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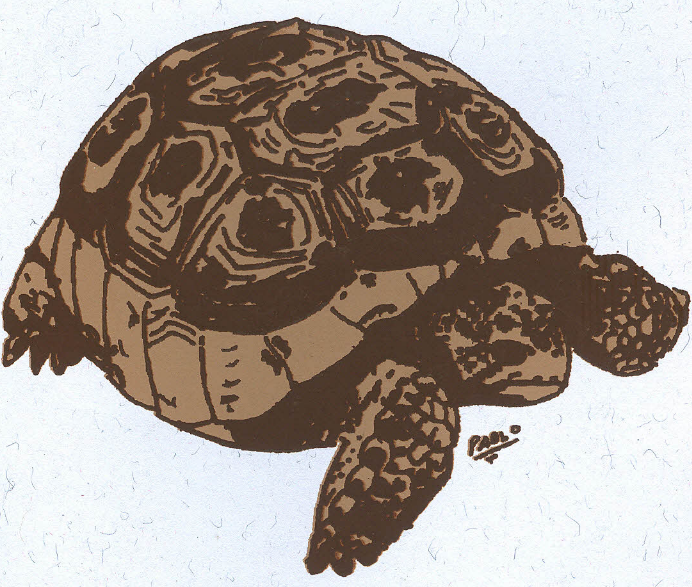
PROCEEDINGS OF NORTH AMERICAN TORTOISE CONFERENCE

Mapimí Biosphere Reserve, Durango, México
October 8-11, 1994



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EDITORS

Gustavo Aguirre
Instituto de Ecología, A.C.

Earl D. McCoy
Henry Mushinsky
University of South Florida, Tampa

Maricela Villagrán Santa Cruz
Rodolfo García Collazo
Gustavo Casas Andreu
Sociedad Herpetológica Mexicana

December, 1995.

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EDITORES

Gustavo Aguirre León
Earl D. McCoy
Henry Mushinsky
Maricela Villagrán Santa Cruz
Rodolfo García Collazo
Gustavo Casas Andreu

Tipografía, Diseño y Armado

Gustavo Aguirre León, Rolando González Trápaga, José Luis Tello Musi,
Rodolfo García Collazo y Marisela Villagrán Santa Cruz.

Dibujo de la portada: Pablo Aguirre Fey

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Dirección de la Sociedad: Lab. de Herpetología, Instituto de Biología, UNAM.
C.P. 04510. A.P. 70-639, México, D.F.

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PRESENTACION

Es muy grato para la Sociedad Herpetológica Mexicana, el presentar los resultados de la "North American Tortoise Conference", desarrollada por el Instituto de Ecología en su Laboratorio del Desierto de la Reserva de la Biósfera de Mapimí, Durango, entre el 8 y el 12 de octubre de 1994.

El documento es el resultado de un esfuerzo entre científicos de México y los Estados Unidos sobre el estudio y conservación de las tortugas del desierto, las que jugando un importante papel en los ecosistemas en que viven, tienen grandes presiones sobre sus poblaciones, debido a modificaciones en un habitat y/o su utilización directa como recursos naturales, lo que establece que se encuentren en permanente necesidad del desarrollo de programas para su mejor conocimiento y adecuada preservación.

La conferencia se orientó, básicamente, hacia la conservación de estas tortugas, con trabajos que revisaron, desde la morfología de poblaciones, pasando por su reproducción, ecología evolutiva y fisiología, hasta estudios estrictamente conservacionistas.

Esperamos que al conjuntar esfuerzos entre los autores de los trabajos, la organización del evento por parte del Instituto de Ecología y la labor editorial de nuestra sociedad, cristalicen en un mayor impacto para la conservación de las tortugas de los desiertos de América del Norte.

Gustavo Casas Andreu

Maricela Villagrán Santa Cruz

Rodolfo García Collazo

PREFACE

The decline of tortoise populations, largely as a result of habitat loss and fragmentation, is virtually universal. If anything positive has become from the decline of tortoise populations, it is the increased research that has been focused on them recently. The four North American species in the genus *Gopherus*, which inhabit arid and semi-arid regions of Mexico and the United States, have been studied by several research groups from these two countries. The resulting data are not equal, and often not comparable, for the four species, however.

We believe that a need exists for binational coordination of comparative research on the ecologies of the four North American tortoise species. Such coordination will reinforce current important studies of some species, while opening the door for new studies of other species. These studies will help to identify commonalities and differences in the biologies of the four species, and to set research priorities. Ultimately, we believe binational coordination will go far in defining sound practical measures for recovery and management of threatened populations in North America.

With the goal of binational coordination in mind, the North American Tortoise Conference took place in October, 1994. It was the second such meeting in the past five years. The conference afforded an opportunity to exchange recent information concerning the study of tortoises in Mexico and the United States, and to establish future conservation efforts. The Laboratorio del Desierto in the Mapimi Biosphere Reserve, Durango, hosted the conference. For the past 18 years, Mapimi has been the focus of study and conservation of the Bolson tortoise, *G. flavomarginatus*.

This publication echoes the desire of participants in the first North American tortoise meetings, which took place in Charleston, South Carolina, in 1990: to make results of research available as quickly as possible, and through a variety of sources. Sociedad Herpetologica Mexicana rapidly took up the idea of publishing this compilation of extended abstracts. Furthermore, this publication serves as an impetus for a full monograph, summarizing current knowledge on the genus *Gopherus* and suggesting future research, to be published in 1996. It is our fondest desire that these efforts will promote interaction among all those persons interested in the study and conservation of tortoises.

We thank the NSF-CONACYT Program for financial aid in the organization of the conference and in the publication of the extended abstracts. Partial support for the North American Conference was provided by a National Science Foundation, Division of International Programs grant (INT-9403039) to Henry R. Mushinsky and Earl D. McCoy, and a Consejo Nacional de Ciencia y Tecnologia, Subdireccion de Asuntos Bilaterales grant (E120.2837) to Gustavo Aguirre. Support from the University of South Florida and the Instituto de Ecologia, A.C. is appreciated. Dr. Maricela Villagran was extremely helpful in editing these publication. Rolando Gonzalez Trapaga assisted us in preparing the final version. We also appreciate the kindness of Juan Francisco Herrera de la Cerda and Agustina Rojas, in the remoteness of the Bolson de Mapimi.

Gustavo Aguirre
Earl D. McCoy
Henry R. Mushinsky

PREFACIO

La disminución universal de las poblaciones de tortugas terrestres y la pérdida y fragmentación de los habitats que ocupan, han dado lugar a importantes avances en el estudio de estos reptiles. Las cuatro especies del género *Gopherus*, distribuidas en ambientes áridos y semi-áridos de México y los Estados Unidos de América, han sido objeto de la atención creciente por parte de varios grupos de investigadores de estos dos países. No obstante, los resultados de las investigaciones no han sido equivalentes y el entendimiento de la biología de las especies de *Gopherus* es todavía desigual.

Estamos convencidos de que es necesario canalizar nuevas acciones en la coordinación binacional para la investigación comparativa de la ecología de estas tortugas así como reforzar algunas de las ya existentes, y de esta manera identificar requerimientos prioritarios de investigación para cada especie así como definir medidas prácticas para el manejo y recuperación de las poblaciones que se encuentran en situación crítica.

Con este espíritu se realizó una reunión de especialistas en el género *Gopherus* en octubre de 1994 con el título *North American Tortoise Conference*, la segunda en su tipo en 5 años, la cual ofreció una oportunidad para intercambiar información reciente sobre el estudio de estas tortugas en México y los Estados Unidos y para establecer futuras acciones de conservación. Esta reunión tuvo como sede el Laboratorio del Desierto de la Reserva de la Biosfera de Mapimí, en el Estado de Durango, en donde se han realizado actividades de investigación y conservación de *G. flavomarginatus* durante los últimos 18 años .

Esta publicación responde a la intención emanada desde la primera reunión, realizada en 1990 en Charleston, Carolina del Sur, en el sentido de divulgar los resultados de la manera más expedita posible y por diversos medios. La Sociedad Herpetológica Mexicana dio pronta acogida a la idea de publicar esta recopilación de resúmenes en extenso de los trabajos presentados, y ha significado un estímulo adicional a nuestros planes de publicar en 1996 una monografía que presente el conocimiento actualizado sobre el género *Gopherus* con sugerencias para investigaciones futuras. Es nuestro deseo que estos esfuerzos sigan aumentando la interacción entre todos los interesados en el estudio y conservación de las tortugas terrestres.

Agradecemos la ayuda financiera del Programa Consejo Nacional de Ciencia y Tecnología-National Science Foundation Primavera 1994 para realizar este evento y publicar estas memorias a través de los apoyos a Henry R. Mushinsky y Earl D. McCoy (NSF, Division of International Programs INT-9403039) y Gustavo Aguirre (CONACYT, Subdirección de Asuntos Bilaterales E120.2837). Agradecemos el apoyo económico otorgado por el Instituto de Ecología, A.C. (cuenta 902-05) y por University of South Florida. Nuestro reconocimiento a la Dra. Maricela Villagrán por su valiosa participación en la edición de este volumen, al Biól. Rolando González Trápaga por su colaboración en la preparación de la versión final, y a Juan Francisco Herrera de la Cerda y Agustina Rojas por su hospitalidad en el Bolsón de Mapimí.

Gustavo Aguirre
Earl D. McCoy
Henry R. Mushinsky

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NATURAL AND LIFE HISTORY OF THE BOLSON TORTOISE, *Gopherus flavomarginatus*

Gary Andrew Adest[1] and Gustavo Aguirre León[2]
[1]P.O. Box 2155 Camp Nelson, California 93208,USA
[2]Instituto de Ecología A.C., Apartado Postal 63,
Km. 2.5 Antigua Carretera a Coatepec
91000 Xalapa, Ver. México

MICRODISTRIBUTION AND HOME RANGE

Within the range of the Bolson tortoise as documented by Bury *et al.* (1988) and Lieberman and Morafka (1988), tortoises exist both as scattered individuals and within high density aggregations termed colonies. Morafka *et al.* (1981) documented the association of tortoises with soils of both high sand content and high salt content. Tortoise burrows are typically associated with sloping grades, often at the base of bajadas and above playas. The range of slopes is 1-3%. Within these areas, tortoise habitat is characterized by shrubs such as *Larrea*, *Prosopis*, *Parthenium*, *Flourensia*, *Opuntia*, and *Agave* and herbs such as *Hilaria*, *Sphaeralcea*, *Bouteloua* and *Tridens*. Tortoise burrow density is highly variable: at Mapimi densities as low as 5 active burrows/km^2 have been documented while at Cerro Emilio in Chihuahua we have counted 7 active burrows/ha. There is a significant correlation between burrow diameter and the width of an inhabiting tortoise ($r = .94$, $p < .01$; Morafka *et al.* 1981). Caution must be used in tortoise censusing using burrows because, as Aguirre *et al.* (1984) have shown, each burrow may be used by multiple tortoises and each tortoise may inhabit multiple burrows. males occupied an average of 3.5 burrows, females 2.7, and juveniles 1.8. Some males used as many as 8 different burrows and more than one tortoise may occupy the same burrow simultaneously. Furthermore, burrow use varies seasonally. Tortoises of all ages/sizes spend about 3/4 of their time in a primary burrow and 1/4 in a secondary burrow.

A well-studied colony at Mapimi is composed of a nuclear area of three tortoises/ha density and a peripheral area decreasing to a density of one tortoise/8-10 ha (± 0.1 tortoises/ha). Burrow distribution within the colony is clumped according to Poisson distribution analysis ($t = 3.66$, $p < .05$). Within this colony, radiotelemetrically-monitored animals exhibited linear movements associated with foraging, apparent exploration, and reproduction. Males moved greater average distances per day (265 m) than females or juveniles; males and females had average maximum distances greater than 500 m and both had statistically greater maximum distance movements than juveniles, who averaged about 250 m. When the effects of season are examined, males and juveniles moved more per day than females during a dry period and all size/sex classes moved significantly more during wet periods.

Various models for home range areal estimation were fitted to the actual tortoise movement data and compared. Most probabilistic and non-probabilistic models overestimated tortoise home ranges. The minimum modified polygon and 68% bivariant ellipse models produced estimates of home range closest to actual tortoise use patterns. Although these results obscure the true pattern of tortoise habitat use, their numerical values for comparison purposes were: males 3.1 and 4.1 ha, females 2.5 and 3.1 ha, and juveniles 0.4 and 1./2 ha. The centers of activity of these home areas were shown to be clumped by Poisson distribution analysis ($t = 5.2$, $p < 05.$) Centers of activity within the colonies are highly correlated with the distribution of burrows; burrows are highly correlated with the distribution of high densities of tobosa grass, *Hilaria mutica*. Long distance movements peripheral to the colony were exhibited by 14% of adults and 18% of juveniles. Following these large displacements, individuals were not seen or recaptured within the colony for 11 months of the study. Distances moved varied from 1500-6000 m.

The social structure of the colony is apparently hierarchical. Individual tortoises defend burrows on occasion and exhibit behavior typical of interindividual distance defense. There is no strong defense of a specific area, or of receptive females by males, nor is there harem formation. Females did not exhibit defense of nesting areas. There is evidence that a small percentage of males is responsible for the majority of reproduction. In an intensively monitored population at Mapimi, there out of seven adult males were responsible for all the copulations observed (Adest et al. 1989a). Centers of activity for these reproductive males are located close to those of the females most frequently courted. However, these sexually active males do not aggressively exclude subordinate males from an area containing receptive females. The most dominant males (those with the greatest reproductive access) studied used the highest number of burrows, they traveled greater linear distences as a result of their courting activities, but they were not the largest size males in the colony. The Minimum modified polygon estimates of the percent of home range overlap were 32% for males, 26% for females, and 9% for juveniles. Interestingly, only about 10% of the area of activity is intensively used for foraging and these areas do not show either intra or intersexual overlap.

CLIMATE AND ACTIVITY

Bolson tortoises inhabit a warm steppe to desert region with low annual precipitation, high evaporation and temperature fluctuation, and high incident solar radiation. Seasonality is pronounced: a dry, frost-dominated winter (November through March), a dry, warm spring (April through May), and a wet summer (June through October.) Monthly temperature, precipitation, evaporation and cloudiness are given for three representative areas in Bolson tortoise range in Morafka (1981). The average annual temperature is 18-20°C, average annual precipitation is 200-250 mm. Adest *et al.* (1989a) note that 72.4% of annual rainfall occurs June through September and 8.1% December through February. The annual activity cycle is correspondingly restricted between November and March with tortoises mostly brumating. Adult tortoises monitored daily exhibited only basking as a surface activity during March April and May. During the hot season, June through September, tortoises spend less than one hour active day in epigean activity and an estimated one day in three active. Intensively-monitored tortoises spent 79% of their time underground, 20% basking and 1% locomoting during the dry period. In contrast, following the onset of the seasonal rains tortoises spent 91% of their time underground, 0.5% basking, and 8.5% in epigean activities. A population of 25 tortoises monitored on an hourly basis exhibited a marked bimodal activity phasing during the hot season (Morafka *et al.* 1981). Peaks of activity occurred between 0900 and 1000 hours in the morning and 1600-1700 hours in the afternoon. In addition, tortoises were active prior to 0800 hours and emerged from their burrows to rest on the entrance mound following sunset. Adest *et al.* (1989a) estimated overall annnual activity at less than 1%.

Heating rates for Bolson tortoises engaged in aboveground activity are high, and cooling rates are significantly lower (Adest and Aguirre unpubl.) Maximum time spent in epigean activity during the hot season appears to be a function of the difference in temperature between tortoise body core and the environment and the degree of hydration of the individual. During locomotion in full sun individuals of both sexes and all age/size classes heat rapidly, reaching body temperatures as high as 41°C, and retreat rapidly to the lower ambient temperatures of the burrow. Mean body temperature is significantly higher (in tortoises with internal temperature-monitoring transmitters) during the hot, wet season as compared to the hot, dry season. All tortoises studied reavched higher body temperatures and spent significantly more time aboveground following the onset of the summer rains. Adest *et al.* (1989a) hypothesized that rehydration permits tortoises to tolerate greater evaporative water loss in the wet season and thus spend more time above ground at higher body temperatures.

POPULATION STRUCTURE

The demographics of Bolson tortoise populations are summarized in Adest *et al.* (1989a). All sites surveyed are similar in exhibiting a paucity of immature animals (Aguirre *et al.* 1984, Adest *et al.* 1989a, Morafka *et al.* 1989). Adult tortoises, defined as individuals >250 mm straightline carapace length, composed 81% of all animals located within the Biosphere Reserve between 1983 and 1985. We have also documented a decline in individuals designated as juveniles and subadults between 1980 and 1985 at our study colony in Mapimi. Whether this is constantly high or fluctuating mortality in immatures is unknown, but it appears representative of chelonians in general. Data from experimental release of captive-reared young bolson tortoises support this result: Nearly 70% of 1-4 year-old tortoises died within 12 months of release (Tom 1988) Adest el al. (1989a) discuss in detail alternative hypotheses explaining the age/size structure of Bolson tortoise populations.

REPRODUCTION

Bolson tortoises begin to court and copulate after emergence from brumation. The earliest record is 20 March at Mapimi. Courtship and copulation peaks during July and August. The latest observation occurred on 5 October.

Six out of 13 (46%) of field-laid clutches were laid on the burrow mound or at the entrance. Three (23%) were located within 10 m of a burrow and four nests (31%) were observed being laid within 150 m of the burrow. Of these latter seven nests, three were laid in the open, two under a creosote bush and one under a mesquite. Twelve of thirteen clutches were laid within 150 m of the laying female; one clutch each laid at the entrance of a resident male's burrow. Clutches were deposited as early as April 8; May and June account for 80% of all clutches laid.

We palpated 56 field-caught females a total of 638 times between 1983 and 1989. Because of the difficulty in recatching females, not all females were caught each year and the catch effort is variable. A total of 48 females produced 100 detected clutches: 60 via oxytocin induction in the laboratory (Adest *et al.* 1989b) and 40 inferred to have been laid in the field. Palpable soft oviductal eggs were detected as early as 24 February, positive palpations peaked during May, and females continued to have palpable eggs through June. Only a few females possessed eggs in July and the latest occurrence of palpable eggs was 22 July.

The minimum size of reproduction of female Bolson tortoises corresponds to approximately 18-20 years of age. We followed two females, with known annuli, by annual palpation until they were 15 and 17 years of age without detection of eggs. These females attained a size of 242 mm and 287 mm when they could first be sexed via cloacal palpation. Females bearing known clutches did so over a range of growth ring cvounts from 16-21, corresponding to carapace lengths from 326-380 mm. One female bore an inferred clutch at 315 mm CL and 18 annuli.

Incubation in the laboratory ranged from 76-149 days and averaged 115.6. One overwintered clutch hatched in 332 days. Mean clutch success overall was 0.59. Hatching success varied by year from 0.48 to 0.65, hatchling probability from 0.28 to 0.60, and egg viability from 0.18 to 0.60. Hatchlings appear in late summer and early fall.

Because Bolson tortoise copulatory activity peaks in July and August along with epigean activity and hard-shelled eggs have not been detected after 22 July, it appears that tortoises are retaining sperm for fertilization of clutches produced the following spring. This correlates with the February detection of eggs at a time when there is little or no epigean activity.

Eggs weigh an average of 54.2 g, are 47.6 mm long and 44.1 mm wide. Clutch size was highly variable and ranged from 2-12 (N = 60). Fifty-seven out of sixty clutches were produced by females with only one detected clutch that year and three clutches were produced by double clutching females. No triple clutches were detected. Clutch size did not vary significantly with laying date, year, or whether a clutch was a first or second one. Total clutch mass averaged 298 g (range 85-708) and no significant association with date of laying, year or first vs second clutch was found. Clutch size ($F(\log)_{1, 56} = 4513$; $p < .0001$; $r^2 = .88$) and clutch mass ($F(\log)_{1, 52} = 4.7$; $p = .04$; $r^2 = .08$) showed a significant positive correlation.

Relative clutch mass (RCM = clutch mass/non-gravid female body mass) was highly variable, averaging 3.80 and ranging from 0.89 to 0.08. RCM was generally uncorrelated with various measures of female body size, except non-gravid female body mass ($F(\log)_{1,52} = 4.1$; $p = .05$; $r^2 = .07$).

Relative egg mass (REM = RCM/Clutch size), representing parental investment per egg, was inversely correlated with all measures of female body size and unrelated to clutch size. If this is valid, it implies that larger females invest lower percentages of their body mass (and supposedly energy) to produce an egg than do smaller females.

The average bolson tortoise hatchling weighed 33.1 g (range 15.4-49.0), was 45.7 mm long (range 33.7-54.4), and 41.4 mm wide (range 34.5-47.0). A single set of twins weighed 19.1 and 15.4 g and measured 38.9 and 38.8 mm CL and 35.7 and 34.5 mm CW.

There were no significant correlations between hatchling mass, length and width versus clutch size. These hatchling size measures, however, are correlated with clutch mass ($F(\log)_{1,108}$ range = 4.9-13.6; p range .0004-.03; r^2 range = .04 -.11).

We defined relative hatchling mass (RHM) as the mass of an individual hatchling divided by nongravid female body mass. RHM represents the percentage of female body mass per hatchling and is significatly correlated with REM ($F_{1,96} = 127$; $p = .0001$; $r^2 = .60$). We interpret this to mean that females so not change the percentage of their body mass per egg as they lay additional eggs. This suggests that optimization of eggs is not occurring-females invest the same amount of body mass in each egg whether that egg is laid in a two-egg clutch or a twelve-egg clutch. The strong relationship between REM and RHM indicates that females who invest more per egg in general receive larger returns in terms of the mass of hatchling in that hatchling mass is generally considered a positive survival trait.

We defined total hatchling mass (THM) as the sum of the wet body mass of all hatchlings born alive per clutch. THM has a com-lex-appearing relationship with clutch size: THM is low at both extremes of clutch size and maximal at intermediate values. This relationship is evident when the zero-hatching success category is included (15 clutches whose eggs were all infetile and 11 clutches which contained at least one fertile egg). The correlation strengthens when all zero-success clutches are removed ($F_{1,30}= 6.1$; $p = .02$; $r^2 = .17$). There is also a significant positive relation between THM and RCMN when all clutches are included. Removing the zero-success clutches improves this correlation as well ($F_{1,27}= 10.1$; $p = .004$; $r^2 =.27$). Total hatchling mass represents our best estimate of the atual return on parental investment. It takes into account all of the factors which compromise the female energy input per egg or per clutch, including fertility/infertility, incubation failures, and hatchling probabilites.

ACKNOWLEDGEMENTS

We wish to thank support from Consejo Nacional de Ciencia y Tecnología, World Wildlife Fund and California State University. Contribution to the MAB-UNESCO Biosphere Reserve Program.

CONSERVATION OF THE BOLSON TORTOISE, *Gopherus flavomarginatus*

Gustavo Aguirre León
Instituto de Ecología A.C., Apartado Postal 63,
Km. 2.5 Antigua Carretera a Coatepec
91000 Xalapa, Ver. México

INTRODUCTION

During the last 15 years the Mapimí Biosphere Reserve in Durango, Mexico (MBR) has been the focal point for developing a program for the study and conservation of the Bolson tortoise. The Mexican Institute of Ecology has been in charge of conducting the majority of the research regarding the biology of this unique species. Continuous collaboration between the Institute of Ecology and U.S. scientists has characterized this program from its start. By the time the MBR was founded, the first comprehensive studies on the species' status and distribution had been completed (Morafka 1977, 1982), serving as a basis to coordinate this binational effort to extend the studies on this tortoise.

STATUS

Gopherus flavomarginatus is endemic to the Mapimian subprovince of the Chihuahuan Desert. It inhabits only some portions of the Bolsón de Mapimí, a series of interconnected closed drainage basins centrally located in the Chihuahuan Desert in northeastern Durango, southwestern Chihuahua and southeastern Coahuila. Tortoises are not common within their limited range and they are usually found in low population densities. Field surveys (Morafka *et al.* 1981, Bury *et al.* 1988, Lieberman and Morafka 1988) resulted in an estimate of nearly 6,000 km^2 as the total area of tortoise occurrence, but the actual area actually occupied by tortoises may be within the range of 1000 to 1500 km^2. Populations are discontinuous and often restricted to narrow belts, below the rocky outcrops and above the more severely flooded plains of the valley floors. Past surveys indicated that a dozen such belt habitats exist. Estimates extrapolated from those belts which have been sampled at the MBR, and Cerros Emilio, Chih., suggested the total number of adults representing the species could be 10,000 individuals as a maximum.

Population and range perturbation of the Bolson Tortoise has been a long and gradual process related to multiple factors such as climatic change, increasing anthropogenic pressure through habitat modification as well as predation by man. Direct human predation and habitat loss has resulted in range contraction. With the exception of a few protected populations, most of the remaining populations are declining. In particular, there is no strong evidence of the existence of any cluster with substantial numbers in the western and northwestern parts of the tortoise's range, which represent about 8% of the actual occupied area. In comparison to the situation documented in 1981 (Bury *et al.* 1988), surveys conducted in 1993 show increasing human occupation of this habitat and reduction of tortoise numbers. This scattered and very isolated individuals are prone to extirpation in the short term. The conservation status of this species remains critical. In fact, its populations continue to be affected by human activities, and in some areas local residents still eat tortoise's meat. Bolson tortoises are effectively protected only in two sites in the States of Durango and Chihuahua. Current information is needed on the status of potentially viable populations in the State of Coahuila.

THREATS TO POPULATIONS

This tortoise has a long history of human predation, both for consumption and for trade. Coupled with a low biotic potential, intensive exploitation has resulted in over-harvesting. Current population trends suggest tortoise declines have been accentuated from about the beggining of this century, coinciding with the impacts of a gradual intensification in local agricultural projects and the expansion of cattle raising in the arid grasslands of the Bolsón de Mapimí.

Bolson tortoise range is fragmented into six recognizable patches, which are internally partitioned by zones of contiguous and apparently ecologically good habitat (Bury *et al.* 1988): Los Americanos Region, Sierra del Diablo Region, Rancho Diana, Ceballos to Yermo Region, Mapimí Core Region, and Sierra de los Remedios Region. Habitat and population fragmentation consequences are not yet fully understood, however, this current patchiness can be interpreted as a rapid deterioration of tortoise range as a result of human influences. Negative correlations between intensive human land use and tortoise densities were demonstrated in part by Lieberman and Morafka (1988). However, this same study indicated that moderately high tortoise densities remain in localities subjected to moderate human land use. Even low levels of collecting may have a deleterious effect on already low-density populations, but the interelationships between variables requires further empirical investigation before they can be resolved. We need to assess which isolated clusters potentially still form a viable system. Continuous monitoring on the clusters at the MBR, shows no evidence of recolonization in extirpated populations from remaining populations (Aguirre *et al.* 1984, Aguirre unpubl.).

PROTECTED POPULATIONS

Tortoise populations are protected at the MBR in northeastern Durango, where viable populations still survive. The Mapimí protection program started in 1976, together with the establishment of the Reserve (Morafka *et al.* 1981, Aguirre and Maury 1990). With the protection afforded by the cooperation of the local people within the reserve, the Institute of Ecology has been able to set up a long term study site of the Bolson tortoise. Population size in the MBR is estimated to be 1,500 to 2,000 individuals, with highly variable densities from 0.1 to 3 tortoises/ha. A medium to high density population in Rancho Sombreretillo comprising a significant number of viable tortoise colonies is now under study. Outside this sites present protective legislation is weakly enforced due to lack of active personnel from the Mexican Wildlife Department.

The operation of formal tortoise protection in Rancho Sombreretillo will hopefully promote similar local efforts in surrounding properties in the States of Chihuahua and Coahuila. A program of public education for the local residents and landholders involved will soon be released.

SECURITY OF LAND OCCUPIED BY EXISTING POPULATIONS

The program for the conservation of Bolson tortoise in Mexico is closely related to the development of alternative ecological conservation policies begun in the mid 70s. In particular, the establishment of Biosphere Reserves as a part of the UNESCO-MAB Programme and their inclusion in Mexican environmental legislation has served as a framework for conservation and protection efforts on behalf of this species. Since 1988, the Mapimí Reserve has been included in the recently created Mexican System of Protected Areas. Its permanency and institutional support is assured through this legal model. Rancho Sombreretillo is currently succesfull in affording protection to tortoises through a voluntary program. Long term protection and conservation of the Bolson Tortoise will be dependent on expansion of efforts already started in these two sites.

We believe we need to take a realistic approach concerning Bolson tortoise conservation, as the species might be functionally extinct in several portions of its current geographic range, and a reversal of the extirpation trend that has ocurred in some areas is unlikely. A recent revision of priorities of the whole system of protected areas supported by the Mexican Government looks promising in this regard. Resultsof this revision are expected to endorse recommendations for executive actions conducive to effective protection in additional areas. Implementation of this sort of plans would eventually mean the protection of natural biological corridors and the establishment of conservation strategies beyond the regional level. In relation to tortoise conservation, the ultimate goal of such an approach would be to broaden site-specific approaches by providing innovative conservation initiatives for habitat protection compatible with the realities of human habitation in the Chihuahuan Desert.

ADEQUACY OF CURRENT PROTECTION

Voluntary cessation of tortoise hunting by reserve inhabitants and cooperation with the MBR policies have been indispensable to the slow recovery of tortoise populations. This reserve actively involves local residents in its education programs and maintenance efforts (Kaus 1993). It excludes hunting and moderates grazing practices in tortoise habitats. While these efforts have met with considerable success, this single reserve can only afford protection to perhaps 10 to 20% of the total number of estimated surviving tortoises. The tortoise protection program will hopefully be reinforced through the operation of a management plan in the area within an economically feasible plan for the local inhabitants.

A program of captive incubation, husbandry and experimental reintroduction aimed to gather information on the biology of the first age classes has been conducted for several years. It was designed as a first step to provide informed management decision in protecting the species. Advantages and disadvantages of this approach have been assessed through this program (Adest *et al.* 1989b), which is at present in the process of redefinition.

ECOLOGICAL SIGNIFICANCE OF CONSERVATION EFFORTS

Ecologically, the Bolson tortoise is a herbivore in the Mapimian tobosa (*Hilaria mutica*) grasslands of the Chihuahuan Desert (Aguirre *et al.* 1979). Its exact contribution to these grasslands is still to be ascertained but most certainly its construction of extensive burrows and pathways and ingestion of fruits and dispersion of seeds would qualify it as a keystone organism in this ecosystem. Bolson tortoises dig burrows up to 10 m long and 2 m in depth for shelter and defense from predators. This structures provide a microhabitat for several species of vertebrate and invertebrate fauna. Successfull restoration of Bolson Tortoise distribution could contribute significantly to the stabilization and enrichment of biodiversity of the Chihuahan Desert.

INTERNATIONAL ASPECTS OF PROTECTION

Since the species description in the late 50's, sufficient distributional information was made available to establish that the species was endangered (Aguirre 1982; Bury *et al.* 1988; Morafka 1982,1988; Morafka *et al.* 1981, 1989). In the course of the last 14 years, *G. flavomarginatus* has been listed as endangered under the U.S. Endangered Species Act, CITES Appendix 1, and the Mexican wildlife laws (most recent update May 1994). In 1991 it was identified as a high priority by the AMNH Turtle Recovery Program (IUCN-SSC Tortoise and Freshwater Turtle Specialist Group's Action Plan).

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TORTOISE MANAGEMENT AS URBANIZATION ENCROACHES

Ray E. Ashton, Jr., Patricia S. Ashton and E. Lynn Mosura-Bliss
Protected Species Services, Water and Air Research, Inc.
6821 S.W. Archer Road
Gainesville, Florida 32608, USA

INTRODUCTION

The state of Florida requires, under law, that significant populations of *Gopherus polyphemus* must either be protected on site or be relocated to suitable recipient sites. In many cases where populations are not significant, the land developer may chose to mitigate by purchasing tortoise habitat at various mitigation parks (Cox *et al.* 1987). Many developers chose to establish on-site preserves where the local tortoise population is to be protected during and after the area has been developed. As upland habitat continues to be developed, mitigation sites and recipient sites for relocating tortoises are becoming more difficult to find, and continuing concerns about disease transmission and the costs of tortoise relocation are making on-site mitigation more attractive. Few data or guidelines are available for establishing on-site tortoise preserves, and these frequently assume that the area will be maintained or redeveloped into the tortoise's upland habitat. Frequently, the mitigation guidelines do not reflect protection of multiple protected species within the same preserves, despite the fact that many of these upland species occur in proposed development areas. The majority of large developments are primarily for human housing and supporting infrastructure, thus creating special problems if the goal is to develop and maintain upland habitat for tortoises or other protected species. Additional problems are created for upland habitats within what will ultimately be urban areas, since most of these habitats are fire maintained. The purpose of our study has been to establish practical methods of establishing gopher tortoise and other protected species preserves within urban settings. Ultimately, the practices that are being developed may have some bearing on other *Gopherus* in North America.

STUDY AREA

The study area is located along the Sumter and Marion County Line and is bordered on the south by the city limits of Lady Lake, Florida. The development, the Villages of Lake Sumter, is a 2,332-acre retirement and golf community that eventually will include 2,597 homes. The density of the houses is from six to eight housing units per acre. Currently, three golf courses are developed, with at least four more planned.

Land use in the area has been in ranching and farming for the past 100 years. Cattle farming has been the primary endeavor, with a row crop rotation every three to six years. Remanent long-leaf pine (*Pinus palustrus*), turkey oak (*Quercus laevis*), and wire grass (*Aristida* spp.), as well as stands of large live oak (*Quercus virginiana*), are scattered over the property and provide an indication of the original plant communities. Approximately 250 gopher tortoises, 26 pairs of Florida burrowing owls, (*Athene cunicularia*), and 3 pairs of state-protected southern American kestrels (*Falco sparverius*) are on site. State-protected tortoise commensals known to be on site include a breeding population of gopher frog (*Rana capito*) and Florida pine snake (*Pituophis melanoleucus mugitus*). Development began in the study area in 1990, and a mitigation plan was developed for the protected species on site. The plan calls for three tortoise and burrowing owl preserves covering a total of 126 acres. An additional 20.5 acres of corridor preserves have been or will be developed, and 267 acres of foraging areas for kestrels and burrowing owls lie within the study area. The owl and central tortoise preserves are bahia grass (*Paspalum notatum*) pastures, and the third preserve is a mixture of pasture and remanent upland habitat. Within the center of the upland habitat preserve is a modified sink hole breeding pond for the local gopher frog population (Ashton 1993).

METHODS

This paper focuses on the methods that have been developed or are in the process of being developed for the establishment of successful, long-term mitigation tortoise preserves that will ultimately be surrounded by high-density urbanization.

Pre-development Phase

Prior to the development receiving state authorization to proceed, a negotiated Wildlife Habitat Management Plan and Conservation Manual (WHMP) were written and approved (Ashton 1993). This manual details plans for the management of protected wildlife from preconstruction and construction phases through the post-development stages. The primary areas addressed included the development of on-site conservation areas; protection of species while farming was continued during development; protection during the construction phase, including education of the construction personnel and contract inclusions for construction companies; and procedures for moving tortoises. The development of conservation areas was spelled out clearly, with the basis being acreages and other basic guidelines required by the state. Educational programs were mandated and are being carried out, including signage, interpretative trails within the preserves, brochures, television, and other educational programs for local citizenry. These efforts are important to ensure residents have a sense of ownership in the preserves and pride in their management. Conservation areas outside of the tortoise preserves are managed to provide forage for protected birds and are suitable tortoise habitat.

Preserve Development

The primary goal for the preserve development was determined to be establishing and maintaining optimal habitats for the three primary protected specyes on site. It was decided not to attempt to reestablish the upland habitat because of cost and long-term management implications. The plan was to modify the bahia pasture to provide optimal forage for tortoises and the two insectivorous bird species. One preserve was designated primarily for burrowing owls, with tortoises and kestrels present as well. The other two preserves were designated as gopher tortoise preserves, with owls and kestrels present in the Central Tortoise Preserve.

Each preserve is surrounded by a 1.5m board fence, which is buried 0.6m underground, with 1.22m wide (2.5cm x 5.0cm mesh) steel hog fence attached to the board fence. This fence is designed to keep tortoises in the preserve and keep stray dogs and cats from entering. A concrete berm was poured, which provides a 36cm wall buried 30cm underground to keep tortoises from crawling under the gate or out of the gate even if it is open. One kestrel nest box is constructed in each of the preserves.

Before construction takes place in an area of the development, the owl and tortoise burrows are excavated using a back hoe. This permits commensals to be captured and moved and data to be taken on burrow depth, length, temperature, and moisture. Prior to release in the preserves, tortoises are sexed, weighed, measured, and marked. Tortoise density increased from 6 tortoises in the owl preserve to 50 tortoises. or roughly one tortoise per acre. The Central Tortoise Preserve has a density of three tortoises per acre from a resident density of one tortoise per acre. The Western Tortoise Preserve currently has eleven resident tortoises in 30 acres.

Forage Management

Preliminary research was conducted on the feeding behavior of tortoises. Of primary importance were scat studies done by MacDonald and Mushinsky (1988) and our unpublished winter scat analysis done on tortoises in 1975. We also investigated how forage studies were undertaken on cattle (L. Sollenberger pers. comm.) and how graze was analyzed (Mislevy *et al.* 1990). Based on observations made on wild and captive *Gopherus* and other tortoise species, it was determined that because of the soft texture and probable digestibility, the largest diversity of plants eaten by tortoises could not be determined from scat analysis. Preliminary efforts to monitor tortoise feeding by video taping has proven to be very successful. Two fifty-meter transects to sample food availability and diversity have been established in two of the preserves. The data collected during seasonal sampling is compared to the plant diversity in feeding areas around a sample of ten numbered tortoise burrows. These areas are measured and the area determined seasonally.

Based on nutritional studies (Moore 1973), grass nutrition was determined to increase with periodic cutting or grazing. Vegetation is also cut to approximately five inches to provide ideal foraging for burrowing owls and kestrels. Soils samples are analyzed for possible nutritional needs. Periodic fertilizer applications may be used as needed. Treated sewage solids may be used routinely when this receives final approval.

CONCLUSIONS

Preliminary results indicate that tortoises are using less than 10 percent of the available forage area with a density of three tortoises per acre. Data also indicate that, within these preserves, tortoises graze grasses within 6 to 12 meters of their burrow in an area of 2 to 40 square meters, depending upon tortoise size. Tortoises graze primarily in front of their burrow, but they range much farther from their burrows when in search of other herbaceous plants. Efforts to determine what plants are important will continue. Early data indicate that, within well-managed pasture-type habitat, the density of tortoises could exceed ten tortoises per acre based on available food supply. Data are not yet available to compare grassland preserve foraging with that of the modified upland preserve.

The multiple species approach to on-site mitigation provides greater acreages to be set aside for all noncompetitive species. In preserves with both tortoises and burrowing owls, owls frequently use inactive tortoise burrows for nesting and use both active and inactive burrows to rear fledglings. Maintaining the grass areas of the preserves to provide proper height for bird foraging also increases its nutritional value for tortoise feeding.

The first five years of this 25-year study have been dedicated to establishing management and monitoring techniques that can be used in an urban environment and by people who have few technical skills. This is important since, like these preserves, most on-site tortoise preserves will be managed by homeowner associations, which will most likely hire lawn care or golf course maintenance people to care for the protected areas.

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CONSTRAINTS OF BODY SIZE, ENVIRONMENTAL STOCHASTICITY, AND LIVESTOCK GRAZING ON THE NUTRITIONAL ECOLOGY OF NORTH AMERICAN TORTOISES

Harold W. Avery
National Biological Survey, Midcontinent Ecological Science Center
Riverside Field Station, 6221 Box Springs Boulevard
Riverside, California 92507, USA

INTRODUCTION

Food and water are essential resources affecting growth, reproduction, and survivorship of wild animals. All species of *Gopherus* are herbivorous, and some live in ecosystems that are characterized by scarce water, varying forage availability, and high ambient temperatures throughout much of the year (Bury 1982). Also, ecosystems inhabited by *Gopherus* spp. pose difficult management problems associated with the influence of expanding human populations that have caused reduction in suitable habitat, extensive fragmentation of existing habitat, and/or have contributed to declines of tortoise numbers through land use.

Understanding the foraging ecology of tortoises can provide useful information for delineating habitat requirements of North American tortoise species. Foraging ecology has been studied in the desert tortoise, *Gopherus agassizii* (Burge and Bradley 1976, Jennings 1993, Avery and Neibergs 1994, Esque 1994) and in the gopher tortoise, *Gopherus polyphemus* (Garner and Landers 1981, Auffenberg and Franz 1982, MacDonald and Mushinsky 1988). Less is known about the foraging ecology of the bolson tortoise, *Gopherus flavomarginatus* (Morafka 1982) and the Texas tortoise, *Gopherus berlandieri* (Auffenberg 1969, Rose and Judd 1982).

Existing information suggests that *Gopherus* spp. exhibit selectivity in the food plants they eat (Auffenberg and Weaver 1969, Garner and Landers 1981, Morafka 1982, MacDonald and Mushinsky 1988, Avery 1992, Jennings 1993, Avery and Neibergs 1994, Esque 1994). In general, *Gopherus* spp. consume forbs, grasses, herbaceous perennials, and some palatable parts of shrubs, with a preference for legumes and other plants having relatively high concentrations of dietary protein (Garner and Landers 1981, Morafka 1982, MacDonald and Mushinsky 1988, Jennings 1993, Avery and Neibergs 1994).

FORAGING AND NUTRITIONAL CONSTRAINTS IMPOSED ON JUVENILE TORTOISES

In light of recent findings that high annual juvenile survivorship (72%) is requisite for maintaining stable populations of long-lived chelonians (Congdon *et al.* 1993), understanding the factors that contribute to juvenile mortality in populations of North American tortoises is essential for designing and implementing effective conservation programs. Factors affecting food and water acquisition and utilization in young age classes are poorly understood, yet can provide critical insight to causes of mortality in these animals. Foraging ecology and nutritional ecology of juvenile tortoises remain among the least known aspects of tortoise ecology.

Body size is an important constraint in the foraging ecology and nutritional ecology of *Gopherus*. Juvenile tortoises may experience different availabilities of forage plants than adults, because larger (and more fibrous) plants are not available to smaller tortoises, and/or may not be digestible, due to limited capacity for gut fermentation in smaller individuals (*sensu* Pough 1973). Differences in body size between hatchling and adult conspecifics range from 5.7-fold (*Gopherus berlandieri*), to 9.5-fold (*Gopherus polyphemus* and *G. flavomarginatus*). It is not surprising that juveniles occupy different microhabitats and have substantially different nutritional requirements and foraging behaviors from adult conspecifics. In addition, juvenile tortoises have maneuverability constraints in the environment due to their small body size (McRae *et al.* 1981; Morafka 1982, 1994; Tom 1988), as do juveniles of other chelonian species (e.g., *Graptemys geographica*, Pluto and Bellis 1986; *Trachemys scripta*, Parmenter and Avery 1990).

Nutrient requirements are undoubtedly different for juveniles and adults. Juveniles have greater mass-specific metabolic rates than larger individuals, which requires juveniles to consume foods that are richer in digestible energy (i.e., lower in dietary fiber). Also, juvenile tortoises have mass-specific rates of water loss that are one to two orders of magnitude greater than those of adults because of their greater surface area:volume ratio (Joyner-Griffith 1991). High rates of water loss set limits on duration of activity, and requires selection of plants having relatively greater water concentrations and lower electrolyte concentrations than adults (see below).

Nitrogen is among the most limited nutrients in the diet of herbivores (White 1993). Juvenile and reproductive animals require proportionately more nitrogen in their diets than non-reproductive adults, because nitrogen is required for growth and development. By selective feeding, juvenile *G. flavomarginatus* consume plants with 16% crude protein, which is twice the concentration of protein found in foods consumed by adults (Adest *et al.* 1989a). Herbaceous plants making up the diets of young *G. polyphemus* are greater in protein concentration than grass diets of adults (Garner and Landers 1981). Other species of juvenile chelonians require greater dietary nitrogen than adult conspecifics as well. Avery *et al.* (1993) demonstrated the importance of dietary protein to growth of juvenile *Trachemys scripta*. Juvenile *Trachemys* fed diets of 10% crude protein (concentration of protein in plants eaten by adults) lose body mass and shrink in size, whereas those fed greater concentrations of protein (25% and 40%) grow significantly during the same period.

ENVIRONMENTAL STOCHASTICITY AND NUTRITIONAL ECOLOGY

Precipitation in North American deserts is scarce, often localized, and highly variable from year to year (Brown 1982, Louw and Seely 1982, MacMahon 1988), and results in spatial and temporal patchiness of primary productivity. Patchiness of food resources contributes to disjunct distributions of tortoises within demes, as observed by Berry (1984), and Lieberman & Morafka (1988). In contrast, more predictable and evenly distributed precipitation in mesic environments inhabited by *G. berlandieri* and *G. polyphemus* results in more even distributions of these tortoises within their demes (Morafka 1994).

Scarcity and unpredictability of precipitation creates special challenges to tortoises, because water affects forage abundance, and is required to utilize dry forage (Nagy and Medica 1986, Peterson 1993). High concentrations of potassium, and low concentrations of crude protein and water, are characteristic of dry desert forbs (Nagy 1973, Nagy and Medica 1986, McArthur 1994). Because desert tortoises are uricotelic (Danztler and Schmidt-Nielsen 1966), as probably are bolson tortoises, substantial amounts of dietary nitrogen are required to excrete potassium in the form of urates. Dry forbs high in potassium and low in crude protein may be avoided because of the physiological challenges they present for maintaining homeostasis.

LIVESTOCK GRAZING AND NUTRITIONAL ECOLOGY

All four species of *Gopherus* have been influenced by livestock grazing that has occurred in North America for over 150 years. Historically, stocking rates were very high in the United States during the 1800's compared to what they are today (Hess 1992). Previously heavy grazing has undoubtedly had profound effects on vegetation and soils in North American tortoise habitat. Killing of tortoises by livestock ranchers has been noted for *G. flavomarginatus* (Pritchard 1979) and *G. polyphemus* (Auffenberg and Franz 1982), because ranchers considered them competitors for forage.

Livestock and tortoises may utilize similar plant species, and thus potentially compete for food in resource-limited years. Few studies have compared the foraging ecology of livestock and tortoises, but Avery and Neibergs (1994) report that in spring following a winter of plentiful rain, range cattle and free-living *G. agassizii* both prefer green annual plants over other available forage in the eastern Mojave Desert of California. In late spring and summer, desert tortoises consume Opuntia spp., while cattle switch to eating perennial grasses (predominantly *Hilaria rigida*) and palatable shrubs (predominantly *Ephedra californica*). In a dry year when spring annuals are not available, desert tortoises and cattle both eat *Hilaria rigida* (H. Avery, unpubl.). Range cattle are removed by mid-spring in a dry year, presumably because of lack of forage.

In conclusion, studies on foraging and nutritional ecology provide essential information on habitat requirements and resource utilization of North American tortoises. Such studies provide information necessary for developing and implementing conservation strategies of North American tortoise species.

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STATUS AND CONSERVATION OF THE GOPHER TORTOISE

Joan E. Diemer Berish
Florida Game and Fresh Water Fish Commission, Wildlife Research Laboratory
4005 South Main Street
Gainesville, Florida 32601, USA

The gopher tortoise (*Gopherus polyphemus*) occurs in the southeastern Coastal Plain from southern South Carolina to extreme southeastern Louisiana (Auffenberg and Franz 1982). The species is peripheral in South Carolina and Louisiana and is found in only the lower parts of Mississippi and Alabama. Florida and South Georgia constitute its current stronghold. The gopher tortoise remains widely distributed in Florida, occurring in portions of all 67 counties (Diemer 1987). However, its current range in southern Florida is fragmented by unsuitable habitat and increased urbanization (Auffenberg and Franz 1982, Diemer 1987, Berish 1991). Tortoise populations occur on Florida's coastal islands and as far south as Cape Sable, at the tip of the Florida peninsula (Auffenberg and Franz 1982, Kushlan and Mazzotti 1984). Throughout much of its range, the gopher tortoise is associated with well-drained, sandy soils and sandhill habitat, characterized by longleaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*). In Florida, tortoises also occur in scrub, scrubby flatwoods, pine flatwoods, xeric hammock, dry prairies, coastal dunes, and disturbed sites (Auffenberg and Franz 1982, Diemer 1987).

The legal status of the species varies among the six states. South Carolina and Mississippi list it as endangered; in Georgia, it is considered threatened. Alabama protects the gopher tortoise as a non-game species. In Florida, the gopher tortoise is a species of special concern. Louisiana does not currently provide protection. However, in 1987, the U. S. Fish and Wildlife Service listed the gopher tortoise as a threatened species in Louisiana, Mississippi, and southwestern Alabama. The gopher tortoise is listed on Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), meaning that commercial trade is allowed only under permit from the country of export.

Habitat destruction, habitat degradation, and human predation have reduced the original number of gopher tortoises by an estimated 80% over the last 100 years (Auffenberg and Franz 1982). Populations in the western part of the range and in the Florida Panhandle have been depleted by past overharvest, exclusion of fire from xeric habitats, and conversion of sandhills to agriculture or dense stands of sand pine (*P. clausa*) or loblolly pine (*P. taeda*) (Auffenberg and Franz 1982, Lohoefener and Lohmeier 1984, Diemer 1987). Gopher tortoise populations in the Georgia Coastal Plain and northern Florida have been fragmented by broad-scale agriculture and development (Landers and Garner 1981, Diemer 1987). Urban growth, phosphate mining, and citrus production have adversely affected gopher tortoises in central Florida. In addition to rampant urbanization and intensive agriculture, invading exotic plants have reduced available habitat in south Florida (Diemer 1987, Berish 1991).

Conservation of the gopher tortoise involves manipulation of the complex interactions among habitats, tortoises, and humans. Key elements are land acquisition, habitat management, and coordination within and among agencies and organizations. Restocking, mitigation, monitoring, education, and research are also integral parts of the scheme to perpetuate this species. In so doing, the broader goal of protecting and enhancing biodiversity will also be achieved. The gopher tortoise's burrowing habits provide refuges for over 360 known species (Jackson and Milstrey 1989), including listed species such as the eastern indigo snake (*Drymarchon corais couperi*), the gopher frog (*Rana capito*), the Florida mouse (*Podomys floridanus*), and Florida pine snake (*Pituophis melanoleucus mugitus*).

Habitat preservation and management require an assessment of currently protected areas and acquisition of remaining critical, unprotected sites. Desoto National Forest in Mississippi and Conecuh National Forest in Alabama are foci for gopher tortoise protection and management in the western portion of the range. However, few sand ridges occur on protected lands in Georgia (Landers and Garner 1981). Relatively large gopher tortoise populations occur on a number of public lands in Florida. McCoy and Mushinsky (1992) surveyed federal lands in Florida and reported tortoise numbers >1000 on Egmont Key National Wildlife Refuge (NWR), Merritt Island NWR (including Canaveral National Seashore), St. Marks NWR, Ocala National Forest, and Everglades National Park (Cape Sable). Cox *et al.* (1994), using Landsat Thematic Mapper imagery and Geographic Information System (GIS) technology, estimated that 93 conservation areas in Florida had sufficient habitat to support tortoise populations >200 individuals (based on assumed densities of 3/ha, which may be high for some sites). Yet, McCoy and Mushinsky (1988, 1992) cautioned that even on reserves gopher tortoises may decline unless the habitat is appropriately managed; they suggested that complacency based on the existence of these currently "protected" lands would be ill-advised. Although current lands may provide the minimum protection required to prevent extirpation of gopher tortoises from Florida, the sandhill and scrub ecosystems, as well as some commensal species, warrant additional attention (Cox *et al.* 1994). The objective, therefore, should be to maximize conservation of xeric uplands through land acquisition, habitat management, and other strategies (e.g., conservation easements). State and local land acquisition programs (e.g., Florida's Preservation 2000) and The Nature Conservancy have acquired exemplary natural areas, but many noteworthy uplands remain unprotected (Berish 1991).

Active management of upland habitats not only increases available gopher tortoise forage and nesting sites (Landers and Speake 1980), but also affects growth rates and age to sexual maturity (Mushinsky *et al.* 1994). Gopher tortoise densities are highest in grassy, open-canopied associations (Auffenberg and Franz 1982). Prescribed burning is the preferred method for managing most gopher tortoise habitats (Landers 1980). The details of the prescription should be site-specific; however, the goal should be to produce a mosaic of vegetation density through variations in fire season and frequency. A multi-aged forest is desirable, ranging from small treeless areas to limited, scattered areas of 50-70% tree canopy cover. Ideally, tree canopy cover for most of the site should not exceed 30-40%. Thinning of oaks and pines may, therefore, be warranted. On lands where burning is not feasible, mechanical removal of woody plants may be useful. Season and frequency of burns should vary with habitat type. In sandhill habitat, burns should be conducted in May or June every 2-5 years. Less frequent, winter burns are recommended in sand pine scrub. Growing season fires every 1-3 years will benefit gopher tortoise populations in pine flatwoods.

Restocking is a conservation measure that differs from relocation in both intent and technique. The goal of restocking is to enhance severely depleted populations or replace extirpated populations. Those populations or lands must first be identified, and the best available source (genetically, socially, and geographically) of gopher tortoises should be used. Gopher tortoise relocation, on the other hand, salvages individual tortoises displaced by development; efforts are made to find "suitable" recipient sites, but the urgency of these endeavors often forces tortoises to less-than-ideal situations. Possible restocking sites include protected lands where gopher tortoises have been overharvested, reclaimed mining lands, abandoned orange groves and pastures, and other "created" tortoise habitats (e.g., areas where the water table has been lowered by drainage) (Diemer 1989). Private lands should be secured by conservation easements or other binding agreements.

Mitigation requirements for gopher tortoises on development sites have evolved over the last decade in Florida. Some mitigation is also occurring in conjunction with highway construction in Georgia (B. Winn, pers. comm.). Current mitigation options in Florida include avoidance of individual burrows during development, habitat protection on or off-site (usually an area equal to 15-25% of the occupied tortoise habitat being affected), and relocation of tortoises to suitable habitat. The habitat protection option may be fulfilled by contributing to a mitigation banking fund to buy the requisite acreage in an existing or proposed mitigation park. Two such parks currently exist and three more are proposed. Tortoise relocation remains a controversial, labor-intensive, and time consuming mitigation option. Biological concerns include disruption of locally adapted gene pools, disease or parasite transmission, population disruption, and dispersal-related mortality (Diemer 1989). Discovery of an upper respiratory tract disease (URTD) in some Florida gopher tortoise populations has increased concern over human-related transmission of infectious disease and prompted draft testing requirements for URTD in relocated tortoises.

Monitoring the status of a widely distributed species is difficult. Remote sensing (e.g., Landsat/GIS data) appears to have the most potential for long-term monitoring of gopher tortoise habitat status. Monitoring of specific populations through burrow surveys or tortoise trapping may also be warranted. Gopher tortoise restocking sites, for example, should be surveyed 5-10 years after stocking.

Posters indicating the gopher tortoise's protected status, informational sheets describing the URTD concerns associated with release of captives, brochures outlining habitat management techniques, and slide series/films on gopher tortoise conservation are educational tools that should be developed and distributed throughout the species' range. Educational efforts on behalf of the gopher tortoise should emphasize that xeric habitats, as well as wetlands, have aesthetic and biological value (Diemer 1986).

Most of the available information on gopher tortoises has been gleaned during the last two decades. Despite recent research efforts, gaps still remain in the knowledge base for this species. Studies regarding gopher tortoise response to development, agriculture, and silviculture are high priorities because the findings have direct application in mitigation efforts. Additional information is needed regarding variations in burrow occupancy rates and tortoise movements in various habitats. Current knowledge regarding URTD is primarily from studies on desert tortoises (*G. agassizii*); research is needed to determine the distribution and evaluate impacts of this disease in gopher tortoise populations.

THE STATUS OF THE DESERT TORTOISE AND CONSERVATION EFFORTS IN THE UNITED STATES

Kristin H. Berry
National Biological Survey,
Midcontinent Ecological Science Center
Riverside Field Station,
6221 Box Springs Boulevard
Riverside, California 92507, USA

Our knowledge and understanding of status and trends in desert tortoise populations and habitats vary considerably depending on location within the geographic range. The most comprehensive body of data available is for the northern and western portions of the range, specifically lands occurring north and west of the Colorado River in the Mojave and Colorado deserts of California, southern Nevada, southeastern Utah, and northern Arizona. Populations in this region were listed as threatened by the U.S. Fish and Wildlife Service (USFWS) in 1990, critical habitats were designated in February of 1994, and a recovery plan was published in June of 1994 (USFWS 1994).

Status and trends in tortoise populations and habitats in the central portion of the geographic range in the Sonoran Desert of Arizona are less well understood, although federal and state agencies have made substantial efforts to gather data since the late 1970's. The data base for the southern part of the geographic range in the Sonoran and Sinaloan deserts in Mexico is even more limited. The discussion on population status and conservation efforts is confined to the two regions within the United States: the northern and western part of the geographic range (Mojave and Colorado deserts), and the central part of the geographic range (Sonoran Desert of Arizona).

POPULATIONS AND HABITAT IN THE MOJAVE AND COLORADO DESERTS

Populations Trends on Study Plots

Because of the longevity of individuals, condition and trends in tortoise populations are best measured using several attributes such as: total population size; population densities; numbers and densities of breeding adults, particularly females; sex ratios; size-age class structure and evidence of recruitment of juveniles and immature tortoises into adult size classes; survivorship rates of the different size classes; causes of mortality; and variations in lambda over time.

Limited data on population attributes are available from 30- and 60-day spring surveys of more than 40 study sites (≥ 2.6 km^2), with more comprehensive long-term data sets available from about 24 sites. Some populations are stable, a few are increasing, and the majority show signs of decline (Berry 1990, Berry and Medica in press, USFWS 1994). The greatest declines in densities (up to 90%) occurred in the western Mojave Desert between the 1970's and 1990's.

Declines of 30-60% occurred in the eastern Colorado Desert between 1979 and 1992, with the greatest declines registered at the Chuckwalla Bench. Declines of 20-25% were experienced in the eastern Mojave Desert at the Piute Valley and Goffs plots. The northeastern Mojave also exhibited declines on some plots (e.g., Ivanpah Valley, Gold Butte, Beaver Dam Slope). In contrast, the northern Colorado Desert population appeared to be growing between 1980 and 1991, at least in numbers of breeding adults in Ward Valley. The Upper Virgin River population is probably stable.

General and Specific Threats to Populations

The greatest threat to tortoises is from people, whether through take of individual animals or as a result of deterioration and loss of habitat or both. Generic threats include: increased human access to remote tortoise habitats, abnormally high mortality rates, fragmentation of populations and habitat, the limited number of established and secure reserves, loss of linkages between small populations, gradual increases in the cumulative impact load of disturbances regionally, and insufficient protection of critical habitats.

The *Desert Tortoise (Mojave Population) Recovery Plan* (USFWS 1994) contains a comprehensive description of specific threats to the species. While the emphasis is on threats facing the listed population in the northern and western portions of the geographic range, the problems are typical of those found range-wide. Threats vary by region and local area, with the types of threats generally being more numerous and severe where human contact is more prevalent.

Humans remove tortoises from wild populations for food, commercial trade and pets; they also vandalize, relocate or translocate tortoises. Humans release captive tortoises, which appear to be the source of upper respiratory tract disease (URTD), an often fatal disease. The URTD, which is caused by a bacterium *Mycoplasma agassizii*, is responsible for catastrophic death rates in the western Mojave Desert and is affecting several other regions as well. This disease is a threat range-wide.

Humans alter and destroy habitat (affecting resident tortoise populations as well) through urban and agricultural development; construction of landfills and deposition of refuse; mining, mineral and energy development; construction and maintenance of freeways, highways, paved and dirt roads, and railroads; construction and maintenance of utility and energy facilities and corridors; military operations; recreational vehicle activity and vehicle travel off road; and livestock grazing.

Where habitats have been damaged or destroyed, exotic and alien plants frequently invade and proliferate. Some alien plants are fire prone, and have contributed to an increase in the numbers of fires and acreage burned in some areas, particularly in the western and eastern Mojave deserts of California and the northeastern Mojave Desert of Arizona. Populations of a native predator, the common raven, have been subsidized by human activities and have grown more than 10-fold in some regions. This native predator has effectively reduced recruitment of juvenile tortoises into the adult population in some areas.

Recommendations for Recovery of Tortoise Populations from the *Desert Tortoise (Mojave Population) Recovery Plan* (USFWS 1994)

The Desert Tortoise Recovery Team recommended that reserves for the desert tortoise be in the range of 520 to 13,000 km^2 with a target size of at least 2,600 km^2. If, for example, densities of adults were at a minimum level of 3.9/km^2, then extremely large reserves of 13,000 km^2 would be necessary to support 50,000 adults. Such large reserves would be necessary for tortoise populations to persist for 500 yrs with a 50% probability of extinction.

Security of Existing Habitats and Populations

Using principles of reserve design and data from three population viability analyses, the Desert Tortoise Recovery Team recommended that six recovery units and 14 reserves or Desert Wildlife Management Areas (DWMAs) be established to enhance opportunities for recovery (USFWS 1994). The six recovery units represent the genetic, morphologic, behavioral, and ecological diversity found within the region. They are called: western Mojave, eastern Mojave, northeastern Mojave, Upper Virgin River, northern Colorado, and eastern Colorado. The USFWS followed by designating critical habitat that covered about 25,900 km^2. In addition to critical habitat, tortoise habitat receives substantial protection within Joshua Tree National Monument and the Desert Tortoise Research Natural Area. Although the majority of most DWMAs are protected by critical habitat status, substantial private holdings remain within the boundaries of most reserves. Pressures for development of both private and public lands are intense within and adjacent to most DWMAs. Government agencies are faced with major challenges to reverse the trends of tortoise population declines, habitat deterioration, and fragmentation.

Management of DWMAs and Recovery Units through Regional Planning

The desert tortoise has acted as an indicator and umbrella species for government land-use planning since the late 1970's. Stimulated by the federal listing of the tortoise as a threatened species in 1990, government agencies are working together and with the private sector to develop regional land use plans known as coordinated resource management plans (CRMPs), habitat management plans (HMPs), and habitat conservation plans (HCPs)). Such plans, which have become large scale biodiversity and multi-species land-use and conservation plans, are in various stages of development for southern Nevada (Clark County HCP), southwestern Utah (Washington County HCP), and the western Mojave Desert (CRMP). A plans for the eastern Mojave Desert (California) and a combined plan for the northern and eastern Colorado deserts are in early stages.

STATUS OF POPULATIONS AND HABITAT IN THE SONORAN DESERT OF ARIZONA

Population Trends at Study Plots

Sonoran Desert tortoises are significantly different from those in the Mojave and Colorado deserts in terms of genetics, morphology, habitat selection, and behaviors. Populations are generally small, fragmented and of low density, rendering sampling more difficult. During the last 5-7 yrs, plots (each ≥ 2.6 km^2) were sampled using 60-day surveys in summer and fall during the monsoon season.

Partial or complete sets of survey data are available from fewer than 12 sites. Sites vary in density and overall population condition. In spite of 16 years of searching, only two sites have been located with densities > 39 tortoises/km^2; one is at Little Shipp Wash and the other is in the Tonto National Forest. Some sites have few or no tortoises and one site (Maricopa Mountains) experienced a substantial die-off a few years ago. Some areas (e.g., Luke Air Force Base) have low tortoise densities of about 3.9/km^2, whereas others (Eagletail and Granite mountains) appear to have moderate densities and have remained stable with little recruitment and low mortality over a 5-yr sampling period. One plot in the San Pedro River Valley supports moderate densities but has an excessive number of recent deaths.

Threats to Populations and Habitat

The threats described for populations in the Mojave and Colorado deserts are similar to those occurring in this portion of the geographic range. Tortoise populations and habitat in the Sonoran Desert of Arizona face additional threats, however. The *Desert Tortoise (Mojave Population) Recovery Plan* (USFWS 1994) outlined sizes of reserves and the numbers of tortoises to be contained within each for the northern and western part of the geographic range. Such large reserves and high numbers of tortoises are probably not be attainable here, because Arizona populations are fragmented and generally small in size. Few blocks of habitat with >39 tortoises/km^2 have been identified and these blocks are generally quite small fragments covering a few km^2. Some large blocks of habitat with low densities of tortoises (3.9/km^2) remain on military installations, but the blocks are still small compared with the 13,000 km^2 reserves described in the *Recovery Plan* for low density populations.

Since most tortoise populations occur on slopes of mountains and the majority of development occurs in the intervening valleys, connectivity of fragments is a serious issue. Private holdings, interspersed with public lands, also contribute to fragmentation. The challenge will be to protect and connect sufficient fragments of habitat and populations to maintain a viable metapopulation.

Security of Existing Populations and Habitat

No reserve system or recovery plan has been developed for desert tortoises within this region. However, some protection is accorded to populations and habitats within Saguaro National Monument, Organ Pipe National Monument, the Barry Goldwater Range and Cabeza Prieta

National Wildlife Refuge, as well as within >50 areas formally designated as wilderness. In addition, two small Areas of Critical Environmental Concern (ACEC) have been designated: Picacho Mountain ACEC (about 25 km^2), and East Bajada near Kingman (about 21 km^2).

ACKNOWLEDGMENTS

References to the material described above can be found in the *Desert Tortoise (Mojave Population) Recovery Plan* (USFWS 1994). The following people provided recent, unpublished information: Ted Cordery of the Bureau of Land Management State Office, Arizona; Todd Esque of the National Biological Survey; and Vanessa Dickinson of Arizona Game and Fish Department.

ECOLOGY OF THE *Agassizii* TORTOISE GROUP

R. Bruce Bury
National Biological Survey
Corvallis, Oregon 97333, USA

The desert tortoise (*Gopherus agassizii*) and Berlandier's tortoise (*G. berlandieri*) are closely related (e.g., central Arizona *G. agassizii* are closest to *G. berlandieri*). Ecologically, they may represent ends of clinal variation or be viewed as adaptations to regional environments. The range of the desert tortoise is the largest of any North American tortoise, covering an area 750 km wide by 1500 km long. Berlandier's tortoise is restricted to southern Texas and northwestern Mexico. The desert tortoise lives in at least three distinct habitats (climatic regimes): the Mojave Desert (hot summers/cold winters; most precipitation in winter-spring), Sonoran Desert (hot summers/cool winters; rainfall mostly from summer thunderstorms), and Sinaloan thornshrub and deciduous forest (hot summers/mild winters; elevated rainfall, mostly in summer). Berlandier's tortoise frequents coastal dunes and Tamaupilan Plain scrub (hot summers/mild winters; elevated rainfall, mostly from summer storms).

The desert tortoise uses the most diverse habitats of any North American tortoise. They range from sea level to mountains over 1500 m elevation. Most surveys for desert tortoises have been on flats or bajadas in the Mojave Desert, where tortoises reach high densities. However, there are no tests of abundance related to elevation and slope. For example, one study indicated tortoises most abundant at mid-elevation slopes (ca. 1200 m) in southern Nevada. Desert tortoises in the Sonoran Desert of Arizona occur on hillsides or rocky uplands and, thus, are on habitat "islands" (hills) surrounded by flats and open desert. Little is known of desert tortoises in Mexico, but recent surveys suggest that they occur in many habitats from sea level to upland scrub forest. Berlandier's tortoise is widespread, but surveys of their habitats are lacking in Mexico.

Use of cover by desert tortoises varies from construction of deep burrows >10 m in the northern portion of its range to hiding in rocky overhangs or use of shallow burrows or pallets in southern locales. Cover use varies greatly in the Mojave and Sonoran deserts. We lack knowledge of their lives in Sinaloan habitats. Berlandier's tortoises mostly construct shallow burrows or pallets.

The desert tortoise reportedly had widespread, high-density populations (>100 per km^2) in the Mojave Desert that have declined since about 1900 to isolated fragments. However, evidence for the long-term decline of tortoise populations is based on unpublished information and may be biased because most of the respondents lived in areas heavily affected by recent habitat loss. Reported declines cannot be extrapolated to undeveloped desert. The scientific literature through the 1970s does not support the contention that desert tortoises once occurred in high densities throughout most of the Mojave Desert. Empirical evidence is inadequate to establish historical population trends in this tortoise.

Low density areas are considered demographic sinks, sustained only by immigration from nearby areas with high densities. However, there is no evidence that supports these conclusions. We do not know if low density populations lack reproductive effort or recruitment. Many tortoise populations with low to moderate density occupy large geographic areas. Thus, on the larger scale, these populations have many individuals. Because of our lack of knowledge about the life history and biology of *G. agassizii* in Sonoran and Sinaloan habitats, analyses of population viability for the species must be viewed with caution. Even for the well-studied tortoise in the Mojave Desert, there is no life table available.

The desert tortoise is a large-bodied herbivore and they eat a wide variety of plant material, often reflecting the abundance of plant species in the environment. They often consume soil, small rocks and bones, possibly as a source of dietary minerals (e.g., calcium). The Berlandier's tortoise is the smallest of the North American tortoises, and eat cactus and forbs.

Reproductive features differ in the two species (Germano 1994). The mimimum age of first reproduction (AFR) for desert tortoises is 13-16 yrs (mean values), with extremes from 9 yrs (western Mojave Desert) to 21 yrs (Sonoran Desert). AFR for Berlandier's tortoise is 13 yrs (range 11-17 yrs). Mimimum size at first reproduction for female desert tortoises is 176-189 mm carapace length; for Berlandier's tortoises, 140 mm CL. Both species are long-lived (estimates >30 yrs old in the wild). So, why do desert tortoises sexually mature at older ages and especially larger sizes than do Berlandier's tortoise?

Clutch sizes vary widely by study and geography (Germano 1994). Mean values for desert tortoises are 4.5 eggs (range 1-8) per clutch and 1.6-1.7 clutches per yr in the eastern Mojave Desert to 6.7 eggs (1-14) per clutch in the "Mojave Desert." Berlandier's tortoises had 1.4, 2.7 and 4.3 eggs in 1-2 clutches per yr in southern Texas. There are no other estimates for desert totoises in other regions or for Berlandier's tortoise in Mexico or inland in Texas.

Populations of desert tortoises are reportedly biased toward adults and, in turn, lack recruitment. However, these analyses usually employ size categories and these frequency distributions tend to clump tortoises in the larger sizes. The categories actually represent different scales. For example, small-sized tortoises are transitory stages (e.g., a juvenile category may include only 2-4 yrs of life) whereas adults are a more permanent group (e.g., including age classes than may span decades). An improvement would be analyses of age structure in populations. Recent studies suggest that there are few individuals in any single age class of tortoise populations because adults represent 10-30+ years of life (and thus need to be divided by this long time span).

Few young are typical in almost all chelonian populations studied to date. Current survey methods likely underestimate young tortoises in populations because these tortoises have small home ranges, tend to hide (perhaps with rare surface activity), and are cryptic.

A drought in the Mojave Desert over the last few years has likely caused the loss of individuals or a few years of recruitment in desert tortoises. However, this alone does not suggest imminent extinction because there is high variation in reproductive success of long-lived, iteroparous organisms like turtles. Successful recruitment may better be considered as a cyclic pattern (e.g., when precipitation regionally is high for two years in a row) or a chaotic phenomenon (e.g., when unpredictable summer thunderstorms drench one area in successive years).

Although most of our knowledge about Berlandier's tortoise is from two coastal areas in southern Texas, it is published in the open scientific literature. Information on the status and ecology of desert tortoises is clouded because of the high volume of gray literature and low output of scientific papers based on field surveys and experiments.

Non-refereed, unpublished reports are now most of the documentation for important decisions on desert tortoise management. In my opinion, this information lacks credibility and may even weaken the arguments for tortoise conservation. Rigor is best achieved by publication of biological information in reviewed outlets, and that open exchange of scientific evidence is the desired means to develop sound management practices. Peer review is the principal means of quality control in science and its necessity is even greater when scientific evidence is offered as guidelines for conservation and policy issues.

MODELLING POPULATIONS OF NORTH AMERICAN TORTOISES: MODEL RESULTS AND ASSESSMENT OF DATA ADEQUACY

David J. Germano
Department of Biology, California State University
Bakersfield, California 93311, USA

INTRODUCTION

In a recent paper I reviewed the life-history data that has been gathered on the four species of North American tortoises (*Gopherus* spp.), and I indicated traits for which greater knowledge is needed (Germano 1994). Morphological and ecological differences among species of *Gopherus* may significantly affect life-history traits. Data on longevity, birth rate, age-at-first reproduction, survivorship, sex ratios, and age distributions are vital to a complete understanding of these species and to their proper conservation. The Endangered Species Act of 1973 (16 U.S.C. 1531-1543; 87STAT 884, as amended) lists all populations of *G. flavomarginatus* as endangered and *G. agassizii* and *G. polyphemus* as threatened in portions of their range. Data on life-history traits can be used to simulate population dynamics and to predict the viability of a population. In this paper I use the data that I collected on the life-history traits of the four species of North American tortoises to model population dynamics of tortoises in variable environments. In addition, I note recent data collected on desert tortoises and I discuss the adequacy of data currently available to model populations of North American tortoises.

METHODS

I used data presented in Germano (1994) as the basis for comparing life-history traits of the four species of North American tortoises: Berlandier's tortoise (*Gopherus berlandieri*), desert tortoise (*G. agassizii*), gopher tortoise (*G. polyphemus*), and Bolson tortoise (*G. flavomarginatus*). In addition, I gathered recent data on these species that was not available when the other paper was written. I used these data to model population dynamics.

I modelled populations of North American tortoises using the age-based model RAMAS/age (Applied Biomathematics 1990). This model can use estimates of variance in life-history traits to simulate population dynamics in a variable environment. I used mean values of fecundity, egg survivorship, and survivorship of individuals post hatching to construct a life table required by the model. In addition, I used proportions of tortoises in various age categories determined in the field to allocate numbers of tortoises to age classes. I used a longevity of 45 years to model populations. However, the model is limited to 17 age categories. Following suggestions of the authors of RAMAS/age, I apportioned numbers of tortoises into 15 age classes (exclusive of eggs) making each age class a three-year time interval. Coefficients of variation (CV) were determined for the mean fecundities and survivorships used in the model. CV is used to estimate the amount of variability of the environment and varies fecundity and survivorship stochastically during model simulation. Each simulation consisted of 100 replications and ran for 200 years from base-line input.

RESULTS AND DISCUSSION

Several additional studies on desert tortoises have been done since my original summarization of life-history traits was written. The number of eggs per clutch for desert tortoises from the Sonoran Desert has been estimated to be 5.7 (range: 3 - 9), and there was no indication of multiple clutches (Murray et al. 1994). Another study in the Sonoran Desert found 5.9 eggs/clutch (range: 4 - 9) and no multiple clutches (B. Wirt, personal communication). A study in the eastern Mojave Desert (Karl 1994) has found lower egg numbers/clutch than in the Sonoran Desert and multiple clutches, confirming data recorded earlier (Turner et al. 1986) in this part of the range of the desert tortoise.

The model results show the wide variation possible in tortoise abundance using realistic values of life-history traits. The starting points I used to model a generalized population of North American tortoise were: Egg Survivorship = 0.10; Egg Output = 8.24 eggs/year (4.12 eggs x 2 clutches, data after Turner et al. 1986); Age at Maturity = 15 years; Survivorship = 0.50/year for ages 1-3 yr, 0.75/year for ages 4-12 yr, 0.90/year for ages 13-15 yr, and 0.98/year for tortoises > 15 yr.

Egg Survivorship:
0.10: Rapid decline in population to extinction in about 60 yr.
0.30: Increase in population for 10 yr, then steady decrease to extinction by about 120 yr.
0.35: Rapid increase in population until 40 yr, then population stabilized at twice starting population abundance.
0.50: Rapid increase indefinitely (exponential growth).

Reproductive Output:
8.24 eggs/year: Rapid decline in population to extinction in about 70 yr.
10.24 eggs/year: Rapid decline in population to extinction in about 70 yr.
13.4 eggs/year: Rapid decline in population to extinction in about 70 yr.
13.4 eggs/year, 0.20 egg survivorship: Increase in population for 10 yr doubling population size, then steady decrease to 200 yr.
13.4 eggs/year, 0.25 egg survivorship: Rapid, steady increase (exponential growth).

Age at Maturity:
14 years: Rapid decline in population to extinction in about 70 yr.
12 years: Rapid decline in population to extinction in about 70 yr.
10 years: Rapid decline in population to extinction in about 70 yr.
8 years: Rapid decline in population to extinction in about 70 yr.
10 years, 0.25 egg survivorship: Increase in population to 40 yr, then steady decrease to below starting population size by 200 yr.
10 years, 0.30 egg survivorship: Rapid increase at 10 yr to three times starting population level, then stable out to 200 yr.
Juvenile Survivorship:
0.90/year at 13 years: Rapid decline in population to extinction in about 70 yr.

0.90/year at 7 years: Decline in population to extinction in about 150 yr.
0.90/year at 4 years: Steady increase in population to five times initial size by 100 yr.
0.90/year at 7 years, 0.20 egg survivorship: Rapid increase indefinitely (exponential growth).

<u>Adult Survivorship</u>: (Egg Survivorshiop = 0.35)
0.95/year Adult, 0.75/year from 1-15 years: Rapid decrease in population, extinct in 94 yr.
0.90/year Adult, 0.90/year at 7 years: Steady increase in population quadrupling population by 120 yr, then rapid increase to 10 - 12 times population size from 160 - 200 yr.
0.98/year Adult, 0.90/year at 7 years: Rapid increase indefinitely (exponential growth).

Model results show that egg survivorship of 0.10 to 0.30 do not maintain a tortoise population, given other trait values I used. If egg survivorship is increased to 0.35, however, tortoise populations increase and then remain stable. Is egg survivorship of 0.35 higher than what is seen in nature? Little data are known for this trait (see Germano 1994). Given the other levels of survivorship for ages 1 to adult that I used in modeling, egg survivorship of 0.35 translates to only a survivorship of 0.000239 (2.4 / thousand tortoises) from egg to maturity at age 15 yr. Perhaps this is realistic.

Changing values of egg output and age at maturity had little effect on tortoise abundance when egg survivorship was 0.10. In both cases, though, increasing egg survivorship led to stable or increasing tortoise populations. For reproductive output, increasing egg number to 13.4/female/year coupled with egg survivorship of between 0.20 and 0.25 gave a stable or expanding population. If age at maturity is decreased to 10 yr along with increasing egg survivorship to between 0.25 and 0.30, an expanding population is achieved.

If adult survivorship (past age 15 yr) is as high as 0.98, setting juvenile survivorship at 0.90/year between 4 and 7 yr will lead to stable or expanding population. This will occur even if egg survivorship is 0.10/year. Adult survivorship can be as low as 0.90/year if juvenile survivorship is also 0.90/year starting at age 7 yr. Obviously many other combinations of survivorship can occur that would maintain stable tortoise populations.

Data are still inadequate to reliably predict population trends for North American tortoises. More data are being gathered on desert tortoises, and recent studies in the Sonoran Desert are much needed. However, survivorship data may be the most important life-history traits to gather to model tortoise populations, yet little headway has been made for this trait.

REPRODUCTION OF THE BOLSON TORTOISE, *Gopherus flavomarginatus*, LEGLER 1959

Rolando G. González-Trapaga
Instituto de Ecología, Centro Regional Durango
Apartado Postal 632, Durango 34000, México

INTRODUCTION

The study of reproduction is one of the basic components of vertebrate wildlife biology. This is particularly important in those species which are threatened or endangered in which one of the principal goals in management of genetic diversity which, in turn, should be the maintenance of genetic diversity which, in turn, depends ultimately on reproduction (Wildt 1989). Although the first studies of reproductive physiology were undertaken many years ago on domestic species of birds and mammals, it is only in the last three decades that the importance of the role of wild populations of fish, amphibians and reptiles has been recognized as contributing to our knowledge of the evolutionary history of distinct groups of hormones and the manner in which they act. The object of this study was to elucidate the reproductive cycle of the Bolson tortoise, *Gopherus flavomarginatus*, evaluate the annual variation in the concentration of specific steroids, and relate these results to the activity and behavior of the species.

STUDY AREA

The study area is situated within the Mapimí Biosphere Reserve, comprising 103,000 ha located between 26° 20' and 26° 52' N and 103° 58' and 103° 32' E in the area known as the Bolsón de Mapimí (Mapimí Basin), a part of the Mesa Central del Norte of the Altiplano of México. Altitude within the reserve varies between 1100 and 1350 m and the climate is arid. Monthly mean temperature varies between 11°C in January-February and a maximum of 28°C during the summer. Annual precipitation averages 230 mm with marked annual variability and a seasonality in which approximately 80% of the annual rainfall occurs between June and September. Vegetation is characterized by matorrales rosetófilos (magueyal: *Agave* spp.), crasicaule (nopalera: *Opuntia* spp.) and spineless microphylls (gobernadora: *Larrea divaricata*) occupying large areas of grassland or pastizal de sabaneta (*Hilaria mutica*).

METHODS

Sampling followed a complete annual cycle of 13 monthly periods beginning in the Spring of 1985 (end of March) to the Spring of 1986 (beginning of May). Collecting was concentrated in high density tortoise sites, defined as colonies with a weak social structure by Aguirre *et al.* (1984.) The original sampling protocol called for 10 adult animals of each sex from natural populations. This protocol was not always obtainable given this species' characteristics: deep and extensive burrows, and seasonal epigean activity restricted to favorable ambient conditions in spring and summer (Adest *et al.* 1989a). Therefore, we also used blood from animals which had remained for varying times under seminatural conditions in the laboratory of the reserve. This group was termed "natural captive." The sample group of animals collected from the field and rereleased subsequently was divided into subgroups according to the duration of confinement. "Wild caught" was used for those animals with less than 24 hours of captivity and "semicaptive" for those with one day or greater. Up to 3 cc of blood was withdrawn in heparinized syringes by jugular venipuncture following immobilization of subjects with 0.5 mg/kg of body weight of succinylcholine. Samples were iced until spun at 20,000 rpm for five minutes in a clinical tabletop centrifuge. Plasma was stored in Nunc tubes in liquid nitrogen, classified according to sex and University of California, Berkeley according to the techniques of Licht *et al.* (1979) for testosterone in males and females, estradiol and progesterone in females, and following Licht *et al.* (1983) for corticosteroids in males and females.

RESULTS

Females. Statistical analysis revealed that length of confinement in the laboratory did not influence circulating steroid levels (testosterone P = 0.06, estradiol P = 0.50, progesterone P = 0.08, corticosteroids P = 0.92), therefore all wild-caught females were treated as a single group: "no captivity." Comparison of this group with captive females produced statistically significant differences for the sex steroids (testosterone P = 0.05, estradiol P = 0.01, progesterone P = 0.03), but not for the corticosteroids (P = 0.15) between mean values. The following description is based on the results of the no captivity group.

Testosterone. Maxima were observed at the beginning of Spring (end of March, 48.95 ± 12.57 ng/ml), which coincides with the period of oviposition and mating, and the beginning of Fall (October, 28.90 ± 8.39 ng/ml), which coincides with the beginning of winter inactivity. The minimum of the cycle (2.54 ± 1.05 ng/ml) was observed at the beginning of July, the transition time between Spring and Summer and the end of the oviposition period. (Fig. 1).

Estradiol. June was the minimum of the cycle (2.50 ± 0.52 ng/ml), while a maximum occurred in November (13.13 ± 2.65 ng/ml), in the middle of the inactive period and at the beginning of April, in Spring (8.83 ± 1.59 ng/ml). (Fig. 1).

Progesterone. The minimum value occurred in the beginning of July, in Summer (1.33 ± 0.23 ng/ml) and the maximum at the beginning of Spring (end of March, 3.53 ± 0.55 ng/ml), at the initiation of the period of oviposition. (Fig. 1).

Corticosteroids. The cycle minimum occurred in October (8.81 ± 1/73 ng/ml) and the maximum in December during the transition between Fall and Winter (20.15 ± 3.47 ng/ml). (Fig. 2).

Males. Statistically significant differences were absent between animals of wild caught, semicaptive and saptive, as between no captivity and captive, and all males were pooled.

Testosterone. The minimum, in the cycle occurred in the middle of April (133.15 ng/ml) and the maximum at the end of July (1028 ± 108.66 ng/ml), after the main part of the reproductive season. (Fig. 3).

Corticosteroids. The minimum value occurred at the beginning of April (5.14 ng/ml) and the maximum at the beginning of June (31.67 ± 9.72 ng/ml). (Fig. 2).

DISCUSSION AND CONCLUSIONS

Females. The statistical differences found according to time in captivity can be related to the reduced sample size of the captive group - an average of 3 individuals per month. The hormonal fluctuations observed in the three sex steroids (Fig. 1) are similar to those reported for other species of chelonians (e.g., *Chrysemys picta* Callard *et al.* 1978, *G. polyphemus* Taylor 1982). As such, testosterone reaches a maximum level before estradiol, suggesting its role as precursor in the synthesis of females, especially with its maximum at the end of Winter and the beginning of the mating period. The variations in the cycle of development. The Fall maximum would coincide with the period of ovarian recrudescence and vitellogenesis and the Spring maximum produces the final maturation of follicles before their release. The minimum estradiol level observed in the summer corresponds to Progesterone changes are inversely related to those of estradiol, maximum only in the period prior to oviposition when the corpora lutea, although transitory, are fully functional and minimum in the summer at the end of the reproductive cycle.

Males. *Gopherus flavomarginatus* males have an associated reproductive cycle in which testosterone reaches its maximum levels in the summer, approximately six months after the initiation of the reproductive season, but a month prior that the cycle maximum (Fig. 3). As a result, it is hypothesized that sperm used in fertilization during the current year was produced during the previous year and stored during the winter.

The high levels of testosterone discovered during this study are much greater than those reported for any other vertebrate species and remain unexplained. Courty and Dufaure (1979) reported a maximum value of androgens (in particular, testosterone) of 445 ng/ml during the mating period of *Lacerta vivipara*. In our case, further studies are required to explain the causes of the testosterone levels we observed. It is very probable that the high levels of testosterone we observed during the Summer are sufficient to explain the reproductive behavior observed in this species during the months of Fall (G. Aguirre, pers. comm.), as well as that reported for *G. polyphemus* (Taylor 1982.)

Corticosteroids. The situation with respect to corticosteroids is similar for both sexes (Fig. 2) and differs from that reported for other species of chelonians (for example, *Chelydra serpentina* Mahmoud *et al.* 1989). In *G. flavomarginatus* the stress of transport, confinement and manipulation does not have a negative impact on the production and metabolism of the sex steroids. The variations in the levels of circulating hormones which were observed in both sexes reflect the energetic demands imposed by unfavorable environmental conditions in that the maximum values occurred in periods of winter lethargy as reported for other species. Females additionally have high levels of corticosteroids during oviposition, as occurs in *Uta stansburiana* (Wilson and Wingfield 1992), an activity which represents a great energetic cost to individuals.

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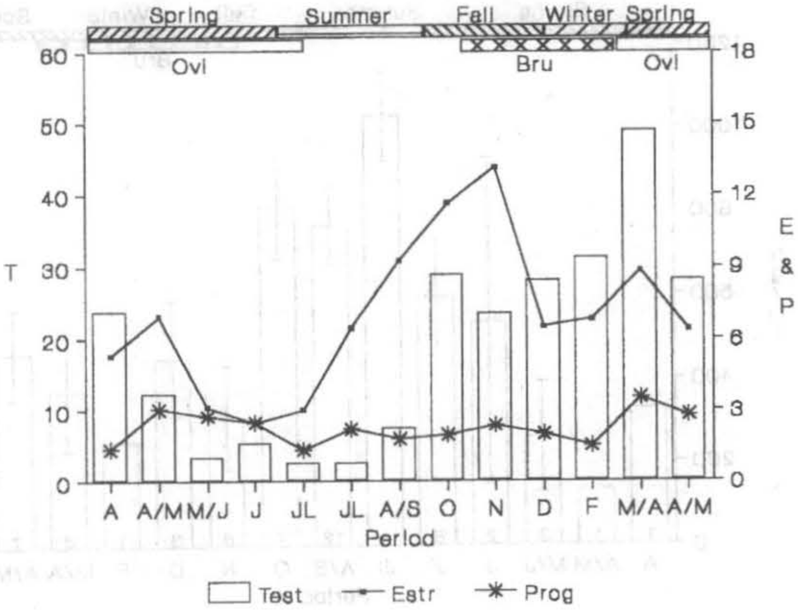

Fig. 1. Sexual steroids of non-captive Bolson tortoises females. The first line of top horizontal bars depict the seasons of the year. The second line, associated events of oviposition (Ovi) and brumation (Bru).

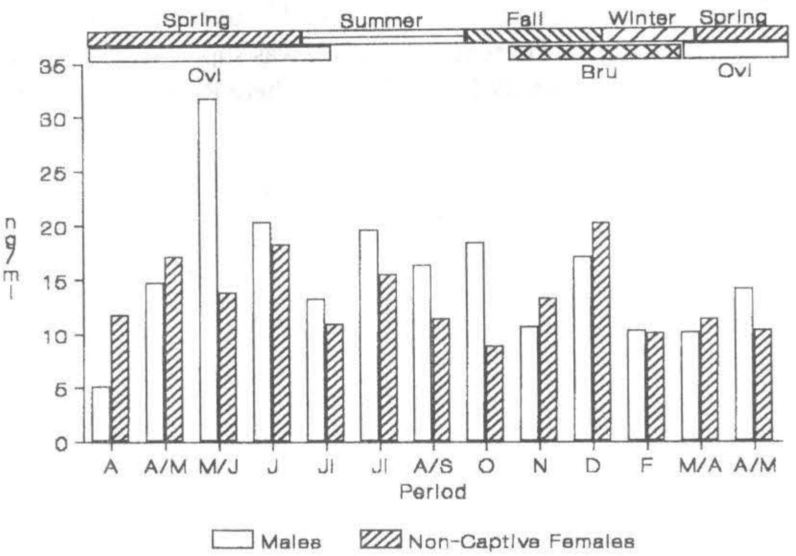

Fig. 2. Comparison of corticosteroids for males and non-captive females Bolson tortoises.

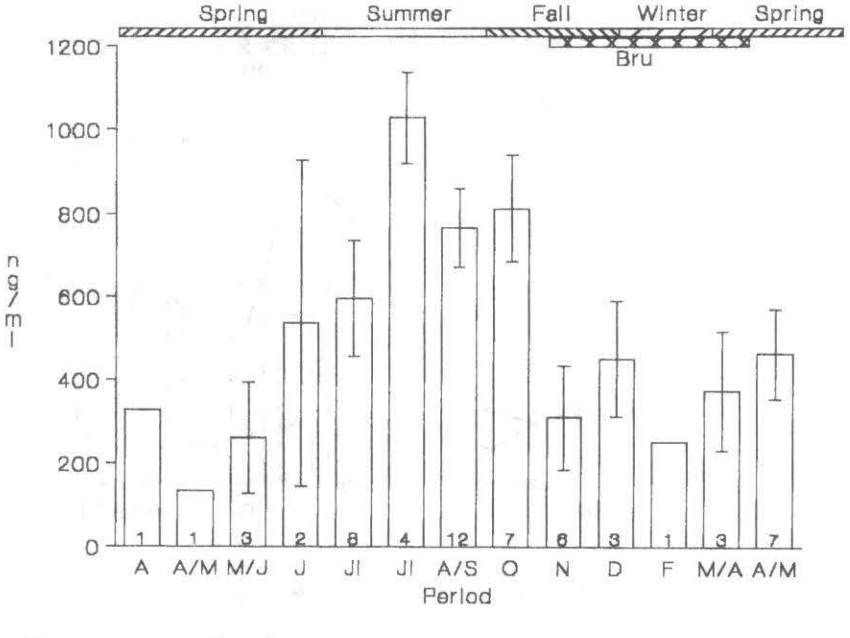

Fig. 3. Testosterone of male Bolson tortoises. Bars represent average monthly concentration. Vertical lines represents standard error. Numbers are sample sizes.

CONSERVATION CONCERNS FOR THE TEXAS TORTOISE, (*Gopherus berlandieri*)

Richard T. Kazmaier
Caesar Kleberg Wildlife Research Institute, Campus Box 218
Texas A&M University-Kingsville
Kingsville, Texas 78363, USA

INTRODUCTION

Several detailed ecological studies of the Texas tortoise, *Gopherus berlandieri*, have been conducted (Auffenburg and Weaver 1969; Rose and Judd 1975, 1982; Judd and Rose 1983). However, these studies were primarily restricted to coastal areas of southern Texas, and little information is available on the variability of life history traits among populations throughout the range of this species, particularly in Mexico. In addition, virtually no data are available on how various land-use practices affect *G. berlandieri*. This paper summarizes current knowledge on the status and conservation of *G. berlandieri*, presents information on a recently initiated study on an inland population of *G. berlandieri*, and points out inadequacies in our knowledge base that impair our ability to make sound conservation and management decisions regarding this species.

Concern over possible declines in *G. berlandieri* populations, primarily by exploitation for the pet trade, prompted the Texas legislature to officially protect this species in 1967. Following development of threatened and endangered species regulations for the state of Texas in 1977, *G. berlandieri* was officially listed as a threatened species (Rose and Judd 1982). As a result, collection of *G. berlandieri* is regulated by the Texas Parks and Wildlife Department and exploitation of this species for the pet trade has been largely curtailed.

There is little information on *G. berlandieri* density throughout its range. Judd and Rose (1983) reported a density of 10.0-22.9 tortoises/ha over 5 years for Cameron county, Texas, but this population was concentrated on lomas (ridges) and densities in more contiguous habitats are unknown. Except for those areas being impacted by habitat alteration, there is no data to suggest that populations of *G. berlandieri* in the United States are unstable. There is, however, anecdotal evidence that some tortoise populations may be declining, particularly in northern parts of their range.

In addition to tortoise density, information on tortoise reproduction is important for making management decisions. Data on sex ratios, age at maturity, clutch size, clutch frequency, and hatchling recruitment are largely lacking. Judd and Rose (1989) do report single clutches of 1-5 eggs for *G. berlandieri* in Cameron county, Texas, but the variability of these traits for different populations has not been addressed. Coastal tortoises tend to be larger than those in inland populations (Rose and Judd 1982), and reproductive characteristics may vary in a similar manner. Longevities and natural mortality rates are also poorly understood. Lack of data pertaining to all aspects of the population dynamics of *G. berlandieri* makes predictions about population stability and viability difficult.

Habitat destruction and fragmentation are often the primary factors causing a species' decline. Fortunately, much of the range of *G. berlandieri* in the United States is composed of large private ranches. Some habitat is being degraded, especially in the lower Rio Grande Valley, for citrus, cotton, and other crop production. Due to the large size of the private ranches north of the Rio Grande Valley, however, extensive tracts of tortoise habitat are being maintained. Many ranches practice grazing, and there has been some concern that grazing may adversely affect the desert tortoise (*G. agassizii*) by competition for forage, direct loss by trampling, or by habitat alteration (Berry 1978, Luckenbach 1982). Presently, the relationship between grazing and *G. berlandieri* is unknown.

Roads, which are often associated with habitat fragmentation, are a concern for certain *G. agassizii* populations due to vehicle-related mortality (Luckenbach 1982). Because much of the range of *G. berlandieri* in the United States is composed of large private ranches, roads probably do not pose a serious threat to this species. However, there are no data on the severity of road-related mortality for *G. berlandieri*.

In addition to possible hazards produced directly by cattle, other factors of the ranching industry in Texas may impact *G. berlandieri*. It is a common practice in southern Texas to employ woven wire high (>2 m) fences, primarily for deer management, and some mesh sizes may entangle tortoises. Immediately after the construction of a high fence surrounding the Chaparral Wildlife Management Area (CWMA) in Dimmit and LaSalle counties, Texas, a large number of tortoises died after becoming entangled in the mesh (D. R. Synatzske pers. comm.). Such deaths have not been encountered recently. High fences may pose a temporary problem to tortoises, until the resident tortoises become accustomed to the barrier and other animals make corridors underneath the fences. Again, the impact such mortality could have on a tortoise population is unclear.

Methods of range improvement have potential to seriously impact *G. berlandieri*. A variety of methods have been employed for the removal of woody vegetation, including roller-chopping, chaining, and root-plowing. Root-plowing consists of plowing an area to a depth sufficient to uproot the woody vegetation. The resulting masses of woody material are pushed into windrows and either burned or left to decompose. These windrows may pose an impediment to tortoise movement, and tortoises present on the area at the time of plowing are undoubtedly plowed over. Chaining and roller-chopping may actually encourage the growth of prickly pear cactus (*Opuntia lindheimeri*). Due to the preference *G. berlandieri* show for prickly pear cactus (Rose and Judd 1982), such alteration may ultimately be beneficial for tortoises. Investigation into the net effect of these range management techniques to habitat quality for *G. berlandieri* is sorely needed.

The use of gopher tortoises (*G. polyphemus*) and bolson tortoises (*G. flavomarginatus*) as food sources for humans has been well documented (Auffenberg and Franz 1982, Morafka 1982). Exploitation of *G. berlandieri* in this manner does not appear to be widespread in the United States. *G. berlandieri* is smaller than those species that have been shown to be heavily exploited for food, and this may make them less desirable for harvest. However, it is possible that exploitation of the Texas tortoise as a food source in Mexico is more severe and similar to that shown for *G. flavomarginatus* (Morafka 1982).

Another area for investigation is the relationship between exotic species and *G. berlandieri*. Landowners in Texas commonly increase their revenue by releasing exotic species and then allowing lease hunting on their property. Many of these released animals, such as Nilgai (*Boselaphus tragocamelus*), have become well established. In some areas, exotics are in high density and may warrant concerns similar to those caused by cattle. Feral hogs (*Sus scrofa*) have become established by both accidental and intentional introduction and are quite common in some parts of the range of *G. berlandieri*. Beshkov (1993) implicated hog predation as a major source of decline for 2 tortoise species (*Testudo graeca ibera* and *T. hermanni*) in Bulgaria. In the literature, there is no evidence to suggest that feral hogs prey upon Texas tortoises, but due to the high concentrations of feral hogs in good tortoise habitat in Texas, the predatory role of feral hogs should not be ignored. Since many exotic species are large ungulates, trampling of young tortoises may also be a cause of mortality.

STUDY AREA AND METHODS

In order to address conservation concerns for *G. berlandieri*, a study has been initiated on CWMA. The principal goal of the project is to address how grazing by cattle affects *G. berlandieri*, but information on many aspects of the ecology of this species is being collected. Managed by the Texas Parks and Wildlife Department, CWMA is 6,150 ha of typical southern Texas scrub habitat and is much further inland than other sites that have been used to study *G. berlandieri*. CWMA consists of a series of grazed and ungrazed pastures. Cattle are allowed on grazed pastures from 1 October to 30 May. Beginning in 1990, Texas Parks and Wildlife Department personnel began marking all Texas tortoises encountered on CWMA by notching marginal scutes, and as of 15 September 1994, over 1160 individuals have been marked on the site (J. C. Rutledge unpubl.).

Fieldwork for the cattle grazing study was initiated in April 1994 and will continue through November 1997. Data will be collected using radiotelemetry for 40 tortoises (20 on grazed sites, 20 on ungrazed sites) to compare tortoise ecology between grazed and ungrazed areas. A Geographical Information System (GIS) is being used to plot relocations. Plant communities have been characterized on a macro-scale for the GIS system by Texas Parks and Wildlife Department personnel. Time budget analysis will be used to compare foraging ecology of transmittered tortoises on grazed and ungrazed areas. Relocations will be conducted throughout daily and annual periods, but will be skewed towards the activity periods of the tortoises. Radiotelemetry information will also allow estimates of adult survival (Heisey and Fuller 1985). Fecal analysis is being employed to determine if tortoise diets differ between grazed and ungrazed areas.

Marking of all tortoises during fortuitous encounters will continue. For each capture, a variety of data are now being collected, including mass, sex (when possible), length (carapace and plastron), width, height, gular measurements (length, width, and spread), scute annuli counts, temperatures (air, substrate, and cloacal), and activity. Information from fortuitous encounters should greatly expand our knowledge of tortoise ecology in areas such as growth, sexual dimorphism, and frequency of annuli deposition.

RESULTS AND DISCUSSION

After 5 years of marking, the recapture rate for this population remains relatively low, being 32% for total captures in 1994 (J. C. Rutledge unpubl.). With the number of tortoises marked since 1990, this recapture rate suggests a large population on CWMA. In 1994, detailed measurements were collected from 270 tortoise captures representing 193 individuals. Between 23 June 1994 and 1 September 1994, over 300 relocations have been made on 22 tortoises with radiotransmitters.

The CWMA study is still in its infancy and conclusions cannot yet be made on grazing effects on *G. berlandieri*. Results from the 1994 field season indicate a high potential for characterizing the ecology and demography of this inland population. For the species, there is a need to determine the status of *G. berlandieri* in Mexico, to more accurately determine the stability of existing populations, to characterize the impacts of land management practices, and to determine the variability of life history parameters across the range of this species. The little available information suggests that, throughout most its range in the United States, *G. berlandieri* seems to be doing well and there is no immediate cause of concern for this species.

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PHYSIOLOGY, GENETICS, AND BEHAVIOR OF *Gopherus polyphemus*

P.A. Kwiatkowski and Kevin Connor
Department of Biology
University of South Florida
Tampa, FL 33620-5150

GROWTH

Gopherus polyphemus shows average annual increases for a Florida population of 11.2 mm in length, 6.1 mm in width, 4.5 mm in height, and 137.3 g in weight (Goin and Goff 1941). In Georgia most rapid development occurs in small individuals with a second growth surge occurring when individuals are approximately 100-120 mm carapace length (CL). Tortoises appear to grow intermittently with CL increases of 10-15 mm occurring every 2.5 yrs. Growth rates are much faster in the southern portions of the range of *G. polyphemus* because of warmer temperatures and a longer growing season. In Georgia, sexual maturity occurs later than in Florida (Iverson 1980, Landers *et al.* 1982). The attainment of a critical minimum body size (240 mm CL) rather than age as the determinant of sexual maturity has been proposed (Mushinsky *et al.* 1994). Substantial variation in the growth rates of localized populations of has also been documented (Godley 1989, Mushinsky *et al.* 1994).

In young tortoises 93% of total growth occurs from April-October (Landers *et al* 1982). Pronounced growth occurs through the age of 11 years, after which growth rates gradually decrease. An average of 18.9 mm/yr for ages 1 through 11 years, after which time growth slows, is reported (Mushinsky *et al.* 1994).

SEX DETERMINATION/SEXUAL DIMORPHISM

The plastron of adult males is known to be more concave than that of females (Goin and Goff 194, McRae *et al.* 1981) with this character being more dimorphic in Florida than Georgia tortoises (Mushinsky *et al.* 1994). Plastral concavity begins to show when males reach 220 mm CL. Males tend to have a plastron which is longer than the carapace whereas, females tend to have a plastron which is shorter than the carapace (Goin and Goff 1941). McRae *et al.* (1981) report that females have greater body widths, body thickness, and CL while males have thicker anal shields. Females have larger anal notches than males while males have greater anal widths. Also, males have greater body thicknesses than females (Mushinsky *et al.* 1994).

DIET PREFERENCES AND REQUIREMENTS

Grasses and grass-like plants dominate the gopher tortoise diet (Garner and Landers 1981). Twenty-six families of plants from 68 genera have been identified in scat analyses and foraging observations of tortoises (MacDonald 1986, MacDonald and Mushinsky 1988). The most common families of plants ingested are the Poaceae, Asteraceae, Fabaceae, Pinaceae, and

Fagaceae; the most common genus being *Aristida*. The gopher tortoise lies between a generalist and a specialist forager being opportunistic; exploiting high quality plant food sources that occur infrequently. Legumes, high in protein and phosphorus, become the diet of choice as grasses become more fibrous in the summer and fall (Garner and Landers 1981). Peak seasonal growth of juvenile occurs at the time of peak legume consumption and growth rates decrease in the fall as tortoises return to a diet of mature grasses (Landers *et al.* 1981).

COMMENSALS

About 60 vertebrate and 302 invertebrate species are known to occur in gopher tortoise burrows (Jackson and Milstrey 1989). In 1019 excavated burrows, Witz and Wilson (1991) report 99 vertebrate symbionts of 19 species. Mammalia were found significantly less than either Reptilia or Amphibia. The most diverse class found was Reptilia, followed by Mammalia, and Amphibia. Habitat type, burrow status, and season all have a significant effect on abundance of commensals (Lips 1991). Habitat type also has a significant effect on commensal diversity. The highest diversity of species was found in burned scrubby flatwoods. A higher abundance of commensals was found in active burrows than in inactive burrows. Additionally, the number of vertebrates found was higher in fall than winter or spring . Burrow size did not have an effect on commensal abundance.

ACTIVITY PATTERNS

Limited activity occurs in Georgia populations from late November through February (McRae *et al.* 1981). Activity increases linearly with temperature as spring progresses. A unimodal activity pattern occurs in Georgia (McRae *et al.* 1981) but changes to bimodal during July and August. In contrast, Douglass and Layne (1978) observed a unimodal pattern of activity throughout the year in their Florida population. Additionally, males are more active earlier during the day and later in the day than females. Ninety-five percent of all feeding activity occurs within 30 m of the burrow (McRae *et al.* 1981). Most individuals feed in circular or elliptical patterns around their burrow with feeding ranges overlapping considerably. Feeding ranges for spring are significantly smaller than for summer-autumn. Males in both Florida and Georgia populations have significantly larger home ranges than females (Auffenberg and Iverson 1979, McRae *et al.* 1981). Diemer (1992), however, found no difference in home range size between sexes for her Florida population and reports considerable individual variation. Extensive movements by large males only occur within the breeding colony (McRae *et al.* 1981). During the breeding season males select and maintain burrows near females. Burrow changes are common, peaking in August. Autumn movements are typified by migration to winter burrows with tortoises remaining in a single burrow.

Juveniles display movement patterns unlike adults. During the 1st year post-hatchling, juveniles remain within 15 m of the nest (McRae *et al.* 1981). Juveniles typically use more than one burrow, however, alternate burrows are rarely more than 10-15 m apart. Juvenile tortoises are most active in the spring (Wilson *et al.* 1993).

GENETICS

Very little genetic information for *G. polyphemus* is known. Information that does exist is mainly in regards to the evolutionary relationships among the mebers of the genus *Gopherus* (see Auffenberg 1976, Bramble 1982, Lamb *et al.* 1989). No studies are known that assess levels of genetic heterozygosity or inbreeding in *G. polyphemus*. No studies of parentage in *G. polyphemus* are known. Only one study of genetic variation within *G. polyphemus* is known (Ostentoski 1993). Three major assemblages across the species' range were identified from mtDNA analyses. The observed phylogeography is suggested to support the influence of regional sea level fluctuations having shaped the tortoise's phylogeography.

PHYSIOLOGY

In a study of body fluid distribution *G. polyphemus* was found to have a lower body water content than freshwater turtle species (Thorson 1964). Extracellular fluid volume (plasma and interstitial fluid) and whole blood volume were higher as well. Blood specific gravity of *G. polyphemus* was more similar to values for aquatic than terrestrial species.

The digestive efficiency of *G. polyphemus* is 68% for organic matter, 61% for energy, 73% for cell walls, and 71% for nitrogen (Bjorndal 1987). The high digestibility of cell walls indicates that celluloytic microflora is maintained in the digestive tract. Transit time is 13 days and body mass has no effect on either passage time or digestibility efficiencies. A pH of 8.0 for the feces of *G. polyphemus*, with acetate being the predominant volatile fatty acid (VFA) in the feces followed by propionate and butyrate is reported (Bjorndal 1987). The predominance of VFA in the feces is also an indicator of celluloytic microflora.

Hypoxia and hypercarbia occur in burrows in both sandy and clayey soils (Ultsch and Anderson 1988). Oxygen decrements and CO_2 increments are greatest in clayey soils and are significantly correlated with burrow length. Additionally, burrows are significantly shorter in clayey soils which they suggest may be due to respiratory limitations. Moderate hypoxia in conjunction with hypercarbia results in increased CO_2 elimination. Additionally, standard metabolic rates are maintained under hypoxia both under normocarbia and hypercarbia.

There is a direct linear relationship between body temperature and duration of exposure to direct sunlight in *G. polyphemus* (Douglass and Layne 1978). Frothing at the mouth, to facilitate evaporative cooling, occurs at $T_b = 38^{\circ}C$. The critical thermal maxima for *G. polyphemus* is $43.9^{\circ}C$; slightly higher than the CTMs for *G. agassizii* ($43.1^{\circ}C$) and *G. berlandieri* ($42.85^{\circ}C$) (Hutchinson 1966).

Water turnover in *G. polyphemus* is reported to be $3.2\ cm^3 \cdot (100\ g)^{-1} \cdot d^{-1}$ (Minnich and Ziegler 1976) which is much higher than that reported for *G. agassizii*. Even during periods of daily rain, *G. polyphemus* is not reported to drink, apparently obtaining water from succulent plants in their diet.

Olfactory neural activity includes two types of slow potentials. The electro-olfactogram was first confirmed in *G. polyphemus* by Shibuya and Shibuya (1963). The second type, DC shifts, are evokable by chemical and electrical stimulation. Mathews and Tucker (1966) report some specificity of neurons, however, Shibuya and Shibuya (1963) found no specificity of receptors. Olfactory nerve fibers are sensitive to chemical stimulation over a broader range of stimuli than are vomeronasal or trigeminal nerve twigs (Tucker 1963). Activity of mitral cells is greater than in epithelial cells (Mathews 1972).

CONCLUSIONS

The gopher tortoise, *G. polyphemus*, is one of four species of North American tortoise. Numbers of gopher tortoises are declining rapidly with loss of habitat throughout its range appearing to be a major attribute of this decline (Diemer 1986). Much more information on *G. polyphemus* needs to be obtained. Studies regarding growth in *G. polyphemus* are well represented and indicate that the geographic location of a population has important conservation implications. Studies of diet preferences have indicated that *G. polyphemus* lies between a specialist and generalist forager. Studies regarding actual nutritional requirements, however, are lacking. Effects of dietary deficiencies have also not been addressed. Activity patterns of both adult and juvenile *G. polyphemus* have been documented. Of importance to conservation efforts is again the geographic variability seen among populations. A few aspects of *G. polyphemus* physiology have been studied. Studies on sensory systems other than olfactory are lacking. No studies are known that address hormonal control mechanisms, or circulation. Additionally, metabolic regulation must be studied in greater detail. One of the most obvious gaps in our knowledge of *G. polyphemus* that exists is its genetics. Nothing is known of levels of inbreeding or heterozygosity within populations. At the present time, nothing is known of parentage (and therefore the reproductive success among males in populations). Determining the genetic relationships within populations is important because it will have important conservation implications (e.g., it will determine the effective population size). As we increase our knowledge in all areas of *G. polyphemus* biology we essentially increase the liklihood of maintaining the long-term viability of existing populations. Because of the great number of commensals associated with *G. polyphemus* burrows, this has great implications for many species other than *G. polyphemus* alone.

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ENDOCRINE PROFILES OF THE REPRODUCTIVE CYCLE OF MALE AND FEMALE DESERT TORTOISES

Valentine A. Lance, David C. Rostal, Janice S. Grumbles and Lisa Morici
Center for Reproduction of Endangered Species
Zoological Society of San Diego, P.O. Box 551
San Diego, California 92112, USA

INTRODUCTION

Hormonal data on the reproductive cycle of a number of chelonian species has been published (Lance 1984, Licht 1984), but very little information is available on tortoises. Plasma testosterone levels during the male reproductive cycle of the old world tortoise, *Testudo hermanni*, were reported by Kuchling *et al.* (1981), but there are no published data on the hormonal changes during the female tortoise reproductive cycle. We have recently published data on the reproductive cycle of male and female desert tortoises from the eastern Mojave area (Rostal *et al.* 1994), but only presented data on plasma testosterone. We now have collected data on plasma testosterone, estradiol-17B, progesterone, corticosterone and thyroxine for two complete reproductive cycles for male and female tortoises from the Desert Tortoise Conservation Center (DTCC) in Las Vegas and from free-ranging animals from the same part of the Mojave. In addition, we have measured plasma calcium as an index of vitellogenesis.

MATERIALS AND METHODS

Thirty adult female and twenty adult male tortoises maintained at the DTCC in ten separate pens each containing 2 males and 3 females were bled from the jugular vein once a month (as described in Rostal *et al.* 1994) from April to October in 1992 and from April to August in 1993.

Free-ranging adult tortoises from the Las Vegas area were also sampled at monthly intervals during 1992 and 1993, but a complete seasonal cycle from all of the individuals in the free-ranging group was not possible. Testosterone only was assayed in blood samples from sub-adult and juvenile tortoises to determine sex. Plasma progesterone, testosterone and corticosterone were measured in duplicate aliquots of plasma extracted with 10 vols of ethyl acetate: n-hexane 3:2 vol/vol and incubated overnight with highly specific antibodies from ICN diagnostics and tritiated steroids from Amersham-Searle (see Rostal *et al.* 1994, for details). Plasma estradiol was measured used a modified iodine-125 kit from Diagnostic Products Corp. The samples were extracted with ethyl acetate:hexane, but incubated with only 1/2 the volume of antibody as specified by the kit, and the bound from free steroid was separated using dextran-charcoal instead of the second antibody. These modifications increase the sensitivity of the assay to 1 pg/tube. Plasma thyroxine was measured using the solid phase G-25 column method (Eales and Shostak 1985). For details see Kohel (1994). When tissues from male animals sacrificed during the URTDS studies were available testicular and epidiymal histological section were made for determining the annual spermatogenic cycle

RESULTS

Male Cycle. It was possible to determine the spermatogenic cycle from the necropsy material, but only in outline. Spermatogenesis begins in late May and June and continues through to spermiation by late fall. On emergence in spring when intense mating activity is seen the epididymides are full of sperm and the seminiferous tubules are completely regressed. Testosterone showed a distinct seasonal cycle with a peak in April and second major peak in August and September. Plasma thyroxine showed a similar biphasic cycle in both 1992 and 1993 with a peak in April and a second peak in July and August (Fig. 1). The peaks in plasma testosterone and plasma thyroxine correlated with peaks in mating activity and male-male aggression. Plasma corticosterone was consistently higher in males than in females in all months of the year.

Female Cycle. Vitellogenesis and follicular growth occurs during late summer and fall and is reflected by increased plasma calcium and estradiol (Fig. 3). Peak levels of testosterone and thyroxine occur in April shortly after emergence. Using ultrasonography 90% of the females in the study were seen to have ovulated by April 30th. First nesting occurred in May. Mean clutch size was 4.68 ± 0.3, n = 19. A second small peak of testosterone occurs in the fall coincident with vitellogenesis and mating activity, but is not accompanied by an increase in thyroxine (Fig. 2). Plasma progesterone was low in all tortoises except around the period of ovulation in April and May (Fig. 4). Individual values as high as 30 ng/ml were found in animals at the point of or recently ovulated. Plasma corticosterone was elevated in May and low in July

DISCUSSION

The male reproductive cycle of the captive group of desert tortoises in Nevada is similar to what has been reported for other tortoise species. The spermatogenic cycle occurs during the summer months when mating activity is at a nadir and mating occurs in the spring when the testes are regressed (Moll 1979). There is evidence for fall mating in a turtle (Gist *et al.* 1990), and although the desert tortoise engages in intense mating activity in the fall, proof of insemination is lacking. We found a similar cycle in plasma testosterone in male captive and free-ranging populations for two consecutive years, a small peak on emergence in the spring and a second major peak in late summer and fall. Levels of testosterone in desert tortoises are at least ten-fold higher than has been reported in *Testudo hermanni* (Kuchling *et al.* 1981), but similar to those seen in the turtle, *Sternotherus odoratus* (MacPherson *et al.* 1982) with a peak of around 200 ng/ml in August. Individual values of as high as 550 ng/ml have been encountered. Plasma thyroxine in male tortoises showed a similar pattern to the testosterone and appeared to be correlated with peaks in feeding and mating activities. Chin gland volume showed a similar seasonal cycle to testosterone, both at a maximum in August when male-male combat was most intense (Alberts *et al.* 1994). Subadult male tortoises also showed a peak in plasma testosterone in August, but only 1/5th that of adult males, and male-male combat was not observed.

Plasma testosterone in the female desert tortoise showed a peak in April and a second small peak in the fall. Plasma thyroxine however, showed a very different pattern from that seen in the male. Levels in the females in April and May were higher than in the males, whereas in late summer and fall thyroxine showed a peak in the males but continued to decline in females. The difference in thyroxine levels could be due to the difference in activity patterns. Males exhibit intense combat activity in August coincident with very high testosterone levels, whereas females show a much lower activity pattern. It is still not clear if testosterone, estradiol and thyroxine secretion are linked. Peak estradiol levels in August are correlated with peak plasma calcium and vitellogenesis and occur when thyroxine is low. Elevated progesterone levels were associated with ovulation and were only seen during April and May. During the rest of the year progesterone levels remained low. As blood samples were collected only once a month it was not possible to examine the dynamics of progesterone secretion around the time of ovulation, and it is still not clear how many days elapse between ovulation and oviposition In the two years of the study only about 10 tortoises out of thirty showed plasma progesterone levels greater than 1 ng/ml during April and May. Only six of the 30 females in the study layed two clutches, 22 layed one clutch. First clutch tended to be larger than second clutch (5.07 vs 3.75).

Both male and female desert tortoises display distinct seasonal cycles in circulating hormone levels that correlate with seasonal cycles in mating and feeding activity cycles. While both sexes show similar patterns in circulating reproductive hormones, they differ in the seasonal variation in plasma thyroxine.

ACKNOWLEDGEMENTS

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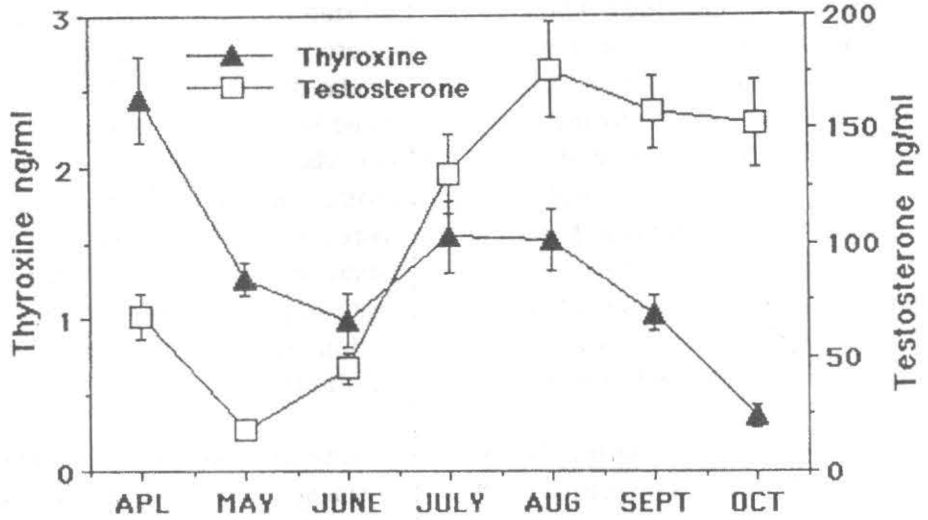

Figure 1. Seasonal changes in plasma testosterone and thyroxine in male desert tortoises

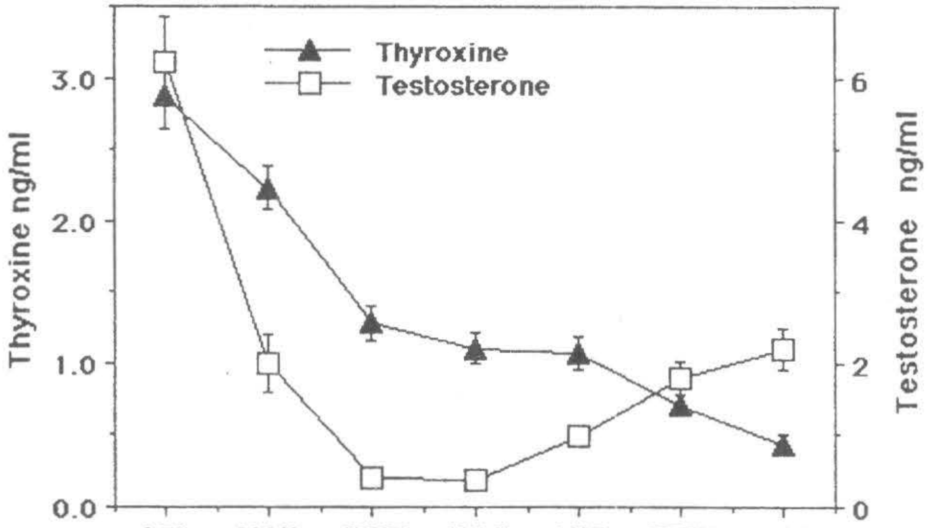

Figure 2. Seasonal changes in plasma testosterone and thyroxine in female desert tortoises

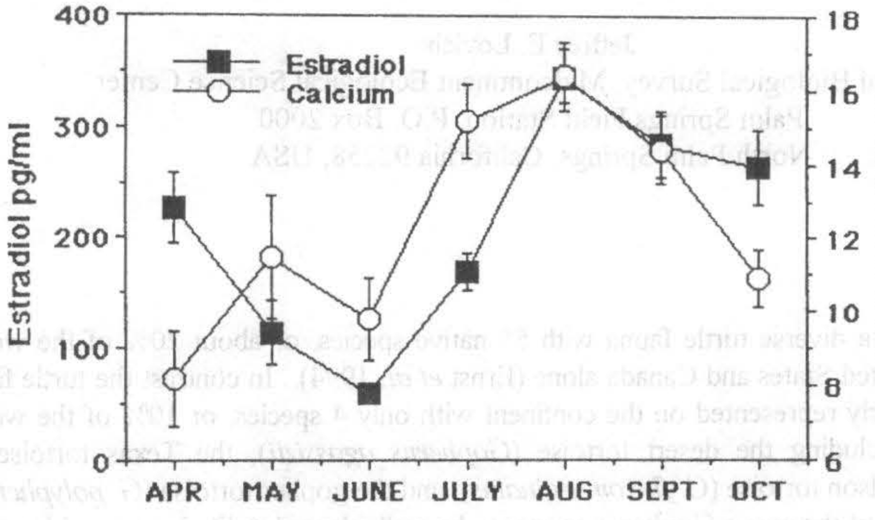

Figure 3. Plasma calcium and estradiol during the reproductive cycle of female desert tortoise.

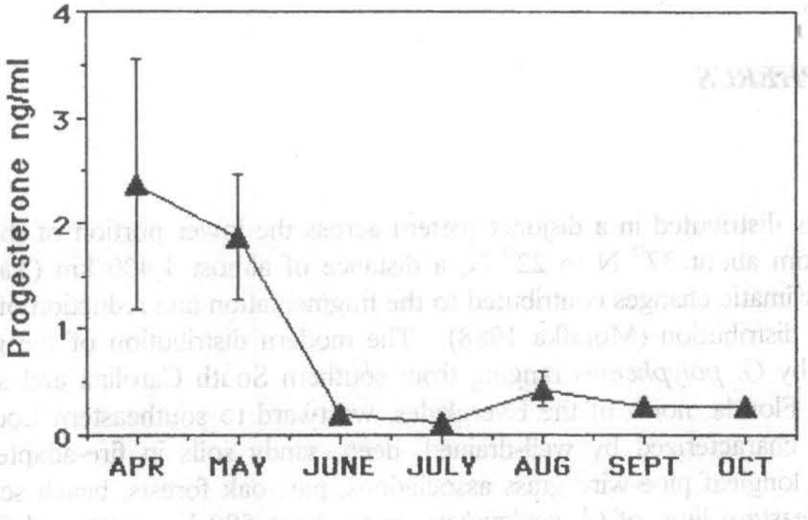

Figure 4. Mean monthly plasma progesterona in female desert tortoise.

ECOLOGY OF NORTH AMERICAN TORTOISES

Jeffrey E. Lovich
National Biological Survey, Midcontinent Ecological Science Center
Palm Springs Field Station, P.O. Box 2000
North Palm Springs, California 92258, USA

INTRODUCTION

North America has a diverse turtle fauna with 55 native species, or about 20% of the world's total, in just the United States and Canada alone (Ernst *et al.* 1994). In contrast the turtle family Testudinidae is poorly represented on the continent with only 4 species, or 10% of the world's tortoise species, including the desert tortoise (*Gopherus agassizii*), the Texas tortoise (*G. berlandieri*), the Bolson tortoise (*G. flavomarginatus*), and the gopher tortoise (*G. polyphemus*). Although members of the genus *Gopherus* appear to be well adapted to life in semi-arid and arid environments, the four species occupy a diversity of habitats ranging from deserts to pine forests and coastal areas. Box turtles (*Terrapene* sp.) are the only other North American terrestrial turtles that share some of the more xeric microhabitats occupied by the genus *Gopherus*. The fact that all four species are in need of some form of conservation action, in all or part of their range (Lovich 1994), underscores the importance of studying their ecological requirements. The purpose of this presentation is to provide a brief overview of the ecology of the genus *Gopherus* with an emphasis on comparing and contrasting the four species. Effective conservation programs can only be implemented with a clear understanding the ecological requirements and limitations of the genus.

ECOLOGY OF *GOPHERUS*

Ecogeography

The genus *Gopherus* is distributed in a disjunct pattern across the lower portion of the North American continent from about 37° N to 22° N, a distance of almost 1,400 km (Table 1). Human predation and climatic changes contributed to the fragmentation and reduction of a more continuous prehistoric distribution (Morafka 1988). The modern distribution of the genus is delineated in the east by *G. polyphemus* ranging from southern South Carolina and southern Georgia, to peninsular Florida, north of the Everglades, westward to southeastern Louisiana. Preferred habitats are characterized by well-drained, deep, sandy soils in fire-adapted plant communities including longleaf pine-wire grass associations, pine-oak forests, beach scrub and oak hammocks. The eastern limit of *G. berlandieri* starts about 580 km westward from the western edge of habitat occupied by *G. polyphemus*. *G. berlandieri* is found in southern Texas and the northern Mexican states of Coahuila, Nuevo Leon, Tamaulipas and San Luis Potosi. Habitats occupied include semidesert scrub and humid, subtropical, coastal areas, perhaps even barrier islands (Ernst *et al.* 1994). The ranges of *G. berlandieri* and *G. flavomarginatus* are separated by another hiatus of about 230 km. Although the distance from its eastern congener is short, *G. flavomarginatus* is completely isolated in remote enclosed basins in the Chihuahuan

Desert. The preferred habitat is the Tobosa grassland, characterized by the perennial grass *Hilaria mutica* (Bury *et al.* 1988).

Almost 600 km west of the basins occupied by *G. flavomarginatus*, the range of *G. agassizii* begins. The desert tortoise is widely distributed in Mojave and Sonoran desert scrub habitats in southern California, Arizona, southern Nevada and southwestern Utah. Throughout this vast area the desert tortoise inhabits desert alluvial fans, washes, canyon bottoms, and rocky hillsides in drylands having sandy or gravelly soil; it occurs to an altitude of at least 1,070 m. The range continues southward into the Mexican states of Sonora and northern Sinaloa, terminating in subtropical thornscrub habitat. In the United States, the particular habitat types utilized vary geographically, gradually changing to rocky slopes in the eastern part of the range. The spatial distribution of desert tortoises in relation to plant communities is not random. High diversity plant ecotones and communities, and possibly soil characteristics, are important features in determining tortoise densities (Ernst *et al.* 1994).

Behavior

Most members of the genus generally construct deep burrows for protection from heat, cold, and predators (Table 1). Burrows of *G. agassizii* can be up to 10 m long while those of *G. polyphemus* may reach 14.5 m. In contrast, *G. berlandieri* rarely constructs burrows but instead constructs a shallow "pallet" or scrape on the surface, normally near the base of a shrub or clump of grass. Surface activity of all species is governed largely by temperature and the availability of food (Ernst *et al.* 1994).

Aggressive interactions and territoriality are displayed by *G. agassizii* and *G. polyphemus*. Both species use head-bobbing as a visual display when confronted by another tortoise. The gular extension of the males is used to ram, hook and sometimes overturn another male. The fights rarely cause any physical harm, but if a tortoise is overturned and cannot right itself it will die. Although not known to be territorial, males of *G. berlandieri* will fight with each other during the breeding season (Weaver 1970). Combat involves biting and ramming. Resident *G. polyphemus* do not necessarily dominate when an intruder is introduced into experimental enclosures (Weaver 1970).

Feeding Ecology

All *Gopherus* are herbivorous, feeding mainly on forbs and grasses, often selectively. The most important foods for *G. agassizii* are desert annuals that often have life spans of less than 30 days and are generally available only from April to June. Since food quality decreases dramatically after June, tortoises must harvest enough energy during the brief feeding period to carry them through summer estivation, winter hibernation and the next reproductive cycle. Cacti and other food plants may be important in dry years. *G. berlandieri* prefers the stems, fruits and flowers of *Opuntia* cactus, but grasses and a variety of forbs are also eaten. Grasses and forbs constitute the majority of the diet in *G. flavomarginatus* (Aguirre *et al.* 1978) and *G. polyphemus* (Ernst *et al.* 1994).

Reproduction

Most species of *Gopherus* have relatively late maturation. *G. agassizii*, *G. polyphemus* (Ernst *et al.* 1994), and *G. flavomarginatus* (Legler and Webb 1961) typically take 10-20 years to reach sexual maturity while maturity in *G. berlandieri* (the smallest species) is reached in 3-5 years (Rose and Judd 1982). Typical clutch sizes and clutch frequencies are summarized in Table 1.

Demography

Like all turtles, the demographic structure of tortoise populations is a reflection of low and variable annual nest success, high adult survivorship, and long life spans (Lovich 1994). Due to the difficulty of locating juvenile *Gopherus* virtually nothing is known of this stage of their life history. Juveniles are poorly represented in all population samples. This could be due to their rarity, their cryptic nature or both. Sex ratios vary widely within and among species of *Gopherus* as does sexual size dimorphism (Table 1). The only life table for the genus is that of Turner *et al.* (1987) for *G. agassizii*.

The Functional Role of Tortoises in the Ecosystem

Tortoises of the genus *Gopherus* play important roles in the ecosystem. Some populations achieve high biomass and may be significant primary consumers. Their burrows provide homes for many commensals including invertebrates, mammals, reptiles and amphibians (Luckenbach 1982, Lago 1991, Witz and Wilson 1991). Activities including burrowing, mound building and grazing by *G. polyphemus* promotes environmental heterogeneity resulting in increased rates of microsuccession and higher plant diversity (Kaczor and Hartnett 1990). Some (perhaps all) species facilitate plant dispersal. The seeds of *Opuntia* that pass through the digestive tract of *G. berlandieri* have enhanced germination rates relative to those that do not (Rose and Judd 1982).

Table 1. Ecological and physical attributes of the genus *Gopherus*. Various references were consulted including Morafka (1982), Aguirre *et al.* (1984), Iverson (1982, 1991), Bury *et al.* (1988), Gibbons and Lovich (1990), Iverson *et al.* (1993), Ernst *et al.* (1994), and references cited therein.

	Species			
Attribute	*G. agassizii*	*G. berlandieri*	*G. flavomarginatus*	*G. polyphemus*
Ecotype	Mojave/Sonoran desert scrub - Sinaloan thorn scrub	Tamaulipian Biotic Province (desert to coastal)	Chihuahuan Desert	Longleaf pine/wire grass
Latitudinal distribution	37° N - 26° N (11°, ≈ 1300 km)	29° N - 22° N (7°, ≈ 770 km)	28° N - 26° N (2°, ≈ 230 km)	33.5° N - 27° N (6.5°, ≈ 800 km)
Longitudinal distribution	118° W - 108° W (10°, ≈ 900 km)	101° W - 96° W (5°, ≈ 470 km)	104.5° W - 103° W (1.5°, ≈ 170 km)	90° W - 80° W (10°, ≈ 950 km)
Max. body size	to 37 cm	to 22.8 cm	40 cm + ?	to 40 cm
Sexual size dimorphism	males larger	males larger	females larger	females ≥
Sex ratio	female biased	male biased	female biased	variable
Biomass/density	0.19-2.05 kg/ha	54.5 kg/ha	10 tortoises/km^2	220 kg/ha
Annualized adult survivorship	0.883	?	?	0.89
Clutch size	4.5	2.6	6	5.2
Clutch frequency	3	1	3	1
Egg mass	38.9 g	26.9	?	40.9
Clutch mass	175.2 g	69.94	?	212.7
Burrower	yes	no	yes	yes
Territorial behavior	yes	no	no	yes

FIELD TECHNIQUES FOR STUDYING NORTH AMERICAN TORTOISES

Earl D. McCoy
Department of Biology and Center for Urban Ecology
University of South Florida
Tampa, Florida 33620, USA

Germano and Bury (1994) provided a critique of research on North American tortoises, with suggestions for the future. Their work uncovered at least two important themes: (1) no topic about North American tortoises has been covered adequately and (2) comparative studies -- among species, within species among areas, and within species among habitats -- should be significant components of future research. Building on these two themes, I shall circumscribe "field techniques," to make the discussion manageable; develop the idea of "scale of investigation"; outline field techniques that have been employed at different scales and some that may be employed in the future; discuss some important areas for future investigation; and show how some of these areas are "technique rich" and some are "technique poor."

Typical sudies of North American tortoises include (from Adest *et al.* 1989a): tortoise density and distribution, burrow density and distribution, population size, individual ages, burrow use status, ethogram and time budget, home range and foraging pattern, diet and energetics, reproductive behavior and success, natality, mortality, survivorship, population growth. For reasons of manageability, I shall need to exclude certain important and interesting topics from discussion. I trust that these topics will be covered, at least basically, in other presentations. First, I note that most studies can be divided into three more-or-less distinct phases, planning, execution, and analysis. The overlap between execution and analysis seems to be greater than that between planning and execution. I shall concentrate here on the execution phase. I shall exclude from discussion: population viability analysis, survivorship analysis, morphometric analysis, ethograms/time budgets, and most other analyses. I shall include certain analyses, however, that are relatively new or have a particularly strong field component: genetic markers, correction factors, home range, diet choice, and habitat correlations. I shall also exclude from discussion: physiological measurements, health assessments, captive breeding and reintroduction, relocation, burrow commensals, and environemntal measurements. I expect most of this last group of topics to be covered in depth in other presentations.

In recent years, ecologists and others have realized the importance of recognizing the scale at which research is conducted. For my purpose here, recognizing scale in research on North American tortoises allows me to organize field techniques into meaningful groups. I shall call the groups, large-scale, medium-scale, and small-scale. The large-scale group includes techniques aimed at finding tortoises in the landscape. The medium-scale group includes techniques aimed at finding tortoises in the habitat. The small-scale group includes techniques aimed at determining what a population or colony or sample of tortoises is doing.

Large-scale techniques map the current and past distributions of tortoises, and account for range restrictions. Current distributions have been mapped in the field by air and ground searches for tortoises themselves or for their signs. Non-field techniques -- for completeness -- include questionnaires, literature, maps, and satellite imagery. Past distributions have been mapped from previous studies and range restriction patterns have been inferred from studies of morphology and genetics (mt DNA). These studies obviously encompass largely non-field techniques. Principal future research needs at the large scale include (Germano and Bury 1994): (1) basic distributional studies, (2) studies of species' variability over their ranges, (3) monitoring of range changes, (4) long-term studies of temporal variability.

Medium-scale techniques are employed for counting tortoises or their signs, inferring numbers of tortoises from numbers of signs, capturing tortoises, measuring their dispersion, and relating numbers and positions of tortoises to habitat variables. Counts have employed transect sampling and complete enumeration. Inferring numbers of tortoises from signs mostly has involved relating tortoises to burrows in some way. Techniques that have been employed are tabulating burrow activity status, including recording of direction of footprints; twigs; physical contact by sewer snake, hose and PVC pipe; listening by physical and electronic amplification; observation with camera. Capturing of tortoises has been by hand when they are away from burrows, including blocking burrow entrances; buckets; handbobbing; tapping; pulling; and burrow excavation. Dispersion has been measured by the point-center and nearest-neighbor techniques, but geostatistics and fractals may be used in the future. Correlations of tortoises with habitat variables has been accomplished with multivariate analysis, by construction of habitat suitability indices (HSI), and by use of null models. Two researchers (Germano and Bury 1994) see principal future research needs at the medium scale as: (1) quantification of habitat use (especially employing random transects), (2) definition of habitat requirements (with special attention to soil types and cover sites), and (3) determination of what constitutes "quality" habitat. Two other researchers (Burke and Cox 1988) see principal future research needs at this scale as: (1) quantification of habitat use and (2) improving ways of determining tortoise density.

Small-scale techniques are numerous, and necessitate my dividing them into three subgroups for manageability. The first subgroup includes techniques for sampling, for marking, and for determining size, sex, age, and burrow characteristics. Sampling techniques that have been employed are enclosures, exclosures, and study plots, while markings techniques that have been employed are drilling, cutting and filing, and painting. The use of PIT tags for marking may be of some use in future studies. Taking measurements of tortoise length and weight and of burrow diameter, placement, and orientation are relatively straight-forward processes. Sex of an individual tortoise has been determined by a variety of field and non-field techniques. Field techniques are behavioral observation, and inferences from size and shell features. Non-field techniques are radiography, laparoscopy, and determination of plasma testosterone levels. Age of an individual likewise has been determined by a variety of field and non-field techniques. Field techniques are mark-recapture studies, counting scute annuli, and noting shell wear. Non-field techniques are inferences from growth curves and captive records, and bone and scute sectioning.

The second subgroup of small-scale techniques includes those used to measure demography: reproduction, reproductive output, mortality, and immigration and emigration. Reproduction has been studied by behavioral observation, measuring subdentary glands; sonograms, palpation, and weight loss in females; and cloacal flushing for sperm in males. Away from the field, reproduction has been studied by radiography, and plasma testosterone and calcium levels. Reproductive output has been studied with egg probes and colored gravel layers at potential nest sites in the field, and by radiography and egg nutrient analysis away from the field. Sonograms may prove useful in counting clutch sizes in future studies. Mortality has been studied by observation, by searches for carcasses and shells, with radio transmitters, and with camera traps at nests. Future studies may make use of egg baits at nests. Immigration and emigration have been studied using mark-recapture information and radio transmitters. Such studies usually are simply extensions of general movement studies, however, and not designed specifically to monitor population interchange. Use of special trapping systems (drift fences) and genetic anlysis may prove useful in future studies. Studies of immigration and emigration are a principal future research need at the small scale, in my opinion. Other researchers see future research needs in other areas of demography. Germano and Bury (1994), for example, see principal needs of: (1) a standardized measure of fecundity, (2) a standardized measure of longevity, (3) a standardized measure of survivorship, and (4) documentation of the relationship between life-history traits and plant reproduction and nutritional value. Spillers and Speake (1988) see need for determination of an optimum age-class structure, while Burke and Cox (1988) see need for more information on early life-histories.

The third subgroup of small-scale techniques includes those used to monitor movement, orientation, and diet. Movement has been studied in the field by direct observation, and through the use of string trailers, radio transmitters, metal detectors (with implants), and micro-switches at burrow entrances. Field data have been used to calculate home ranges using four methods: probability-density function, mean distance between successive captures, maximum distance between capture points, and minimum convex polygon (both uncorrected and corrected for sample size). The few orientation studies on North American tortoises used direct observation and string trailers to gather data. Based on their data, many researchers then used some type of manipulation to attempt to explain patterns in orientation. These manipulations have included habitat alteration to examine the role of well-worn paths as cues and blocking of nares to examine the role of olfaction. Studies of diet have employed mostly direct observation in the field. Away from the field, researchers have also used analyses of scat contents and food nutrients and energy content. Information gathered in the field has been used to calculate diet choice with indices and null models.

Returning now to principal future research needs, I shall illustrate how some areas are technique-rich and others are technique-poor. Recall that two potential areas for future research at the small-scale are developing a standardized measure of fecundity and developing a standardized measure of survivorship. For the first area -- measuring fecundity , Germano and Bury (1994) propose the following five-step model. (1) Equip about 30 mature female tortoises with radio transmitters. (2) Relocate the female tortoises about every ten days during the reproductive season. (3) Use radiography or sonograms to reveal presence of eggs, until no more eggs are observed. (4) Capture smaller female tortoises during the reproductive season to determine the size (age) at which they can produce eggs. (4) Observe and/or capture male tortoises during the breeding season to determine the size (age) at which they are sexually mature. This model, in my opinion, is technique-rich, because all of the techniques necessary for its implementation are readily available. Therefore, developing a standardized measure of fecundity is currently possible, both in principle and in practice. For the second area -- measuring survivorship, Germano and Bury (1994) propose the following four-step model. (1) Use estimated ages of tortoises to yield a "snapshot" picture of survivorship. (2) Locate hatchlings and juveniles. (3) Follow hatchlings and juveniles with radio transmitters. (4) Attach biological meaning to age/size distributions. This model, in my opinion, is technique-poor, and for at least three reasons. First, static analysis of life tables requires assumptions that many tortoise populations are not likely to meet. Second, locating hatchlings and juveniles is a difficult undertaking, and requires better methods than now are employed. Perhaps dogs might be employed with success in this area. Third, the relationship between age and size in tortoises is not well enough understood to translate measurements of size into meaningful survivorship curves. Therefore, developing a standardized measure of survivorship does not appear to be currently possible, in practice. This area -- and others as well -- will require substantial attention to developing techniques if future progress is to be made.

WHAT DOES EVOLUTIONARY ECOLOGY AND PHYLOGENETICS REVEAL ABOUT CONTEMPORARY GOPHER TORTOISES (TESTUDINIDAE: *Gopherus*), THEIR MORPHOLOGY, LIFE HISTORY STRATEGIES, AND ECOLOGICAL NICHES?

David J. Morafka
Department of Biology
California State University, Dominguez Hills
Carson, California, 90747, USA

No genus of extant reptiles has a more complete fossil record than the North American gopher tortoises, genus *Gopherus*. This robust record consists of an array of exceptionally complete fossils representing more than a dozen taxa. Furthermore, this paleontological history includes burrows in their original matrices, revealing the nature of past microhabitats. Several parsimonious phylogenies (and/or cladistic networks) drawn independently from osteology of both fossil and living forms (Crumly 1984, 1994), allozyme (Morafka *et al.* 1995), and mitochondrial DNA restriction fragment data (Lamb *et al.* 1989) are now available. No interpretations of gopher tortoise morphology, life history, habitat associations, or even their general distribution have been made in light of the new paeloecological and phylogenetic evidence since Auffenberg (1974) and Bramble (1982). This review will attempt to remedy this situation in all four contexts.

A brief review of the early history of tortoises demonstrates that many characters which are commonly considered as species specific adaptations, were, more probably, fixed as unique traits (synapomorphies) in Asian batagurine turtles, or their descendants, the manourine tortoises. Long before the gopher tortoises (genera *Stylemys* and *Gopherus*) large hard shell eggs were produced by their Oriental progenitors among the herbivorous and amphibious or mesic terrestrial batigurines. Chin glands, found only in the extant tortoise genera *Manouria* and *Gopherus*, are most certainly, synpleisomorphies retained from these same ancestors. Gaffney and Meylan (1988) and Crumly (1984, 1994) have established that *Gopherus* is derived from an Asian tortoise stock , the manourines, which already had manifest general flattened shell morphology, some aspects of skull and appendicular osteology, and possibly such behaviors as burrow excavation, vocalization, and defense of egg nests.

A number of gopher tortoise attributes, now associated with arid North American grassland and scrub microhabitats, are more accurately considered as exaptations originally evolved in mesic tropical Southeast Asia. In this context, burrows, for example, are more probably evolved originally as a defense against large predators, than as a refuge from climatic extremes. So also, large eggs and neonates, produced from small clutches, are more probably an adaptive accommodation to the biomechanical demands of terrestrial herbivory, rather than as resistance to dehydration through the more favorable surface to volume ratios generated by the production of larger young (Morafka 1994).

The differentiation of the *Stylemys-Gopherus* lineage from Old World manourine tortoises took place in North America, minimally back to the Oligocene Period, but quite possible occurred earlier in the Cenozoic. Given the equal antiquity and Laurasian distribution of the genus *Geochelone* and its tribal allies, comparisons seeking sister lineages with *Gopherus* should utilize *Manouria*, not the phylogenetically more remote, but physically more proximate tortoises of Western Hemisphere.

Gopher tortoises seem to be clearly adapted, or at least exapted, for sandy grassland microhabitats. However, the presence of this lineage in fundamentally modern and fossorial morph by Oligocene times indicates that its evolution may have actually preceded the development of widespread, arid temperate prairies in North America. Retallack (1983) has suggested that Oligocene grassland mammals may have evolved many of their adaptations before such habitats had developed into dominate features of the landscape. Rather these adaptations were responsive to selection in localized, perhaps edaphic patches of sandy well drained soils (and ,or, rain shadow locations) prior to regional shifts toward more arid climates (Morafka *et al.* 1992). The disclimax patches of grassland, which open and close in response to fire in sandy pine/hickory/oak forests of *Gopherus polyphemus* habitat in the Southeast U.S. may be good models for the early evolution of this lineage.

The four extant gopher tortoises may share a common history in which selective pressures are generated more often by the edaphic habitats and microclimates they encounter on the well defined home trails and in the burrows in which they spend more than 90% of their lives. These ambient conditions may contribute the conservatism of the genus, even when individual taxa vary in their affinities across the entire spectrum of lowland ecosystems found across southern temperate North America.

Microhabitats and edaphic conditions, may also have contributed significantly the later Tertiary differentiation of the *G. polyphemus-flavomarginatus* clade with their specialized fossorial synapsomorphies. Crumly (1984, 1994) has established that *G. agassizii* and *G. berlandieri* (along with the several fossil "*Scaptochelys/Xerobates*" of Bramble 1982) do not constitute a sister group, but are simply an assemblage of less specialized tortoises, bound together only by unresolving synpleisomorphies. Allozyme based genetic distances (Morafka *et al.* 1995) indicate that the divergence of the more fossorial clade was much more recent the suggested the early-mid Miocene suggested by Bramble (1982). Coarse molecular clock dating calibrated against genetic distance suggests a divergence of perhaps five millions years. This later estimate is more compatible with Auffenberg's (1974) reports of the first tortoises resembling "*polyphemus*" from the Late Pliocene of Texas. Revised mtDNA clock estimates by Lamb (pers. comm.) lie somewhere in between , about 10 MYBP.

Estimations of early divergence often rely on vicariance scenarios to explain the differentiation of these two "groups" of tortoise species. Usually either a Miocene orogeny in the Cordilleran (Rocky Mountains) Province, or a northern intrusion of the Gulf of Mexico embayment has been invoke to separate "*Xerobates*" to the west and "true *Gopherus*" (in the sense of Bramble 1982) to the east. Neither molecular clocks nor the available fossil record support such a scenario. It seems more probably that now obscure local events sequestered tortoises into different microhabitats, hilly scrub lands with variable soils for the less specialized "*Xerobates*" and lowland sandy grassland pockets for "*Gopherus*." Morafka (1988, p.49) suggested a possible complementarity between "upland' and lowland tortoise, without directly indicating whether such resource partitioning in sympatry might have been primary or secondary: the upland distribution of *Gopherus agassizii* in the eastern Sonoran Desert today may have been reinforced by past coexistence with *Gopherus flavomarginatus*, which seems better adapted to valley floors and margins than does *G. agassizii*. In contrast, historically allopatric *G. agassizii* populations in the Mojave Desert, while topgraphically widespread, have no particular affinity to upland habitats." Van DeVender *et al.* (1976) reconstructed an even more complex assemblage of terrestrial chelonian sympatry in New Mexico where *Terrapene*, *G. agassizii*, *G. flavomarginatus*, and a small *Geochelone* may have occurred together in the late Pleistocene.

Allopatric speciation and vicariance are more credible in the end Pliocene differentiation of Mojave from Sonoran *G. agassizii*, as a result of the northward extension of the Gulf of California to the Mogollon Rim, as suggested by Lamb *et al.* (1989). Both Lamb's mt DNA distances and allozyme studies by Morafka *et al.* (1995) suggest that this divergence predates the speciation of *G. berlanderi* from Sonoran *G. agassizii* by several million years. If behavioral and morphological data were subordinated to molecular evidence, *G. berlandieri* would be considered no more than a dwarf of Sonoran *G. agassizii*, a race lacking in fixed allelic differences, without significant differences in gene frequencies (undistinguished even by standard F statistics for inbreeding when compared to Sonoran tortoises).

Current taxonomy then presents a paraphyletic definition of *G. agassizii*, in which one more closely related taxon, *G. berlandieri* is excluded, while the more distantly related Mojave, Sonoran, and Sinaloan metapopulations are clustered together. Given the latitude of definition provided by the evolutionary species concept, the current *G. agassizii* probably should be divided into four species. A recent morphological comparison of juvenile Sonoran and Mojave *G.agassizii* confirms that they differ from each other by more characters than does *G. carbonaria* from *G. denticulata* (M. Joyner, pers. comm.). In fact some of the same character states are involved in both pairwise comparisons (i.e., smooth versus dentate posterior marginal scutes).

Consideration of the evolutionary ecology of Pleistocene tortoise habitats indicates that for as much as 94% of the past two million years, gopher tortoises have been evolving in more mesic environments, especially those taxa occurs to the west of central Texas (Van DeVender and Burgess 1985). For the two more eastern extant taxa, the increasingly chaotic Holocene fluctuations toward greater aridity and temperature extremes may have had only modest ecology impact. Perhaps distributional limits were dipalced southward and eastward. However, in the more arid Southwest, not only were limits displaced, but tortoises were often placed at limits of their physiological tolerance polygons. Burrow occupation, stored water and lipid reserves, and low metabolic rates of adults considerably buffered the impacts of newly fluctuating and extreme climates. However, it should not be surprising that western tortoises, already marginal in their ecological settings of the past 10,000 years, are differentially more vulnerable to post- Columbian anthropogenic changes in forage, subsidized predation (ravens), and the stress of epidemic diseases.

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ECOLOGY OF THE GOPHER TORTOISE

Henry R. Mushinsky and Earl D. McCoy
Department of Biology and Center for Urban Ecology
University of South Florida
Tampa, Florida 33620, USA

The gopher tortoise, (*Gopherus polyphemus* (Daudin)), is one of four tortoise species in North America, and the only species found east of the Mississippi River. The range of the gopher tortoise extends from eastern Louisiana to southern South Carolina. Within its geographic range, the gopher tortoise is found almost exclusively on deep, sandy soils suitable for construction of extensive burrows (Hansen 1963). Its dependence on sandy substrates places the gopher tortoise in direct conflict with humans who modify upland habitats for mining, agriculture, or other uses. Fragmentation and loss of lands with suitable substrate are likely the most important factors contributing to the decline of gopher tortoises (Auffenberg and Franz 1982, Diemer 1986).

Gopher tortoises are restricted to habitats that permit them to excavate their burrows which average about 5m in length and extend to a depth of 2m (Hansen 1963). Although they reside in several types of upland habitats (i.e. pine flatwoods, scrub and sandhill), sandhills support the greatest densities of gopher tortoises. Sandhill habitat occurs on well-drained deep yellow sands (Myers 1990). Sandhill habitat is characterized by a lush ground cover of grasses (*Aristida* spp.) and herbs (especially Asteraceae and Poaceae), partially covered by a shrub layer of saw palmetto (*Serona repens*), under a patchy canopy of longleaf pine (*Pinus palustris*), turkey oak (*Quercus laevis*), and sand live oak (*Q. geminata*). Sandhill is a pyrogenic habitat (Abrahamson 1984); hence, the time interval between fires strongly influences canopy cover and the herbaceous and grassy ground cover (used as forage by gopher tortoises). Campbell and Christman (1982) suggested that gopher tortoises are attracted to the "openness" of the habitat and McCoy and Mushinsky (1992) reported that tortoises abandon habitats that become overgrown. On average, sandhill burns naturally about once a decade (Myers 1990). In the absence of fire for several decades, the patchy tree canopy is replaced by a dense canopy of other plant associations (Veno 1976, Myers 1990).

The life history of the gopher tortoise conforms to the following pattern. Males court and mate with females in the spring and fall of the year. Females deposit their eggs during May and June, often in the sandy spoil mounds immediately outside their burrows. Following an incubation period of about 95-105 days, eggs hatch from mid-August through September (Landers *et al.* 1980). Males achieve sexual maturity one to four years before females which begin to reproduce when their carapace lengths are about 240 mm at an age of 9 to 18 years (Auffenberg and Iverson 1979, Alford 1980, Mushinsky *et al.* 1994). Each female may produce a single clutch of eggs per year with a mean of five (Iverson 1980) to eight (Linley and Mushinsky 1994) eggs. Gopher tortoises grow less rapidly after sexual maturity than before (Mushinsky *et al.* 1994) and may live to an age of more than 60 years (Landers *et al.* 1982).

Considerable geographical variation exists in the number of years required for gopher tortoises to attain sexual maturity. In southern Georgia, females attain sexual maturity at 250-265 mm CL and an age of 19-21 yr, and males attain sexual maturity at 230-240 mm CL and an age of 16-18 yr (Landers *et al.*, 1982). In northern Florida, females attain sexual maturity at about 230 mm CL and an estimated age of 12-15 yr (Iverson 1980, and included references). In a central Florida, females grow to 240-250 mm CL in 9-11 yr and some can reproduce at an age of 9 yr (Mushinsky *et al.* 1994). Thus, size, rather than age, appears to be closely related to the attainment of sexual maturity in *Gopherus polyphemus*: females begin reproducing at about 240 mm CL across much of the species' range.

The level of predation on gopher tortoise eggs and young individuals is high. For example, over a two year period in South Carolina, 17 of 24 (74%) nests were destroyed (Wright 1982). In Georgia, an average female produces a successful clutch of eggs (eggs are not destroyed prior to hatching) once a decade (Landers *et al.*, 1980), because about 90% of their nests are destroyed annually. Hatchling gopher tortoises (individuals in their first year of life) also are subjected to high levels of predation. From egg laying to one year of age, gopher tortoises in northern Florida were estimated to have a mortality rate of 94.2% (Alford 1980). Results from another study in central Florida, which also combined mortality of eggs and hatchlings, suggested an annual mortality rate of 92.3% (Witz *et al.* 1992). Estimated rates of survivorship of juvenile gopher tortoises (age 1 to 4 years) have been reported from one location in central Florida. Predation of juvenile tortoises was higher in October-November and April-May than any other two month interval of the year (Wilson 1991). Juvenile tortoise are known to bask at the mouths of their burrows more often in the spring and fall of the year than during the summer or winter months (Wilson *et al.* 1994). It appears that a juvenile tortoise, when positioned at the mouth of the burrow to thermoregulate during the cool months of the year may be quite vulnerable to predation by avian and mammalian predators (Wilson 1991).

Few, if any, gopher tortoise populations have not been influenced directly or indirectly by human activities. Human predation on gopher tortoises is well documented (Taylor 1982), but likely has declined over the past decade. At present, the most apparent threat to the survival of individual or entire populations of gopher tortoises is the alteration of the upland habitats where gopher tortoises reside. For example, in Florida Auffenberg and Franz (1982) calculated that an 80% reduction in the number of tortoises had occurred over the last 100 years, largely as the result of suitable habitat reduction. They estimated that 70% of the remaining tortoise habitat would be lost by the year 2000, and that virtually all would be lost by the year 2025.

During the past decade, surveys of more than 50 tortoise populations (including 10 island populations) in Florida were conducted to collect data to: (1) construct a demographic profile, (2) assess the extent of the area occupied, (3) evaluate the vegetation structure, and (4) determine the extent of habitat reduction, if any, for each population (Mushinsky *et al.* 1995). The areal extent of gopher tortoise habitat for each population was determined by the occurrence of tortoises, not by our subjective evaluation of habitat suitability. We visually estimated the density of plant cover at three levels: (1) from the ground to 1m above ground, (2) between 1 and 3m above ground (low canopy), and (3) above 3m (high canopy). To quantify area reduction, we obtained a temporal series of aerial photographs of each site. We used the photographs only to construct broad, arbitrary categories of area reduction. For example, an area reduction of less than 25% was considered moderate, while area reduction of greater than 25% was considered severe. Each population was surveyed by three researchers walking side by side on 10m wide transects. We located and measured all burrows on a transect and classified each as active, inactive, or abandoned (McCoy and Mushinsky 1992, Mushinsky and Esman 1994). We measured burrow widths to the nearest 0.5cm with a pair of meter sticks fastened together at the 50cm mark to form a connected pair of calipers.

Gopher tortoise populations residing on sites that had experienced severe area reduction, or occurred on sites with greater than 50% tree canopy, or occurred on sites of small size (< 2ha) tended to have truncated demographic profiles. A truncated profile suggests little recruitment of individuals into the population and abandonment of the site by mature individuals. In contrast, tortoise populations on sites with no or limited area reduction, or sites with less than 50% tree canopy, or relatively large sites (> 2ha) tended to have a high proportion of mature individuals and evidence of recruitment of young into the population (McCoy and Mushinsky 1988). We cannot address the potential influence of past harvesting of large adult tortoises (for human consumption); however, the collection of tortoises in Florida was banned in 1988.

Comparisons of tortoise populations on true islands with populations on the mainland suggests that tortoises do respond to relatively small, isolated habitats. Both island and mainland tortoise populations show a positive relationship between the number of active and inactive burrows and the area of habitat. Density of burrows, however, decreased as area increased on the mainland, but density of burrows was not related to area on the islands. Also, the ratio of inactive to active burrows (a measure of the tendency of individuals to construct new burrows) increased with area of habitat, and burrow density increased with increasing herbaceous vegetation, on the mainland sites, but neither of these relations could be demonstrated on island sites. Collectively, these findings suggest that tortoises have a greater selection of habitats on the mainland than on islands.

Tortoises on islands are confined and forced to live in less than ideal conditions. The implications of these findings are profound for tortoises living in small, fragmented "habitat islands" on the mainland which also may be confronted with less than ideal conditions. In time, perhaps a few decades, as the quality of their habitat island is degraded, mature adults may be forced to abandon a site in search of better habitat quality. Such individuals, which may be forced to abandon isolated patches of habitat in areas surrounded by human dwellings seem doomed to perish. From a practical perspective, prior to our study (McCoy and Mushinsky 1988, Mushinsky and McCoy 1994), observing large numbers of active and inactive gopher tortoise burrows in a confined area likely would have been viewed as indicators of a "healthy" population, however, our findings suggest just the opposite. Rather than a signal of a healthy population, large numbers of active and inactive gopher tortoise burrows, relative to the actual number of tortoises, may signal a stressed population.

Gopher tortoises function as "keystone species" (Campbell and Christman 1982, Jackson and Milstrey 1989, Witz and Wilson 1991), and because of their role in maintaining biodiversity, even in small patches of habitat, they merit special consideration in ranking conservation priorities (see Soule and Simberloff 1985, Soule 1987). As a keystone species, the gopher tortoise may facilitate the continued existence of other species on patches of habitat that may be too small for the long-term persistence of tortoise itself, but are suitably sized for these other species.

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PHYSIOLOGICAL ECOLOGY OF THE DESERT TORTOISE (*Gopherus agassizii*) CONSTRAINTS ON LIFESTYLE AND KEEPING UP WITH THE JONESES

Michael P. O'Connor and James R. Spotila
Department of Bioscience and Biotechnology
Drexel University
Philadelphia, Pennsylvania 19104, USA

The desert tortoise, *Gopherus agassizii*, is a turtle that, by virtue of living in a desert, faces an unusual set of physiological, behavioral, and ultimately ecological challenges. Its basic physiology is turtle-like. Water, temperature and energy availability constrain the ecology of the desert tortoise throughout its range.

Temperature affects both the seasonal and diel activity times of desert tortoises. In California and Nevada the activity season extends from March through October. Near Las Vegas, some tortoises are active for most of the daylight hours in early April and October. From late April until late September tortoises adopt a bimodal activity pattern which is most restricted during the hottest part of the summer in July and August (Ruby *et al.* 1994). This behavior pattern is consistent with daily and seasonal patterns in solar radiation and air and ground temperatures (Zimmerman *et al.* 1994). Operative environmental temperature (T_e) is a good predictor of tortoise activity, especially when the thermal lag in body temperature (T_b) is considered. Thermal physiology of desert tortoises has been little investigated. The CTM's range from 38.6 to 45.1°C and appear to decrease somewhat in older, larger animals (Naegle 1976). Preferred temperatures, measured in the same study, are more difficult to interpret but ranged between 29 and 33°C. Hence, during most of the activity season of tortoises near Las Vegas, T_e on the surface is lethal for tortoises during midday and well beyond the preferred range for nearly all of the day (Zimmerman *et al.* 1994). Tortoises avoid these conditions for much of the day by retreating to their burrows. During surface activity, T_b is more variable than has been observed in other large reptiles. Desert tortoises do not exhibit the thermoregulatory shuttling characteristic of desert lizards (Cowles and Bogert 1944). However, they do thermoregulate by postural adjustments, limiting daily activity, seasonal shifts in activity and by microclimate selection (McGinnis and Voigt 1971). Adult tortoises rely on inertially damped heating and cooling rates and the thermal buffering capacity of the shell (inertial homeothermy) as part of their thermoregulatory strategy (Zimmerman *et al.* 1994). In addition, tortoises typically use burrows as heat sinks and sources and may use nighttime temperatures to affect their thermal regime during morning activity periods during the hot summer months (Zimmerman *et al.* 1994). Minimizing energy expenditures and water loss through reduced activity and by selecting cooler microhabitats may be essential for desert tortoises to maintain energy and water balance annually.

Tortoises also use burrows to moderate the temperature of their nests. Spotila *et al.* (1994) reported that temperature determined the sex of desert tortoise embryos with a pivotal temperature of 31.8 °C. New data (Rostal *et al.* unpubl.) indicated that pivotal temperature was

31.3 $^{\circ}$C. Hatching success and survival was very good between 28.1 and 32.8 $^{\circ}$C in dry sand (-5000 kPa) while wet sand (-5 kPa) was lethal for desert tortoise eggs. Therefore by placing their nests within burrows, tortoises insure maintenance of suitable temperatures for the development and sex determination of their eggs. Hatchlings from warm eggs were significantly smaller than those from small eggs, although hatching mass had no effect on later growth of hatchlings. Temperature selection by hatchlings in a thermal gradient was not affected by prior incubation condition and averaged 26.6-29.2 $^{\circ}$C (Spotila *et al.* 1994).

The effects of water limitation on desert tortoise activity have been better studied. Tortoises tolerate temporary imbalances in water, salt, and nutrient balances as do other desert reptiles (Minnich 1970, 1976, 1977, 1979). Mojave Desert tortoises are thought to experience positive water balance during the early spring as they feed on relatively succulent plants that grow in response to winter rains. As temperatures increase, vegetation dries, and tortoises enter negative water balance and are faced with a dilemma. They need to feed to balance their energy budgets, but feeding on dry plants does not provide water but does provide high concentrations of potassium (K^+) that can only be excreted in the urine in a kidney that cannot concentrate urine. High serum concentrations of K^+ have a variety of adverse physiologic effects not the least of which is that the function of excitable tissues (muscle, nervous tissue) is disrupted. The tortoise deals with this problem by a combination of 1) tolerance of high K^+ concentrations, 2) using the large bladder as an osmotic sink, and 3) complexing K^+ with urate to form poorly soluble salts which are precipitated and excreted in semi-solid form. Late summer rains, when available, provide free water allowing tortoises to void concentrated urine, dilute concentrated blood, and refill the bladder with dilute urine (Minnich 1977, Nagy and Medica 1986, Peterson 1993).

Minnich (1977) measured water turnover using tritiated water in a free-living population of desert tortoises near Barstow, California. During July and August tortoises have very low water intakes (0.27 ml $(100g)^{-1}$ day^{-1}) which approximates rates of metabolic water production (0.22 ml $(100g^{-1})$ day^{-1}). Tortoises lose water rapidly (0.46 ml $(100g^{-1})$ day^{-1}), while losing body mass slowly (0.28 g $(100g^{-1})$ day^{-1}), primarily through evaporation. They retain a concentrated urine in their bladders and excrete urinary pellets containing electrolytes (Na, K, NH_4). The low solubility of these cations, together with the high urate content, low chloride content and high urine pH, suggests that most cations are bound as urate salts. (Minnich 1972).

Relatively low field metabolic rates (Nagy and Medica 1986, Peterson 1993), and low rates of transcutaneous and pulmonary water loss compared to similar animals are also thought to aid in water conservation. Indeed, despite a severe drought in 1989 in the western Mojave, Peterson found very small deficits in net water flux throughout the drought (Peterson 1993).

Of great interest are the interactions of a desert tortoises water budget with other budgets the animal must balance and activities it must perform. First, as already noted, water economy interacts with energy and nutrient acquisition. During the relatively "wet" early spring when tortoises maintain positive water balances, they are thought to be in negative water balance (Nagy and Medica 1986, Peterson 1993) for reasons that are not entirely clear. As the vegetation dries and the tortoises start hemoconcentration, they also enter positive energy balance. Thus it is not possible to avoid activity before the late summer rains because of the need to balance the long term energy/nutrient budgets. Medica *et al.* (1975) report that annual growth increments are positively correlated with winter rainfall. Peterson (1993) noted correlations between feeding activity, metabolic rate, and the availability of rainwater.

Second, activity carries a cost in terms of water loss both for thermal (Naegle 1976) and other reasons (C.R. Tracy, pers. comm.). Thus, the activity necessary for feeding, mating, movement, and social interactions all carry a cost in terms of water loss. Finally temperature selection may also affect water economy (Naegle 1976).

O'Connor *et al.* (1994) monitored hematologic and plasma biochemical parameters in free-ranging and captive tortoises, maintained in 4 ha pens, at the Desert Tortoise Conservation Center (D.T.C.C.) near Las Vegas, Nevada. Captive animals were exposed to different levels of water supplementation to mimic different levels of hydric stress. Significant increases in plasma electrolyte and urea nitrogen concentrations occurred in captive animals without water supplementation. Differences in electrolytes and BUN among treatments were consistent with altered water balance. A gradient in water availability, from excess water provided three times a week in the supplemented pens to no water provided in the unsupplemented pens, resulted in a similar gradient in physiological responses that were related to hydric stress. Behavioral differences between tortoises in the unsupplemented and supplemented pens (Ruby *et al.* 1994) suggested that the tortoises responded to the treatments behaviorally as well as physiologically. Tortoises in the unsupplemented pens reduced the length of above ground activity time, but increased levels of movement and feeding activity. Tortoises in supplemented pens remained active and fed throughout the summer. They acted more like tortoises maintained in captive situations that receive regular food and water.

This is in contrast to tortoises in other sites in California and Nevada (Medica *et al.* 1975, Minnich 1977, Nagy and Medica 1986) where activity stops or is greatly reduced during hot dry summers. During these periods tortoises remain in their burrows. When rain falls these tortoises then drink rainwater, void urinary wastes, and store rainwater in their bladders as a dilute urine. They also resume activity and feeding. They consume plants high in K^+, but are able to excrete the K^+ load because the dilute bladder urine is utilized as a water reserve (Minnich 1977). Tortoises in the D.T.C.C. study appear to have received sufficient water, even in the unsupplemented pens, to remain active throughout the summers of 1991 and 1992. The same was true for nearby free ranging tortoises. This apparently occurred because 1991 and 1992 were relatively wet years. After a severe drought that lasted several years it rained in February and March, 1991 as well as later that year, and even more extensively in 1992 (O'Connor *et al.* 1994). Thus, free ranging tortoises and those in the unsupplemented pens had enough water available to maintain balanced electrolyte concentrations while remaining active, at a reduced level, throughout the hot summer months.

There is an ongoing search for a physiological indicator that will identify tortoises that are under stress before they develop noticeable pathology. O'Connor *et al.* (1994) employed a standard clinical panel of diagnostic blood tests to determine the physiological response of desert tortoises to thermal and hydric stress. Significant increases in plasma electrolyte and urea nitrogen concentrations and white blood cell counts occurred in captive animals without water supplementation when compared to free-ranging and water-supplemented, captive animals. The differences among water supplementation treatments, while significant, were not sufficient to distinguish among animals from different treatments. No reliably predictive indicators of water stress, or other stresses, were found. Blood profiles from free-ranging animals more closely resembled profiles from captive animals that received supplemental water than profiles from animals that did not receive supplemental water. Captivity , thus, altered blood profiles in a manner similar to that seen with decreased water availability. The extensive blood profiles obtained for tortoises in this study indicate that reliably predictive indicators for water or other stresses may be very elusive indeed. Blood profiles may be more profitably used to search for specific hypothesized stressors in populations rather than as assays of unspecified stress on populations of tortoises.

Desert tortoises are faced with the problem of balancing a cascade of interrelated demands placed upon them by their physical environment. First, they must remain in thermal balance by behaviorally and physiologically thermoregulating in a harsh and complex microclimate. They do this on an hourly and daily basis. Second , they must remain in water balance in an environment where there is no free standing water and rainfall is usually available seasonably, although unpredictably within a season and not at all during some drought years. They maintain water balance on a seasonal or annual basis. Third, they must remain in positive energy and nutrient balance in a habitat where they are limited by both thermal and hydric constraints. They do this on an annual, or perhaps longer, basis. Finally, they must balance nutrient levels in their food and avoid accumulating toxic concentrations of ions such as K^+, Na^+, and $NH4^+$. They do this by selective feeding and by using water stored in the bladder to excrete excess amounts of these ions or by sequestering them in urate salts in the bladder. Only in this way can a turtle live in the desert.

DISEASES OF NORTH AMERICAN TORTOISES (*Gopherus* spp.)

Isabella M. Schumacher[1] and Elliott R. Jacobson[2]
[1] Interdisciplinary Center for Biotechnology Research (ICBR)
University of Florida, Gainesville, Florida 32611, USA
[2] Department of Small Animal Clinical Sciences
College of Veterinary Medicine, University of Florida
Gainesville, Florida 32610, USA

INTRODUCTION

Most tortoise species are experiencing population declines. Although habitat degradation and destruction are considered the most significant threat to wild populations of tortoises, disease is being observed more frequently in certain populations. Of the various causes of mortality in wild populations of tortoises the effect of infectious agents and disease on the structure of wild tortoise populations have been the least studied. Much more information is available on diseases of captive tortoises than on those of wild tortoises. Of infectious diseases, viral, bacterial, mycotic, and parasitic diseases have all been reported. Non-infectious diseases identified in tortoises include trauma, various nutritional diseases, and growth anomalies. Virtually nothing is known about the effects of pollutants and toxicants in tortoises. Because health and disease are directly related, one cannot be understood without appreciating the other. This paper describes health assessment of tortoises in the field and gives an overview of infectious and non-infectious diseases most frequently encountered in wild populations of North American tortoises (Jacobson 1994).

HEALTH ASSESSMENT

When evaluating the health status of tortoises in the wild, one must be able to distinguish between diseases, both infectious and non-infectious affecting individual animals and those affecting whole populations of tortoises in a certain area. A number of pathogens have the ability to spread rapidly through an entire population and cause high rates of morbidity and mortality. In most cases of diseases caused by nutritional deficits or toxins, entire populations in a certain geographic area are seen with characteristic symptoms. Therefore it is essential when conducting a health survey to collect accurate data about the symptoms observed in individual animals, the number of animals affected and the location of sick and dead tortoises and their remains.

Prior to assessment of health in tortoises it is essential to understand what is normal and what are potential signs of disease. While a variety of diagnostic tests is available, the most useful step is an initial thorough physical examination of the tortoise. Critical evaluation of all accessible organ systems will hopefully lead to an initial diagnosis. At the same time appropriate specimen can be collected for various laboratory tests and examinations. In most cases, especially if it is anticipated that an entire population is affected, specimens from several animals should be collected and evaluated. In cases where disease is associated with high morbidity or mortality, preferably representative live animals should be collected and presented to a diagnostic facility for collection of specimens.

A systematic approach including examination of all organ systems of the tortoise is critical to obtaining the most accurate information. The most commonly seen diseases in wild populations of North American tortoises are described below.

Trauma

A wide range of traumatic injuries is commonly seen in wild tortoises. Most commonly encountered are crush injuries to the shell resulting from vehicle accidents and bites in the shell and the limbs from both wild predators and dogs. In addition, drowning in canals, pools and ponds is often observed. While fresh injuries to the skin and the limbs often have a better prognosis than shell trauma, it is essential to administer supportive and antimicrobial treatment as soon as possible. This includes also surgical debridement and treatment of the injury. The prognosis for shell trauma is directly dependent on the location of the injury. Penetrating wounds can result in pneumonia if the lung is exposed, while injuries on the midline of the carapace often result in partial or complete transection of the underlying spinal cord. In these cases the prognosis is poor. In general shell trauma should be treated as an open wound, which includes restoration and alignment of shell fragments and wound management. The tortoise should receive antimicrobial and supportive treatment. The healing process is long and it has to be critically evaluated if the condition of the shell allows successful return into the wild without exposing unprotected areas of the body to predators due to missing parts of the shell.

Shell

The appearance and composition of the shell (carapace and plastron) is often a good indicator for the overall condition of the tortoise. Except for signs of normal wear which increase with the animal's age, the horny layer of the shell surface should be smooth and continuous without discoloration. Various nutritional but also fungal and bacterial diseases will affect the shell and produce typical lesions. If an infectious cause is suspected, a scraping of the shell submitted for culture and a biopsy either taken from the edge of a lesion or from the edge of the carapace for histological evaluation will give important information about the cause of disease. If nutritional deficits are suspected as the cause of abnormal shell composition, several animals should be evaluated and a thorough history of past droughts, etc., be taken to identify any abnormalities in plant growth, thus resulting in an inadequate diet for the tortoise.

Since 1975, the desert tortoise (*Gopherus agassizii*) population on the Beaver Dam Slope, Arizona and Utah has experienced a high mortality rate. An analysis of skeletal remains revealed a pronounced spongy appearance due to osteopenia (Jarchow *et al.* 1989). Malnutrition was considered responsible in this case (Woodbury *et al.* 1948). Cutaneous dyskeratosis in all age classes of tortoises has been observed on the Chuckwalla Bench Area of Critical Concern, Riverside County, California (Jacobson *et al.* 1994). The lesion commenced at seams between adjacent scutes and spread towards the middle of each scute in an irregular pattern. Nutritional deficiencies or toxicosis are suspected to be the cause of this disease. Few primary bacterial infections of the integument have been described in tortoises. Sloughing of the horny shell plates. with local bacterial infection, occurs in tortoises that are kept under unhygienic conditions (Rosskopf 1986). Shell anomalies, like scute reductions or supernumerary scutes have been reported for the desert tortoise on the Beaver Dam Slope, Washington County, Utah and in the Desert Tortoise Natural Area, Kern County, California (Good 1984). Shell anomalies may be environmental and/or genetically based.

Skin

Both infectious and non-infectious disease processes may result in typical lesions of the skin. Scrapings of the skin for cultures and biopsies will hopefully lead to an accurate diagnosis. Hyperkeratotic skin lesions at multiple soft tissue sites have been seen in four captive desert tortoises in Arizona. A *Dermatophilus* -like organism was suspected, but could not be verified upon microbial isolation attempts (Jacobson, pers. obs.). Ticks and mites are frequently seen on tortoises, but do not seem to cause any harm. Larval stages of the dipteran fly *Cistudinomyia cistudinis* frequently parasitize gopher tortoises (*Gopherus polyphemus*) in the southeastern United States (Knipling 1937). The larvae can cause significant tissue damage and death. Lesions are typically located on the perineum and caudal aspects of the hind legs. Following removal of the larvae the cavity should be cleaned with dilute povidone-iodine solution.

Ears

The tympanic scale covering the ear canal should be flat and dry, without perforations. Diseases of the middle ear have been seen in tortoises (Graham-Jones 1961, Keymer 1978). Bulging of the tympanic scale can be seen when purulent material fills the ear canal. A variety of gram-negative microorganisms have been cultured from these lesions.

Eyes

Eyes should be clear without discharge and eyelids should not appear puffy. Palpebral edema and conjunctivitis have been seen in desert tortoises and gopher tortoises in connection with URTD (see under Respiratory Tract).

Oral Cavity

The mucosal surface of the oral cavity should be of a light pink color and slightly moist. There should not be any discharge. Herpesvirus-like agents have been reported in association with stomatitis, necrosis of the oral mucosa with accumulations of necrotic debris around the glottis, the roof of the oral cavity, and the internal nares (Jacobson *et al.* 1985, Cooper *et al.* 1988). In a captive desert tortoise herpesvirus-like agents have been found in a pharyngeal abscess (Harper *et al.* 1982). Treatment of stomatits with 5% acyclovir ointment has been described as encouraging.

Respiratory Tract

The nares should be dry and free of discharge. There should be no loud breathing sounds. Rhinitis with clear to purulent discharge, conjunctivitis, palpebral edema and labored breathing are characteristic signs of an upper respiratory tract disease (URTD). Severely affected tortoises appear depressed and emaciated, and may die of starvation. URTD was first seen in 1988 in the Desert Tortoise Natural Area, Kern County, California (Jacobson *et al.* 1991). Since then, URTD has been seen in desert tortoises throughout the Mojave Desert of southern California, the Las Vegas Valley, Nevada, the Beaver Dam Slope, Utah/Arizona, and the Sonoran Desert, Arizona. Various gopher tortoise populations throughout their range have been found to test seropositive for URTD but, except for a few individuals in Central and Southwest Florida and some captive tortoises, they did not show clinical signs (Schumacher pers. obs.). URTD is a contagious disease caused by *Mycoplasma agassizii,* a small pleomorphic bacterium (Brown 1994). A serologic test can be used to confirm the diagnosis (Schumacher *et al.* 1993). Symptomatic treatment with enrofloxacin (5mg/kg i.m., every other day for a total of 10 treatments) is possible.

DISEASE PREVENTION

While preventing disease in wild populations is impossible, preventing the spread of disease is all the more important. Many predisposing factors for an outbreak and spread of disease, like stress caused by habitat destruction through urban development or unfavorable weather conditions, unfortunately are not easily or not at all controllable. Responsible handling of wild tortoises, keeping stress to a minimum and making informed decisions in relocating tortoises are important steps in disease control (Klein 1993). Responsible handling of tortoises includes wearing a separate pair of gloves for each animal examined and collecting tortoises in individual containers which can either be discarded or disinfected after being used. If necessary, responsible relocation includes surveying the relocatees as well as the host population for diseases to prevent the spread of contagious diseases. Captive animals should never be allowed back into the wild. They could be silent carriers of pathogenic agents which are nonexistent in wild populations and therefore would pose a potentially deadly threat to naive wild populations.

MORPHOLOGICAL DISTINCTIVENESS OF THE NORTHERN POPULATION OF THE BOLSON TORTOISE, *Gopherus flavomarginatus*

Eddie Treviño[1], David J. Morafka[1], and Gustavo Aguirre León[2]
[1]Department of Biology
California State University, Dominguez Hills
Carson, CA 90747-0005, U.S.A.
[2]Instituto de Ecología A.C., Apartado Postal 63,
Km. 2.5 Antigua Carretera a Coatepec
91000 Xalapa, Ver. México

INTRODUCTION

Under IUCN sponsorship, a team of U.S. and Mexican investigators have been assessing the distinctiveness of a population of the endangered Mexican Bolson tortoise, *Gopherus flavomarginatus*. Studies of Bolson tortoise biology were conducted initially at the Mapimí Biosphere Reserve (Morafka *et al.* 1981, Morafka 1982,) a protected area within the MAB-UNESCO international network of biosphere reserves. Further research on the Bolson tortoise population at Mapimí comprised different aspects of its ecology, life history and conservation (Aguirre *et al.* 1984, Adest *et al.* 1989a,b, Morafka *et al.* 1989).

Previous studies at Cerros Emilio, in souhtwestern Chihuahua (Morafka 1982, Bury *et al.* 1988) revealed robust tortoise populations, possibly warranting reserve status. Current studies support this conclusion.

STUDY AREA

This tortoise occurs at Rancho Sombreretillo in the state of Chihuahua (27° 24' 58" N and 103° 58' 15" W, elevation 1264 m), and situated along the northern edge of the Bolson de Mapimi. This bolson, or valley, lies between the Sierra del Diablo to the west, the mountain ranges of the Sierra de Almagre to the northeast, and the Sierra Mojada to the southeast. This is most of the current range that contains several demes of these tortoises.

RESULTS

Surveys conducted in 1992, 1993, and 1994 yielded carapace measurements that confirmed that the Sombreretillo tortoise yellow pigments are largely confined to the marginals, especially in sub-adult to adult individuals. Juvenile carapaces presented more extensively distributed yellow than previously reported.The carapace sizes are used to establish four age classes based upon carapace length and the carapace width of the fourth marginals (Germano 1988). A suite of shell measurements will determine differences in shell morphology between the two populations at Mapimí and Sombreretillo.

DISCUSSION

Habitat quality at Rancho Sombreretillo had deteriorated since the late 1980's due to increased cattle grazing. Cattle densities had increased, in part, as a result of expanded pumping of underground water to local troughs and reservoirs. However, tortoise populations remained robust, with ample evidence of nests, hatchlings, and particularly juvenile age size classes. Juvenile and sub-adult age classes are well represented and may be adequate for recruitment into a stable population (C.R. Tracy, pers. comm.).

The impacts that ranching methods used at the Sombreretillo area has had on this population will be studied and the result compared to other studies. These studies investigated the potentially negative impacts livestock grazing has had on desert tortoise populations in the Mojave desert (Berry 1978, Oldemeyer 1994). At the other extreme, Bostick (1990) suggested that cattle grazing may even be benefitial to desert tortoises. Analysis of data collected will be useful in resolving these differing views, especially when regional climatic diferences are taken into account.

CONCLUSION

The IUCN team concludes that Rancho Sombreretillo is still suitable and appropriate as a Bolson tortoise reserve. The Instituto de Ecología has experience addressing the socio-economic issues in establishing the Mapimi Biosphere reserve and has succeeded in protecting the Bolson tortoise with the cooperation of local resident (Kaus 1993) and will provide support for monitoring Rancho Sombreretillo.

Therefore, a cooperative agreement between local landowners, residents, Mexican government agencies such as the Instituto de Ecología, and NGOs such as Fundación Chihuahuense de la Fauna is recommended as most effective in order to promote local community support for tortoise conservation. Outright land acquisition would be exploited by local poachers if responsible and cooperative residents were displaced to establish a remote and inadequatelly patrolled reserve.

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