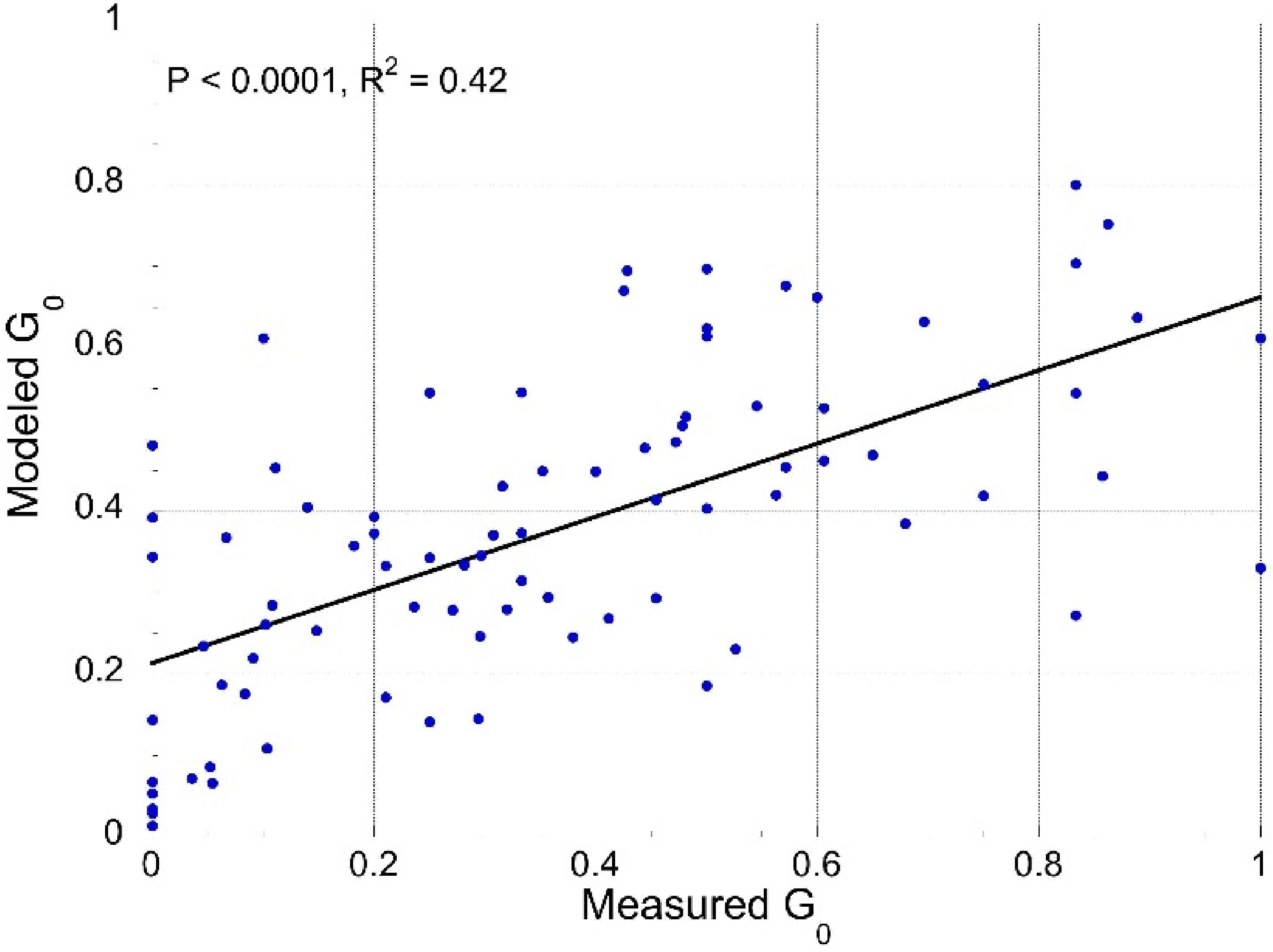
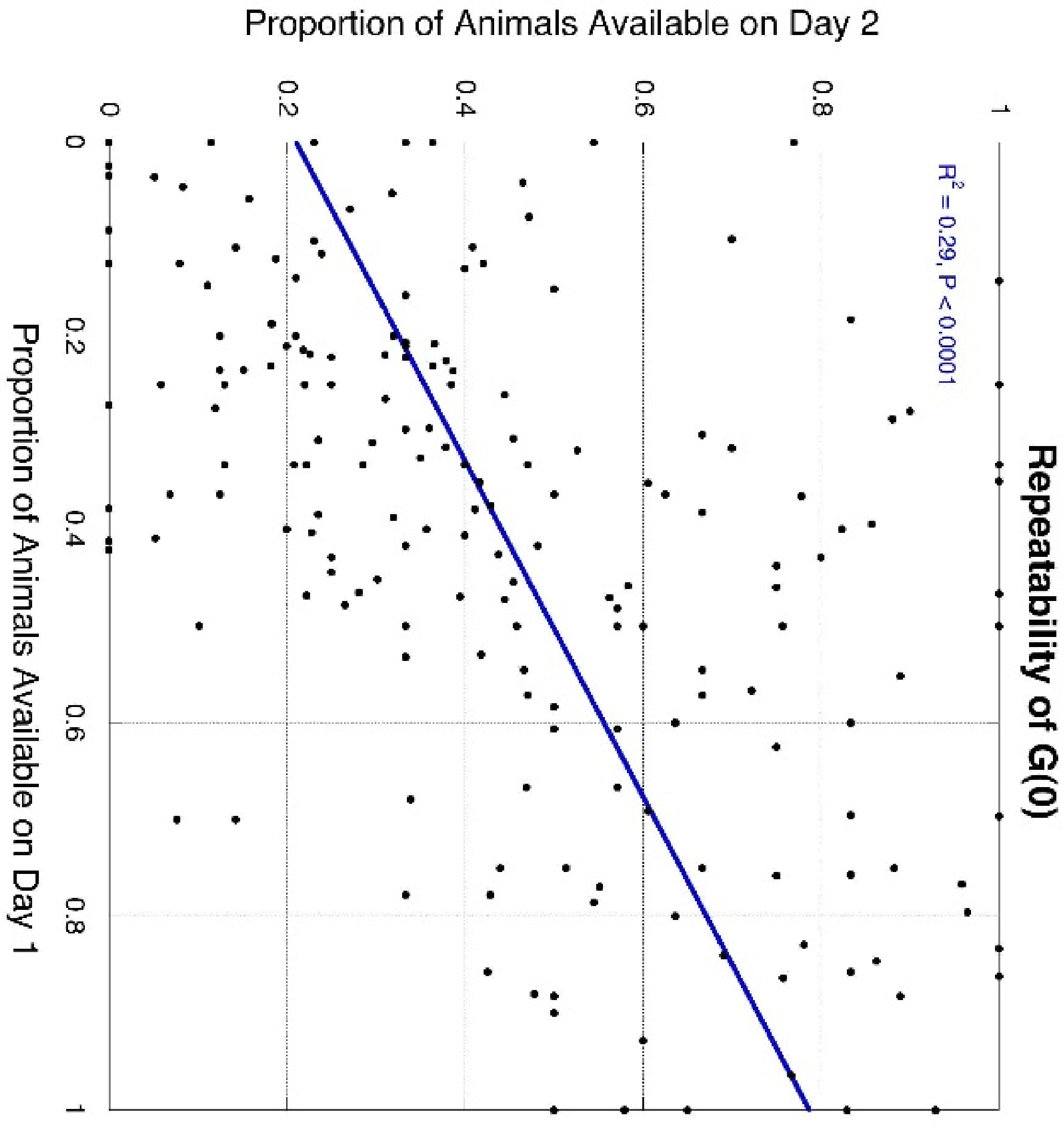

P < 0.0001, R² = 0.42
Modeled G0
Measured G0
0
0.2
0.4
0.6
0.8
1
0
0.2
0.4
0.6
0.8
1

Fig. 7


Repeatability of G(0)
$R^2 = 0.29$, $P < 0.0001$
Proportion of Animals Available on Day 2
0
0.2
0.4
0.6
0.8
1
Proportion of Animals Available on Day 1
0
0.2
0.4
0.6
0.8
1

BEFORE THE ENERGY RESOURCES CONSERVATION AND DEVELOPMENT
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APPLICATION FOR CERTIFICATION FOR THE *PALEN SOLAR POWER* PLANT PROJECT

Docket No. 09-AFC-7

PROOF OF SERVICE

(Revised 8/27/10)

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*indicates change

DECLARATION OF SERVICE

I, Marie Mills, declare that on October 22, 2010, I served and filed copies of the attached MECHANISTIC INVESTIGATION OF THE DISTRIBUTIONAL LIMITS OF THE DESERT TORTOISE, dated May 2004. The original document, filed with the Docket Unit, is accompanied by a copy of the most recent Proof of Service list, located on the web page for this project at:
[http://www.energy.ca.gov/sitingcases/solar_millennium_palen]

The documents have been sent to both the other parties in this proceeding (as shown on the Proof of Service list) and to the Commission's Docket Unit, in the following manner:

(*Check all that Apply*)

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OR

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Attn: Docket No. 09-AFC-7
1516 Ninth Street, MS-4
Sacramento, CA 95814-5512
docket@energy.state.ca.us

I declare under penalty of perjury that the foregoing is true and correct, that I am employed in the county where this mailing occurred, and that I am over the age of 18 years and not a party to the proceeding.

Marie Mills

Marie Mills