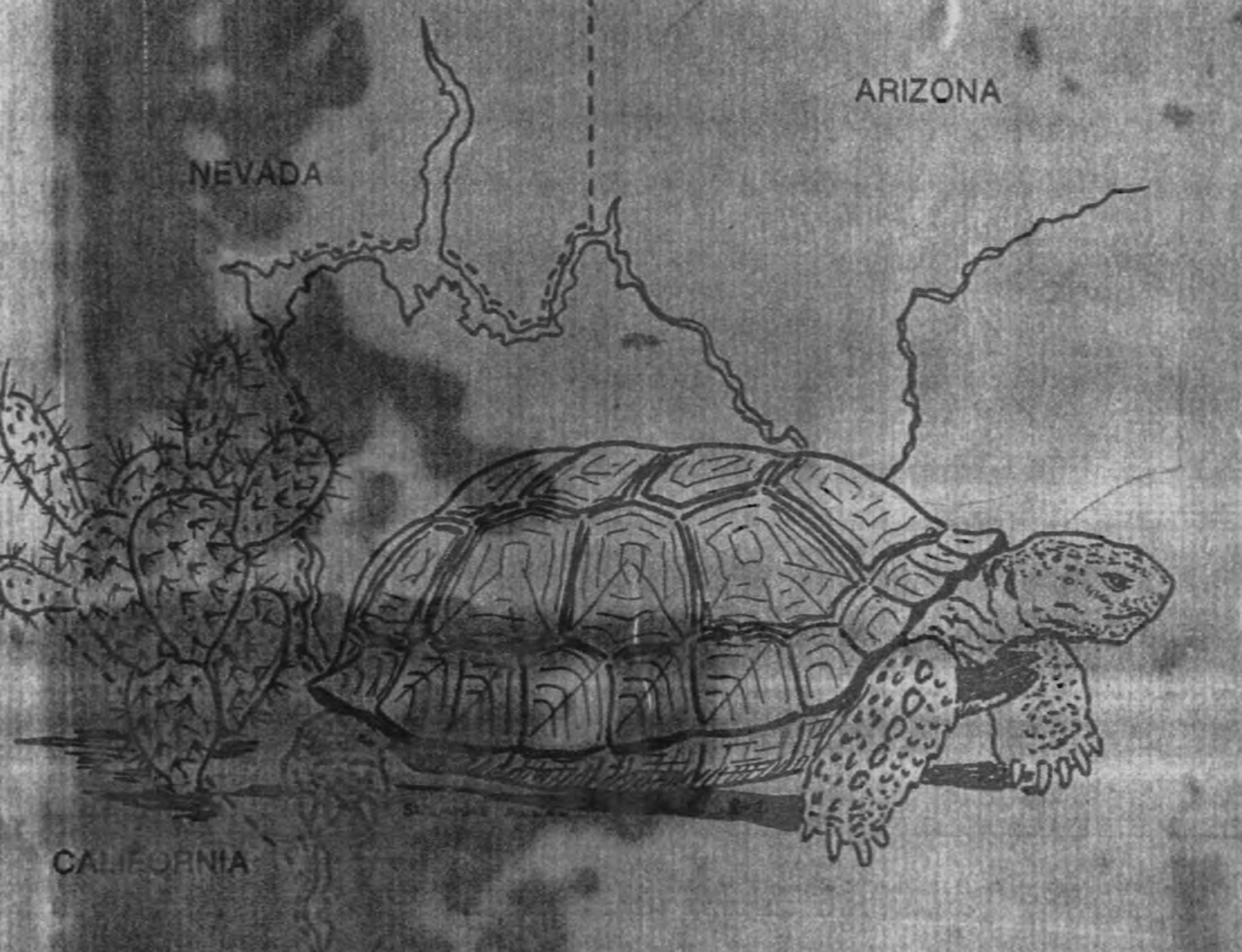
THE

DESERT TORTOISE COUNCIL



PROCEEDINGS OF 1977 SYMPOSIUM

DESERT TORTOISE COUNCIL

PROCEEDINGS OF 1977 SYMPOSIUM

A compilation of reports and papers presented
at the second annual symposium of the
Desert Tortoise Council, 24-26 March 1977,
in Las Vegas, Nevada

Copies of these proceedings may be obtained by
sending $5.00 to: Desert Tortoise Council,
1835 Klauber Avenue, San Diego, CA 92114.
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DESERT TORTOISE COUNCIL

-Editorial Committee-

Acknowledgment

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Photographs

A Female *(left)* and a Male Desert Tortoise Outside a Burrow in the Mojave Desert, California

Photo by Beverly F. Steveson

The Desert Tortoise Council

James A. St. Amant

The Desert Tortoise Council, in its 2nd year of commitment of assuring the continued survival of viable populations of the desert tortoise throughout its existing range, has made major strides toward this goal.

Growing in stature and number, the Council has stimulated interest in saving the tortoises and the once neglected desert habitat as an important part of our western heritage. The Council, functioning as a coordinator, has proved to be an unprecedented example of effective combined efforts of state and federal agencies, academies, zoos, institutions, museums, turtle and tortoise clubs and societies and concerned citizens, to help the tortoise.

The Council's main functions include:

1. To serve in a professional advisory manner, where appropriate, on matters involving management, conservation and protection of desert tortoises
2. To support such measures as shall work to insure the continued survival of desert tortoises and the maintenance of their habitat in a natural state
3. To stimulate and encourage studies on the status and on all phases of life history, biology, physiology, management and protection of desert tortoises, including studies of native and exotic species that may affect desert tortoise populations
4. To provide a clearinghouse of information among all agencies, organizations and individuals engaged in work on desert tortoises
5. To disseminate current information by publishing proceedings and transactions of meetings and other papers as deemed useful
6. To maintain an active public information and conservation education program
7. To commend outstanding action and dedication by individuals and organizations fostering the objectives of the Council.

We still have a long way to go, but through your efforts the tortoise now has a chance. Keep up the good work. See you at the Third Annual Desert Tortoise Council Symposium, 1-3 April 1978, in Las Vegas, at the Flamingo Capri.

California Department of Fish and Game
350 Golden Shore
Long Beach, California 90802

The Second Annual Meeting and Symposium

Our sincere thanks to keynote speaker, Dr. Kenneth S. Norris of the University of California, Santa Cruz, for setting just the right tone for our Second Annual Symposium with his thought-provoking address, "The Subtle Desert--Conservation's Orphan."

Our deepest appreciation also to our after-dinner speaker, Dr. Thomas H. Fritts of the San Diego Museum of Natural History, for his very informative and entertaining slide presentation regarding conservation efforts with the giant tortoises of the Galapagos Islands.

Excerpts from the Minutes of the Second Annual Business Meeting

Dr. Crawford G. Jackson, Jr., and David W. Stevens, members of the Public Information Committee, reported that more than 200 copies of the Proceedings of the 1976 Symposium were mailed without charge to college and university libraries, museum libraries, and several community libraries throughout the United States.

Dr. Thomas H. Fritts recommended that, because the Bolson tortoise *(Gopherus flavomarginatus)* is endangered and is being heavily exploited, the Desert Tortoise Council write the Mexican Wildlife Service endorsing research on and enforcement of laws protecting this species. (Such a letter was sent to the appropriate agencies.)

RESOLUTIONS

RESOLUTION No. 1 (sent to the appropriate Fish and Wildlife and land management agencies)

RESOLUTION ON THE MANAGEMENT OF THE FERAL BURROS

WHEREAS, feral burros are capable of damaging desert tortoise and other indigenous wildlife habitats, and

WHEREAS, feral burros compete for limited forage available to desert tortoises and other wildlife on arid lands where plant productivity is low, and

WHEREAS, burro populations are not adequately maintained within ecosystem carrying capacity, therefore, be it

RESOLVED, that the Desert Tortoise Council recommends control of feral burro populations on public lands where burros are protected by the Wild and Free-roaming Horse and Burro Act. Burro populations should be maintained within the habitat carrying capacity which must include provisions of forage for resident native animal species, and be it further

RESOLVED, that burros should be excluded from national parks and other reserves established for the protection of indigenous wildlife.

Research Proposal (related to Resolution No. 2)

The Halfway House has been an experiment in captive tortoise rehabilitation, and has approximately 50 tortoises ready for release. Each released tortoise must be closely studied to determine the effectiveness of the rehabilitation program. Thus a formal research program must be approved to determine these results.

Dr. Glenn R. Stewart proposed that a research proposal reviewed by the Research Advisory Committee be submitted to the Los Angeles County Fish and Game Commission. This proposal is for $4,950 to cover travel expenses and radiotelemetry equipment to assist California State Polytechnic University (Pomona) graduate student James C. Cook to research the released captives. Dr. Stewart moved that a proposal with the Desert Tortoise Council's endorsement be submitted to the Los Angeles County Fish and Game Commission. David Stevens seconded the motion.

Discussion: Dr. Norma J. Engberg recommended that the study also include an evaluation of the Quarterway and Halfway Houses, crowding, carrying capacity, and stress of the rehabilitation areas. Dr. Stewart stated that these factors would be included in the study. The motion was carried.

RESOLUTION No. 2 (sent to the Los Angeles County Fish and Game Commission)

RESOLUTION IN SUPPORT OF A STUDY OF THE CALIFORNIA DEPARTMENT OF FISH AND GAME CAPTIVE TORTOISE REHABILITATION PROGRAM

WHEREAS, The California Department of Fish and Game has been developing a rehabilitation program for captive desert tortoises for over two years, and

WHEREAS, a detailed study of the program, including intensive radio tracking of tortoises released from the program, is urgently needed to evaluate the program's effectiveness, and

WHEREAS, the first 50 tortoises to complete the rehabilitation program are ready to be released in the Antelope Valley of Los Angeles County in May 1977, and

WHEREAS, California State Polytechnic University graduate student James Cook is prepared to carry out the needed study under the direction of Dr. Glenn R. Stewart, and

WHEREAS, several potential sources of funding have not been able to provide money for the study, and

WHEREAS, funds to purchase radio tracking equipment and cover travel expenses are essential to carry out the study, now therefore, be it

RESOLVED, that the Desert Tortoise Council, meeting in Las Vegas, Nevada, on 25 March 1977, herewith declares its full support for the study and urges the Los Angeles County Fish and Game Commission to provide the necessary funds.

Attendees - Second Annual Meeting and Symposium

Jeffrey B. Aardahl	Bureau of Land Management, Bakersfield District Office, CA
Suzanne Allan	Las Vegas, Nevada
Dale K. Arhart	Bureau of Land Management, Cedar City District Office, Utah
Michael Banks	Student-University of California at Riverside
Dr. Gilbert B. Becker	San Bernardino County Museum, Redlands, CA
Dr. Kristin H. Berry	Bureau of Land Management, California Desert Plan Staff, Riverside
Betty L. Burge	Student-University of Nevada at Las Vegas
Dr. Nathan W. Cohen	University of California at Berkeley Extension
James C. Cook	Student-California State Polytechnic University, Pomona
Eric M. Coombs	Student-Utah State University, Logan
Mark Davidovich	California Turtle and Tortoise Club, Las Vegas, Nevada
Dr. Mark A. Dimmitt	Bureau of Land Management, Riverside, CA
Deborah Dorsett	Student-California State Polytechnic University, Pomona
John A. Edell	CALTRANS, Bishop, CA
Frederick H. Emmerson	Las Vegas Valley Zoo, Las Vegas, Nevada
Dr. Norma J. Engberg (Thoemmes)	University of Nevada at Las Vegas
Richard E. Enriquez	Bureau of Land Management, Las Vegas District Office, Nevada
Ann Farber	Desert Tortoise Preserve Committee, Edwards AFB, CA
Elizabeth W. Forgey	Desert Tortoise Preserve Committee, Boron, CA
Warren Forgey	Desert Tortoise Preserve Committee, Boron, CA
Rochelle Freid	California Turtle and Tortoise Club, Fullerton, CA
Dr. Thomas H. Fritts	Museum of Natural History, San Diego, CA
Stan Hillyard	University of Nevada at Las Vegas
Bruce Hird	Bureau of Land Management, Ridgecrest, CA
Mark Hoffmann	Santa Monica College, Santa Monica, CA
Jeanne B. Hogg	Santa Monica College, Santa Monica, CA
Judy P. Hohman	Student-Arizona State University, Tempe
Paul B. Holden	Logan, Utah
Lita L. Holmgren	California Turtle and Tortoise Club, Los Angeles, CA
Frank Hoover	California Department of Fish and Game, Chino
Alex Jaramillo, Jr.	California Turtle and Tortoise Club, Fontana, CA
Vicki Jaramillo	California Turtle and Tortoise Club, Fontana, CA
Gail C. Kobetich	U.S. Fish and Wildlife Service, Las Vegas, Nevada

Attendees (Continued)

Mary Ann Lewis	California Turtle and Tortoise Club, Los Angeles, CA
Thomas A. Lules	Arizona Game and Fish Department, Kingman
Paul Lucas	Nevada Fish and Game, Ely
Charles W. Marshall	California Department of Fish and Game, Chino
Philip A. Medica	UCLA-Nevada Test Site
Dr. John E. Minnich	University of Wisconsin-Milwaukee
Shirley Moncsko	Desert Tortoise Preserve Committee, Ridgecrest, CA
Dr. David J. Morafka	California State College, Dominguez Hills
Dr. Kenneth A. Nagy	University of California, Los Angeles
Dr. Kenneth S. Norris	University of California at Santa Cruz
Robert G. Patterson	Independent Researcher, Orange, CA
Evelyn Perrine	Long Beach, CA
Presley Pickell	Student-Chaffee College, Alta Loma, CA
Diana Pickens	California Turtle and Tortoise Club, La Puente, CA
William Radtkey	Bureau of Land Management, Sacramento, CA
Wilma S. Rogers	Las Vegas, Nevada
Frank Rowley	Bureau of Land Management, District Manager, Cedar City, Utah
James A. St. Amant	California Department of Fish and Game, Long Beach
Peter G. Sanchez	National Park Service, Death Valley National Monument, CA
Robert B. Sanders	San Bernardino County Museum, Redlands, CA
James L. Schwartzmann	Arizona State University, Tempe
Donald J. Seibert	Bureau of Land Management, Arizona State Office, Phoenix
Harold F. Snowden	San Diego Turtle and Tortoise Society, San Diego, CA
Patricia Snowden	San Diego Turtle and Tortoise Society, San Diego, CA
David W. Stevens	Southern California Edison Company, Environmental Planning, Rosemead, CA
Dr. Glenn R. Stewart	California State Polytechnic University, Pomona
Caroline Stiles	Las Vegas, Nevada
Edward C. Thoemmes	Las Vegas, Nevada
Mary Trotter	Desert Tortoise Preserve Committee, San Diego, CA
Dr. Thomas T. Van Devender	University of Arizona, Tucson
Ann E. Weber	Student-California State Polytechnic University, Pomona
Melvin J. Wilhelm	Bureau of Land Management, Arizona Strip District
Darrell M. Wong	California Department of Fish and Game, Blythe
Dudley Zoller	Nevada State Federation of Garden Clubs, Las Vegas

1977 Annual Award - A Profile of Recipient, Dr. Kristin H. Berry

Dr. Kristin H. Berry was born in Walla Walla, Washington, in 1943. When she was just four years of age, her family moved to China Lake in the Mojave Desert of California. There she developed an avid interest in desert natural history, and, over the years, felt increasing concern for desert flora and fauna in the wake of agricultural and urban development, livestock grazing, and growing off-road vehicle use.

Photo by Beverly F. Steveson

Dr. Kristin H. Berry

Dr. Berry attended Occidental College for three years, and was graduated from Stanford University in 1964. She earned her master's degree in 1968 under Dr. Kenneth S. Norris of the University of California at Los Angeles. The subject of her thesis was the desert spiny lizard. Four years later she received her Ph.D. at the University of California, Berkeley. Her dissertation, under the supervision of Dr. Robert C. Stebbins, was on the ecology and social behavior of the chuckwalla.

In 1971 Dr. Berry undertook a three-year, $15,000 contract for the State Department of Transportation (Division of Highways) to study the feasibility of relocating desert tortoises away from the highway corridor between Barstow and Mojave, to find sites for the relocated tortoises, and to study the behavior of the transplanted tortoises. She gathered data on almost

160 marked wild tortoises at two study sites during this period, on a small number of former captives, and several dozen transplants. Since 1974 she has been employed as the Lead Biologist for the California Desert Program, Bureau of Land Management.

During the course of her studies for the Division of Highways, Dr. Berry became aware of human encroachment on many tortoise populations. The population of highest known density was threatened by off-road vehicles, and agricultural and suburban development. In 1972 she approached the Bureau of Land Management and asked them to establish a preserve to protect the desert tortoise. In April 1974, she organized, the Desert Tortoise Preserve Committee which has the goal of establishing a preserve or natural area. Through this Committee, she has worked to establish a natural area north of California City to protect that high-density population; has spearheaded a massive letter-writing campaign; has developed—with noted wildlife photographer Beverly F. Steveson—four slide programs (three of which are being sold by the Committee) to educate the public; and has lectured and given numerous programs on the subject. She is now working through The Nature Conservancy to further the goals of land acquisition, and is on the Board of Directors of the Southern California Chapter.

In addition to the above accomplishments on behalf of the desert tortoise, Dr. Berry has developed and produced transect forms for determining relative densities of tortoises (with the help of colleagues); has promoted the study of desert tortoises through the Bureau of Land Management in Arizona; has established, through contracts with the Bureau of Land Management and her own funding, several permanent study plots in the California desert with the goal of determining the status of the desert tortoise in California; and has generally tried to develop an awareness of the problems of the desert tortoise management among the scientific community and land-use managers.

She is past co-chairman of the Desert Tortoise Council, and has been its program chairman since the Council was formally organized.

Thomas A. Liles

State Reports - Arizona

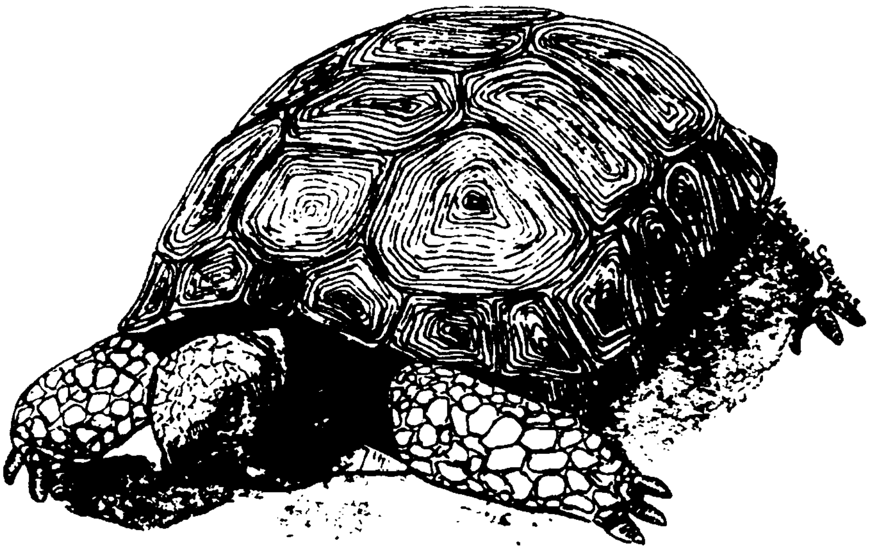
Donald J. Seibert
Bureau of Land Management

Inventories of the desert tortoise populations of that portion of the West Beaver Dam Slope within Arizona and north of the Virgin River were completed this past year.

An intensive study to determine the impact of livestock grazing on the tortoise has been started in the same area. This study is proposed as a long-term project of which the initial phase will be 2 to 4 years in duration.

A paper relating to both the inventories and the ongoing study will be presented by Judy Hohman later on the agenda.

Bureau of Land Management
Arizona State Office
2400 Valley Bank Center
Phoenix, Arizona 85073



State Report - Arizona

Thomas A. Liles
Game and Fish Department

State Law under Title 17 of the Arizona Revised Statutes allows for the possession of 1 desert tortoise *(Gopherus agassizi)* per person. None may be killed or exported from the state, and a person who possesses a desert tortoise must be age 14 or older and must have a valid Arizona hunting license. Exceptions to this are individuals who have been issued special permits (i.e., Scientific Collector's Permit or Zoo Permit) by the Arizona Game and Fish Commission. These individuals are then bound by the specific conditions set forth in their permits.

The Arizona Game and Fish Department has prepared a list of "Threatened Wildlife of Arizona" which covers native mammals, birds, reptiles, amphibians, and fish. It is scheduled to be revised during the summer of 1977. If the revised edition is approved by the Arizona Game and Fish Commission, it will then become an official state list and not merely a department list as at present.

In an effort to get away from the terminology of "Rare and Endangered" or "Threatened", species warranting concern were placed in 1 of 4 groups. These categories are as follows: Group I - species or subspecies formerly resident in Arizona that may possibly be reestablished; Group II - species or subspecies in danger of being eliminated from Arizona; Group III - species or subspecies whose status in Arizona may be in jeopardy in the foreseeable future; Group IV - species or subspecies sufficiently limited in distribution in Arizona that major ecological disturbances could jeopardize their existence in the state.

The present list includes 11 species of reptiles and 7 species of amphibians. All 7 amphibians (4 species of frogs and 3 species of toads) and all 9 species of snakes are listed in Group IV. The other 2 reptiles, the desert tortoise *(Gopherus agassizi)* and the Gila monster *(Heloderma suspectum)* are listed in Group III.

The Arizona Game and Fish Department is presently involved in the preparation of a "Statewide Fish and Wildlife Plan". We are due to complete the inventory phases 30 June 1977. This phase has been primarily the compilation (for centralization) of all past data. This should aid greatly in delineating data gaps and other areas of concern on a statewide basis.

The Arizona Game and Fish Department is not presently considering to propose any changes in the regulations concerning the desert tortoise. We are familiar with the difficulties the California Department of Fish and Game encountered when they first prohibited collecting of the tortoise. However, information gained from the preparation of the "Statewide Fish and Wildlife Plan" and input to the "Threatened Wildlife of Arizona" list may well warrant revision of our present reptile regulations in the future.

Arizona Game and Fish Department
1420 West Beale Street
Kingman, Arizona 86401

State Report - California

Kristin H. Berry
California Desert Program, Bureau of Land Management

The Bureau of Land Management report for the California deserts is subdivided into several parts: a study of desert tortoise distribution and density in the Colorado Desert and eastern Mojave region; the establishment of a permanent study plot in the western Mojave Desert in an area used by off-road vehicles; projects proposed for the desert tortoise during spring 1977 in the California deserts; and a status report on the Desert Tortoise Natural Area. Dr. Mark Dimmitt and Jeff Aardahl will present papers on the Colorado Desert study and Desert Tortoise Natural Area, respectively.

The wildlife staff of the California Desert Program has identified the desert tortoise as one of the more important species occurring in the California deserts and plans several projects to determine status and distribution. The goals of the staff during the next few years include: mapping quantitively (and in detail) the distribution and relative densities of tortoise populations in California; determining absolute densities in 10 or more areas in habitats typical of large parts of the desert; establishing several permanent trend study plots to determine population density, age structure, sex ratios, population condition, and habitat condition; and studying impacts of such human-related activities as effects of off-road vehicle use, livestock grazing, and presence of highways and unpaved roads.

Studies on Distribution and Relative Density. During 1975 and 1976, over 40 transects were made in the eastern Mojave Desert of San Bernardino County in a study area called the East Mojave planning unit. This area encompasses about 8,100 km^2 [= two million acres] and includes Cima Dome, the Granite, Providence, New York, Ivanpah and Piute mountains, and Ivanpah, Fenner and Lanfair valleys. Concentrations of tortoises were found in the Budweiser Wash area west of the Granite Mountains, in southern and western Ivanpah Valley, and near Goffs. Virtually no tortoises were found in areas above 1,220 m [= 4000 ft] in elevation.

During 1976, 80 transects were made in the Colorado Desert region by Marshall Yacoe, who worked for Dr. Mark Dimmitt on the Sundesert Power Plant Project. Mr. Yacoe found concentrations of tortoises in some of the major washes with microphyll woodlands, particularly in the region between the Chuckwalla and Chocolate mountains.

Permanent Study Plot in Western Kern County. A permanent study plot 2.59 km^2 [= 1 square mile] in size was established in the Fremont Valley—Rand Mountain area of western Kern County. The study plot lies in a region of high tortoise densities and also in the Rand Open Area, an approximate 337 km^2 [= 130 square mile] area of public land used intensively by off-road vehicle recreationists. Marshall Yacoe (in a privately funded study) marked 118 tortoises and collected 44 shells during a 20-day period in May 1976. Data were recorded on size, sex, behavior, condition, and locations of all tortoises. Twenty-seven feeding observations were made on 26 individuals. The population was found to consist of 41% adults, 17% subadults, 34% immatures and 8% very young individuals; there were no hatchlings. The sex ratio of adults and subadults was 119 males: 100 females. Density was estimated at 58-77 per square kilometre [= 150-200 tortoises per square mile].

This study cost approximately $600 and produced valuable results. Similar study plots should be established both in typical habitats and in disturbed areas throughout the range of the desert tortoise.

Proposed Studies for 1977. The California Desert Program wildlife staff anticipates establishing 5 permanent trend study plots in the Mojave and Colorado deserts of California during spring 1977. Each plot will be 2.59 square kilometres [= 1 square mile] in size. Data will be collected on size, sex, behavior, and location of every live tortoise, and on size, sex and condition of every shell. Hopefully the data can be used for 2 purposes: to establish base-line information on the condition of certain desert tortoise populations, and to determine densities, age structure, sex ratios, and mortality factors in certain habitat types.

More transects are planned. The staff anticipates undertaking transects in the northeastern, southeastern, central, and western Mojave Desert. However, it is unlikely that transect data will be collected in the military reservations and National Monuments.

Zoologist
California Desert Program
Bureau of Land Management
3610 Central Avenue, Suite 402
Riverside, California 92506

State Report - California

Jeffrey B. Aardahl
Bureau of Land Management

Thank you for inviting the Bureau to give a report on the Desert Tortoise Natural Area, or I should say proposed Desert Tortoise Natural Area. Yes, the area is still in a proposed stage but in reality the designation as such is not hindering the primary objective of the project which is habitat protection for all wildlife species naturally occurring in the area.

As many of you know, the Bureau has been fortunate to receive generous funding for management of the habitat in the natural area. In fiscal year 1976, the Bakersfield District Office received $135,000 and this year we were allocated about $60,000. With this money we have hired a full-time wildlife biologist to work on development of the area, contracted for construction of a protective fence around the area, contracted for an interpretive plan and materials with the Desert Tortoise Preserve Committee, and removed trash from the area. During the next 2 months we will contract for construction of interpretive facilities and nature trails and possible color infrared aerial photography of the area.

We are fortunate to have one of our Desert Rangers in the Federal Law Enforcement Training Center in Georgia. I expect he will be a valuable asset in enforcing the vehicle closure, grazing closure, and helping in controlling vandalism. Presently, at least one person from the Ridgecrest Office patrols the natural area every day except Mondays.

The Habitat Management Plan is complete and will be sent to the Department of Fish and Game for their final approval. Briefly, the plan will protect and enhance the habitat and wildlife populations in the area by:

1) Eliminating vehicle use

2) Eliminating grazing

3) Acquiring private land

4) Rehabilitating disturbed areas

5) Managing public use, including scientific research

6) Withdrawing public lands from future appropriation and mining laws. The withdrawal is being resubmitted for congressional approval under terms of the newly passed "Organic Act" or Federal Land Policy and Management Act. Congress will have 2 years to act on the proposal. As you may recall, the original proposal was submitted in 1975 and no action was taken up to the end of last year. We believe that the new congressional approval approach will be superior to what has occurred in the past.

Let me expand on the Land Acquisition Program. There are about 300 private parcels of land within the boundary. Acquisition priorities are based on wildlife habitat value as specified in the Habitat Management Plan.

No land has been acquired by the Bureau as yet. Shortly, we will program for manpower and money for next year for acquisition of our first priorities. The acquisition program will be very costly under the traditional exchange program because all parcel exchanges require mineral, land, archaeological, and environmental reports. Under existing manpower we could acquire 1 to 2 parcels per year. We hope to acquire land under the Land and Water Conservation Funds as authorized under the Organic Act. We also hope for assistance from the Department of Fish and Game in our Land Acquisition Program.

We are very pleased that our Land Acquisition Program is being bolstered by assistance from The Nature Conservancy. They are in the process of acquiring private land in the northern extension which will be added to the proposal.

As far as scientific research is concerned, we have developed guidelines for evaluation and the permitting of research. The Research Advisory Committee of the Council and Department of Fish and Game will jointly review and evaluate proposed research for the natural area. The following guidelines will be used in the evaluation process:

1) Research will be permitted to the extent that natural conditions are not adversely altered.

2) Research must be based on scientific principles.

3) Results of research should make a significant contribution to science.

4) Research should provide needed information on life history and habitat requirements of plants and animals.

5) Research should provide needed information for habitat management.

6) Research must not unnecessarily duplicate or conflict with other research.

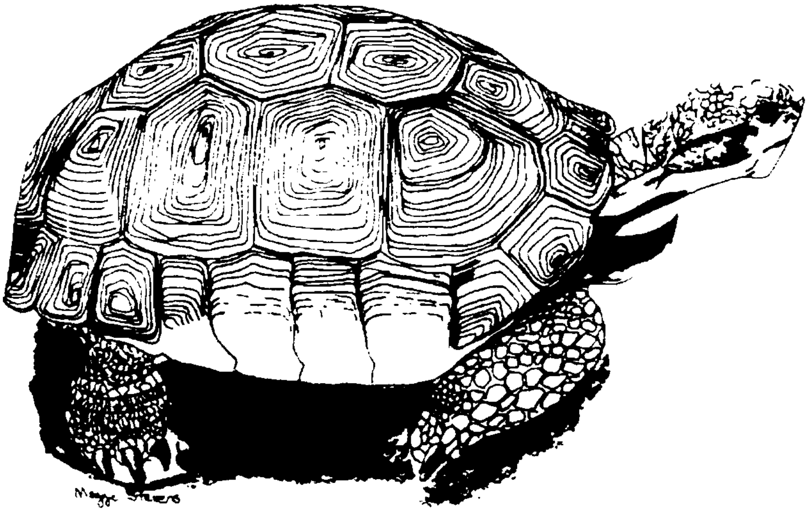
7) If the same results can be obtained, the research will be conducted outside the natural area.

Our office initiated the review process of research proposed by Mr. and Mrs. Ron Marlow of the University of California at Berkeley. I believe Dr. Glenn Stewart has received correspondence regarding this.

The Bakersfield District received the research paper "Respiratory Disease in the Desert Tortoise" completed under contract with Murray Fowler, D.V.M., University of California, Davis. One of Dr. Fowler's findings was that he does not believe respiratory disease in captive tortoises is contagious. He believes respiratory disease results from undernourishment which allows infection by opportunistic bacteria. During the next year Dr. Fowler will continue this research by testing the susceptibility of healthy tortoises to bacteria isolated from diseased tortoises.

In closing, I would like to say thank you to the Desert Tortoise Council for its support of our program and the assistance provided, especially in evaluation of research proposals. I do not have any details for next year's funding for the natural area but I would expect it to be similar to this year's figure.

Bureau of Land Management
Ridgecrest Resource Area
P. O. Box 219
Ridgecrest, California 93555



Special Report - California

Tortoise Adoption Program of the California Turtle and Tortoise Club

Mary Ann Lewis

Evolving from the simple exchange of turtles and tortoises between members of the California Turtle and Tortoise Club, the Tortoise Adoption Program for Region 5 of California is now a strong and viable force.

As evidenced by these figures, the California Turtle and Tortoise Club Adoption Program has been gathering momentum year by year. In 1974, 104 *Gopherus agassizi* tortoises were adopted. In 1975, 222 were adopted and in 1976, 389 were adopted. While our State Reptile is the foremost consideration in our adoption program, we also offer for adoption other species; for example, in 1976 we placed 76 *Gopherus berlanderi,* 27 box turtles, 32 aquatic and 8 miscellaneous. And do not forget the hatchlings; 84 of these were placed.

As you undoubtedly know, permits are required for all *Gopherus* species. In addition to the 726 *G. agassizi* and 76 *G. berlandieri* permits filled in and sent to Sacramento, we also handle permit registration at the various turtle and tortoise club shows. For example, in 1976 at the California Turtle and Tortoise Club, Foothill Chapter, show we gave out 32 permits to the public and registered 75 tortoises, and at the Pomona Fair we gave out 26 permits and registered 56 tortoises, while at the Westchester Chapter show we gave out 72 permits and registered 162 tortoises.

We must have help in the Adoption Program. At the present time we need 25 team workers around Region 5 to assist us. Team workers are chosen for their ability to: (1) deal with people, (2) recognize sick tortoises, (3) answer questions about turtles and tortoises, (4) identify different turtles and tortoises, and (5) give out care sheets on turtles and tortoises. If someone in San Francisco or San Diego adopts a turtle or tortoise, we can usually find someone to do the transporting for us.

The Adoption Program is not a status-seeking program or an undercover pet store program, but has a very definitive place in the chain of events regarding the health, habitat, and security of captive *Gopherus agassizi.*

Although a program is underway to relocate the captive tortoise in his pristine habitat, results so far indicate only a qualified success. Overcrowding, stress factors and various degrees of illness all contribute to the welfare of the tortoise.

The tortoise is by nature a partly solitary creature and requires individual attention. The Adoption Program stresses this one need above all other requirements.

The turtles and tortoises we receive are given to us by private individuals and by a few agencies. When we receive them, we determine their sex, measure and weigh them, and record this information along with other pertinent facts. They are then checked healthwise and treated, if required. We do not knowingly place sick tortoises unless the adopting person is advised and agrees to the added responsibility. We actively endeavor to choose people in the drier areas of Region 5 who desire to adopt tortoises. We ask these people to contact us if they have any problems thereby reducing the work load of others, and to return the tortoises to us if they move or do not wish to keep them any longer.

At the time of the adoption a permit is completed in the presence of the Adoption Committee by the person adopting the animal. This permit is later sent to the Department of Fish and Game in Sacramento.

We try to satisfy most requirements of people as to size and sex of the tortoise they request—but not always. One boy requested 2 female tortoises, one of whom had to be pregnant. This requirement we could not guarantee.

While we are in sympathy with all programs regarding the welfare of the desert tortoise, we believe the Captive Adoption Program helps to assure the health and longevity of *Gopherus agassizi*.

3245 Military Avenue
Los Angeles, California 90034

Special Report - California

Desert Tortoise Preserve Committee

Elizabeth W. Forgey

The Desert Tortoise Preserve Committee welcomes this opportunity to present a report at this second annual meeting of the Desert Tortoise Council, for it has been an effectual and productive year for the Committee. But first, a brief summary of the group's commitment is in order.

The Committee, now a 16-member group, was organized 2 April 1974, just 3 years ago, to establish a preserve as a natural area on the Mojave Desert in eastern Kern County for the protection and welfare of the desert tortoise. Additional goals were to raise funds for the purchase of private land, to purchase fencing for the area, and to develop public use facilities. Coupled with the Committee's goals was its undertaking to publicize uses of the preserve, and to give the public an understanding of the desert tortoise in the wild.

This reporter noted at the 1976 Desert Tortoise Council Symposium that on 22 March 1976 the Committee had received the contract from the Bureau of Land Management to develop recommendations for interpretive facilities and structures on the preserve/natural area and to propose locations for same; to lay out nature trails and parking areas; to develop a long range plan for a road system in the natural area; to design a natural history brochure and natural history summary pamphlet and general use pamphlet; to prepare the interpretive material for the interpretive centers; and lastly, to submit slide programs for elementary, general, and special interest groups.

That was a large order for a 16-member committee. Suffice it to say, the past several months have been studded with activity. But there were other stellar events occurring almost monthly. The appropriation received by the Bakersfield office of the Bureau of Land Management early in 1976 benefited the Committee in that the group will receive $9,500 for developing the Interpretive Contract. Then in April, the Bureau of Land Management purchased 45 kilometres [= 28 miles] of fencing material, and reported at the August meeting of the Desert Tortoise Council held in Baker, California, that the fencing construction contract had been let for February of this year. This freed the Desert Tortoise Preserve Committee of the fencing responsibility, allowing it to focus on the critical task of acquiring land within the preserve boundaries.

This was perfect timing, for in July a special meeting of the Committee was called to meet with a Western Regional representative of The Nature Conservancy to discuss the advantages of becoming a Project Committee of The Nature Conservancy to expedite land acquisition. This was a landmark decision to be affiliated with, and have the expertise of, this national conservation organization

Female Desert Tortoise by a Desert Candle (a food source), Desert Tortoise Natural Area, California

Photo by Beverly F. Steveson

whose objective is to preserve and protect environmentally significant land and the diversity of life it supports. So now the Committee is under the wing, so to speak, of the prestigious Southern California Chapter of The Nature Conservancy. To date 65 hectares [= 160 acres] of private land have been purchased at a cost of $14,600, and the Committee has transferred an additional $23,000 to the Conservancy account for land acquisition.

This past November there was more good news, at which time BLM distributed their El Paso Management Framework Plan. It was stated that the preserve, 80 square kilometres [= 31 square miles] in size when the Desert Tortoise Preserve Committee was formed, had been expanded to approximately 98 square kilometres [= 38 square miles]. Also, pending acquisition of 7.8 square kilometres [= 3 square miles] of private land, a critical 13 square kilometres [= 5 square miles] on the northeastern edge of the preserve would be considered for inclusion. This area, aside from having worthy natural values, is desperately needed as a buffer zone between the preserve and the nearby Rand open area, an intensive off-road vehicle use area. The 65 hectares the Committee has acquired is in the 7.8 square kilometre section mentioned above, and BLM is negotiating land exchanges in the remaining 2 parcels.

The Committee has addressed its objective of educating the public in several ways. The Program Chairman traveled nearly 6,400 km [4,000 mi.] in the past year to present the Desert Tortoise Preserve slides to over 3,000 viewers. During the spring months of 1976, 6 organizations were given guided tours of the preserve. (Because it was a poor year due to the dry season, the Committee did not encourage tours.) Another 10,000 brochures were printed and distributed, and now have a fund-raising products insert.

There was sparse publicity for several months, the Committee not being endowed with a member versed in journalism. However, when an unauthorized and inaccurate article appeared in a turtle and tortoise oriented publication in the Bay Area and was repeated in a conservation leaflet for western readers, the Committee was aroused and a spark was drawn in several members to remedy the situation. As of this writing, the Committee's efforts to protect the tortoise and bring to fruition the tortoise preserve/natural area has received excellent publicity in several conservation magazines, periodicals, Ecology Forums in newspapers, 2 feature articles in San Diego daily papers, a "story" in Desert Magazine, and a feature article in the Los Angeles Times. And lastly, the Committee's historian prepared a 3-page history delineating the group's activities and accomplishments from the time of their organizational meeting through January 1977. Several hundred of these brief histories have been distributed, and a supply is on hand at this symposium for all who would be interested in a copy.

Inasmuch as the deadline for the Interpretive Contract proposals is at hand, making this a total-involvement situation for the Committee at the time of this writing, this reporter is prompted, in closing, to list the subjects that will be depicted on each of the 8 panels of the principal interpretive structure:

Panel 1)	A distribution map of the desert tortoise in the Southwest, and more specifically the Mojave Desert, with densities color-coded and a legend on the rationale for the Preserve
Panel 2)	The life cycle of the tortoise with drawings (by a Committee artist) tracing the life span
Panel 3)	Seasonal activities
Panel 4)	Daily activities
Panel 5)	Spring wildflowers and favored foods of the desert tortoise
Panel 6)	Some reptiles of the Natural Area
Panel 7)	Some birds and mammals of the Natural Area
Panel 8)	Conservation problems of the desert tortoise.

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State Report - California

James A. St. Amant
Department of Fish and Game

California discovered when it started to develop a desert tortoise program there were two "populations" to manage: captive tortoises and wild tortoises.

The captive tortoise program developed due to increased enforcement of the then existing regulations and the addition of new regulations. The main intent of the regulations is to assist in reaching the same goal as the Desert Tortoise Council: To maintain viable desert tortoise populations in its native range. More specifically, the regulations are directed to prevention of tortoise collecting from the wild, without preventing people from possessing legally acquired animals—consequently, the permit system. At this time last year 4,406 permits had been issued. The number issued is now 8,290. A big portion of these now are tortoises hatched in captivity. Although we believe there are still a number of unregistered captive tortoises, there is a definite increased awareness by the public of the regulations; mainly, that it is illegal to collect tortoises from the desert.

As a result of our regulations, we did have a number of tortoises turned in to the Department. We now have a program to handle these unwanted captives. We have found that survival of captive tortoises released directly to the desert is very low. In addition, there is a threat to wild tortoise populations by introducing diseased or exotic species, and overcrowding populations that may already be under stress.

The Department, working with the Desert Tortoise Council, has a program for acclimating captive tortoises for eventual release to the desert.

Tortoises turned in are taken to our field station at Chino for identification and are checked for tagged individuals. The desert tortoises, *Gopherus agassizi*, are then transported to holding pens at the Palm Desert Living Preserve (Quarterway House). Here, diseased tortoises are quarantined and treated under a veterinarian's supervision. Those invididuals that appear healthy are placed in a fenced enclosure for additional observation. At this point the de-programming of domestic behavior of the tortoise begins. This includes attempting to reduce association with humans to a bare minimum, limiting contact to viewing them from a distance. It also includes a reduction in availability of water and the changing of diet from lettuce-type foods to desert vegetation. We believe this de-domestication program is necessary if tortoises released back to the wild are to survive.

Following a suitable observation period at the Quarterway House, the tortoises are then moved to the Halfway House at Fort Soda for further adjustment to desert living. After a full year at this site, they will be released back to the wild. Only those that are in good health will be selected for release. We plan to include X-raying as part of the physical examination. The first "graduates" completing the course will be released this spring. Dr. Glenn Stewart is directing this study.

In addition to this study to obtain additional data on survival of released captives, areas where tortoises have been released in the past will be investigated. This includes Anza-Borrego State Park and Joshua State Park.

As with other state fish and game agencies, our Department is funded mainly by the sale of hunting and fishing licenses and, therefore, is severely limited in funding and manpower. Recently some additional funding has been made available to work exclusively with nongame species. Although most attention must be given to species that are now on either the federal endangered or threatened list or the state rare and endangered list, some funding is available for inventory of other nongame species such as the desert tortoise. What this means is manpower assistance will be given to our area biologists to conduct surveys to determine more accurately the status of our desert tortoise populations. Cooperating with state and federal land management agencies, we will work toward suitable habitat protection.

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State Report - Nevada

Richard E. Enriquez
Bureau of Land Management

Preliminary inventories have begun on the tortoise populations in southern Nevada.

A survey was conducted on a population found in the Coyote Springs Valley which is 88 kilometres [= 55 miles] northeast of Las Vegas. This area lies within the Caliente Planning Unit, which is scheduled for the District's first grazing impact statement.

Objective. To check for possible locations of winter dens by concentrating on walking washes with relatively high banks of consolidated gravels. Also to derive an indication of a crude density estimate of tortoise, if possible.

Coyote Springs Valley, Lincoln County, Nevada. The habitat is variable having washes, gently rolling hills with desert pavement and scattered rock.

Vegetative cover consists primarily of creosote bush, *Larrea divaricata*; burrobush, *Ambrosia dumosa*; globemallow, *Sphaeralcea ambigua*; desert trumpet, *Eriogonum inflatum*; filaree, *Erodium cicutarium*; and cheatgrass, *Bromus tectorum*.

Date: 23 February 1977. Time walking and recording burrows - 4 hours. Number of good burrows located was 18. Collapsed and/or excavated (by predators) was 11, 6 of which were probably used this winter. Density of burrows calculated at 4.5 burrows per hour.

One tortoise was found in a burrow and was measured. Measurements of the tortoise were 80-61-32 mm. The tortoise was also marked with the number 350. The tortoise was located in burrow facing in. Burrow was 40 cm long facing south under dead *Larrea* at base of gentle sloping NE bank of wash. The tortoise had 6-7 growth ridges with the last 2 being wider than the others. Betty Burge did the notching and she also took photographs.

The topography and suitability of burrow sites is quite similar to Betty's study area (Arden Study Area).

Rough estimate of tortoise density may be indicated by comparing rate of sighting burrows at this site to Betty Burge's rate at her study area where study was concentrated over 1½ years. On the first transects of Arden Study Area:

1) Sample size 73 cumulative hours 433 burrows found— calculated at 6 burrows per hour

2) Tortoise density calculated at 45 per square kilometre [= 117 per square mile].

My thanks to Betty Burge for devoting her time to helping me make this preliminary inventory.

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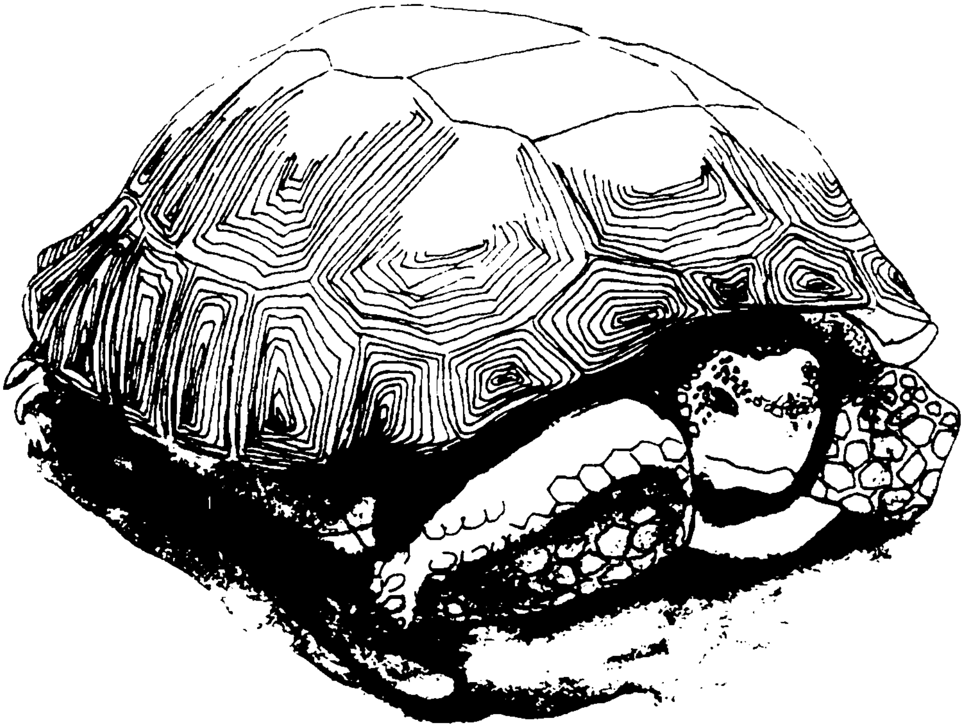

State Report - Nevada

Paul Lucas
Department of Fish and Game

Nevada Law and Regulation

Nevada law and regulation remain the same as reported last year. The captive tortoise question remains unanswered. A proposal that would allow for possession of tortoises presently in captivity but strongly discourage future capture is being worked up by biologists and enforcement personnel for administrative consideration. Our proposal is being patterned after California's system. If the proposal is determined to meet Department needs adequately, additional input will be obtained before any new regulations are established.

Maximum protection of viable wild populations remains the Department's main goal.

Biological Surveys

The lack of data on desert tortoise distribution, status and trend in Nevada has been the biggest problem in establishing an adequate program. The Department's nongame program still has only 2 people. Emphasis continues on raptors because of the numerous species in the group, their relationship in the food chain and their ability to act as indicators of environmental health. Limited funding has been allocated this year from an over-stressed budget to gather tortoise data, but funding from additional sources will be necessary before intensive inventories can be conducted.

An early May survey is planned for the Flat Top—Mormon Mesa area in an effort to collect more data on the Beaver Dam Slope population. A Bell 47G3B1 helicopter will be tested for use in delineating distribution and key use areas. If found feasible, the helicopter could become a valuable tool for some aspects of desert tortoise censusing. We have determined from other wildlife surveys that the helicopter is much faster and usually cheaper than ground coverage. It will be quite a job to survey all the desert tortoise habitat in Nevada.

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Report of Nevada *Ad Hoc* Committee

E. C. Thoemmes, Chairman

At its June 1976 meeting, the Council, at the request of Nevada members, appointed an *ad hoc* committee to assist Nevada State Department of Fish and Game in formulating and implementing a species management plan for the desert tortoise in Nevada. As part of its supportive role, this committee could assist in the identifying and inventorying of wild populations, could help educate the general public to leave wild tortoises in the wild, could bring pressure on the state legislature to set aside funds for the establishment of desert tortoise preserves, and could educate citizens in the conservation of the tortoise.

Also effected at the June meeting was the acceptance by the Council of a draft version of a letter, prepared by the Nevada members, to be sent by the Co-Chairmen, to the Director, Nevada State Department of Fish and Game. In this letter, which was mailed 20 August, the Council recommended that Fish and Game begin studies on the desert tortoise, leading to the formulation of a species management plan. Inventory of wild populations in order to identify portions of tortoise habitat in need of protection was of special concern. In addition, the letter advocated the hiring of additional nongame biologists within the state. It further emphasized that tortoises currently being held in captivity should be given legal status, perhaps by means of a permit system with Fish and Game having the right of inspection. The granting of such legal status would also permit citizens to proceed openly to find new homes for captives whose owners could no longer keep them. The letter promised that the Council's *ad hoc* committee would work with Fish and Game to create public support for these goals.

The answering letter from Fish and Game was received on 3 September. The Council was informed that Fish and Game had only $2,500 in its budget to use in acquiring information on the distribution of the desert tortoise in the state. It concurred in the need for some change in the legal status of the captive tortoises and in the need for education of citizens; however, since implementation required money, the agency could foresee no definite timetable for carrying out these desirable goals.

Meanwhile, Nevada State Fish and Game corresponded with representatives of the California State Fish and Game, asking about California's experience with the permit system for captives.

The *ad hoc* committee discussed various possibilities for immediate action. One suggestion was to invite prominent citizens to form a "Committee for the Conservation of the Nevada Desert Tortoise." This committee would then bring political pressure on individual members of the state legislature during the upcoming session to fund studies leading toward the desired species management plan, to fund the hiring of nongame biologists and to alter the current wording of the law so as to recognize and distinguish the large captive tortoise population in the state.

In November, members of the ad hoc committee met with representatives of Fish and Game. Various alternatives to a permit system were discussed. These ranged from simply removing the tortoises from the "Protected-Rare" category to a possession system which might tie the number of tortoises held in a given household to the number of persons residing in that household. Another possibility was that the Commission could make a change in its own regulations to legalize the holding of tortoises which were already in captivity and to distinguish them from those presently in the wild.

Members of the ad hoc committee, after the November meeting, were left uncertain as how best to proceed. It seemed inadvisable to contact a legislator and attempt to have him introduce a bill in the upcoming session when we could not be sure that Fish and Game would like to have in the bill.

As of the first of January 1977, the ad hoc committee is continuing to accommodate those tortoises which are handed over to Fish and Game either by individual owners who no longer want them or by persons who find them wandering in the streets. Members have had to house these animals in their own yards and have been forced to accept numbers of these animals, way in excess of the carrying capacity of their yards. As a result, a very high percentage of these animals have succumbed to a respiratory infection, due probably to the stress associated with overcrowding. As long as possession of the captives is illegal in the state, the committee cannot openly advertise for persons willing to take these animals into their homes. Consequently the high death rate is likely to continue.

The legislature met in January, but the plight of the desert tortoise was not brought to its attention. Citizens of Nevada desiring to support the desert tortoise will apparently have to wait another 2 years until the next session of the legislature.

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State Report - Utah

Dale K. Arhart
Bureau of Land Management

Last year the Bureau of Land Management financed studies of desert tortoises and other species on the Beaver Dam Slope and other portions of Washington County. The Utah Division of Wildlife Resources carried out the studies under contract for BLM.

We have just recently received a rough draft of the written report. I'll limit my discussion to some general comments about the study. Eric Coombs, who did most of the work for the Division of Wildlife Resources, will be discussing some of the findings in greater detail later in the agenda.

The study gave us a good picture of our tortoise population in terms of total numbers, age and sex classification, and geographical distribution.

One of the goals of the study was to define the food habits of the Beaver Dam Slope population to better understand the relationship between tortoises and livestock use. In this regard the study was only marginally successful.

To augment the data from our contracted study, we, that is the BLM, began some fecal analysis studies of both tortoise and cattle fecal samples from the Beaver Dam Slope. We send the samples to the Composition Analysis Laboratory at Colorado State University where they are analyzed microscopically at 100-power magnification.

Because we decided to start the fecal analysis studies so late in the '75-'76 grazing season, we were unable to collect seasonal samples. We collected only 1 set of samples at the end of the grazing season from each of 3 of the major tortoise denning areas.

Each of the tortoise scats was examined separately, but the cattle samples were analyzed as composites consisting of at least 25 subsamples. Twenty-five tortoise scats from each of the 3 areas were analyzed.

The analyses indicated that the tortoises rely primarily on *Erodium cicutarium* and grasses, including annual *Bromus* species, *Tridens pulchellus*, and some *Stipa*. In all, 16 species of plants were found in the tortoise scats.

Similarity indices comparing cattle diets to tortoise diets in each area indicate dietary overlaps of 34 to 40%.

These figures, of course, must be used cautiously, especially because we did not sample seasonally. It is possible that the similarity indices are much different in certain seasons than our samples indicate.

During the '76-'77 grazing season we collected fecal samples from cattle seasonally. We do not have the results yet, but hope we will get better data on seasonal use by cattle.

We hope to have more tortoise scats analyzed this year also, but unfortunately we are not sure we can find sufficient tortoise scats for seasonal sampling. Every tortoise scat found was collected last year so, if suitable samples can be found this spring, perhaps we can at least get a good spring sample.

In addition to the studies, we have some significant changes in management of the Beaver Dam Slope to report, plus an update on the status of the Livestock Grazing Livestock Impact Statement covering that area.

The BLM's Dixie Resource Area Manager from St. George, Mr. Frank Rowley, will discuss these topics.

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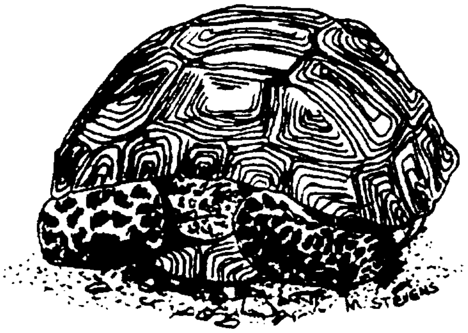

State Report - Utah

Frank Rowley
Bureau of Land Management

General Description. The desert tortoise *(Gopherus agassizii)* in Utah is located in the southwest corner of the state in the area known as the Beaver Dam Slope. This area is approximately 180 square kilometres [= 70 square miles] in size. The vegetative aspect for the area is a Joshua tree-creosote bush type with a variety of annual forbs and grasses.

Hot Desert Grazing Environmental Statement. A draft report for Chapters 1 and 2, description of the existing situation and description of the existing environment, is complete.

Chapters 3, 4, and 5, which anlyze associated impacts, mitigating measures, and adverse impacts which cannot be mitigated, is currently being worked on.

The preliminary draft is scheduled to be completed by 15 June 1977. Final environmental statement for public review will be completed and published this fall.

Proposed Management of Desert Tortoise Area. An allotment management plan has been developed for the desert tortoise area. The grazing system is a three-pasture rest rotation, modified to mitigate heavy cattle concentrations and limit competition for green forage during the spring grazing period. This plan covers the entire desert tortoise area on the Beaver Dam Slope.

Two management areas have been established for the desert tortoise with Highway 91 acting as the division line. The area west of Highway 91 will be managed for multiple use purposes, but with the following stipulations:

1) Cattle grazing will continue, but under the guidance of an allotment management plan.
2) Vehicle use will be restricted to existing roads and trails.
3) Oil and gas exploration or development work will not be allowed between 1 April and 1 November.
4) No surface disturbing activities will occur within 150 metres [about 500 feet] of winter dens.
5) Sheep trailing through the tortoise area will be eliminated.
6) Removal of predators from active denning areas will be recommended to the Fish and Wildlife Service for control work.

In addition to the above stipulations, an interim management stipulation for grazing will be required until the allotment management plan can be implemented. This additional stipulation requires the removal of cattle from the area by 15 March.

Management of the area east of Highway 91 will be multiple use management except for the proposed Research Natural Area which will restrict some uses. This proposal includes an addition of approximately 1,200 hectares [about 3,000 acres] to the existing Joshua Tree Natural Area, making the size of the total area approximately 1,600 hectares [about 4,000 acres]. It will also include the Hardy-Woodbury "tin can" study area. The area will be established as "The Woodbury Desert Study Area," with the following restrictions being placed on the area:

1) Elimination of livestock grazing
2) Withdrawal from mineral activity
3) Vehicle use restricted to designated roads and trails
4) No removal or sale of vegetative products
5) Prohibit rights-of-way, etc., in the area
6) Fencing the area
7) Establishment of base-line studies for both wildlife and vegetative species for a comparison with the multiple use management area west of Highway 91.

Managers in Utah feel that they have been responsive to the problems and needs of the desert tortoise. We want to thank you for the opportunity of outlining our management objectives.

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Native Animal Habitat Protection: A Solution Becomes a Problem

Peter G. Sanchez

Burros, *Equus asinus*, compete with native animals for food, water, and space. Changes in native plant community composition are occurring and may threaten rare and endemic species of plants and animals. Soil erosion resulting from tracking and trailing is locally severe. Disturbances have degraded springs and water holes. Burros range over 2,070 km^2 [= 512,000 acres] within Death Valley National Monument and number 1,600 animals. Unless controlled, impacts by feral burros will result in the continued decline of native species and the alteration of natural habitats, which national parks are mandated to protect. There are few technical difficulties involved in managing burros; obstacles to ecologically sound management are sociopolitical. United States National Park Service habitat management problems and efforts to control burro impacts in Death Valley are discussed.

The burro *Equus asinus* ranks with the House Sparrow and Starling as one of the most successful introductions of exotic species into North America. Most free-roaming burros are descendants of pack animals abandoned by prospectors and miners during the heyday of mining activity in the late 1800s and early 1900s (Hansen, 1973). The burro (a native of Africa) is preadapted to a desert climate and terrain, and has no natural predators or diseases capable of controlling its numbers. Largely because of their legal status as a protected species, burros are increasing in numbers and range throughout the Southwest. Finding an acceptable remedy to burro overpopulation has become a problem.

The impact of burros on the desert—mountain ecosystem of Death Valley National Monument has been known for more than 40 years (Sumner, 1959). Studies stress the competitive nature of burros toward native species for food, water, and space. It has been estimated that burros in Death Valley consume ≈ 6,600 kg [= 14,500 lb] of forage daily or ≈ 2,408,000 kg [= 5,310,000 lb] per year (Sanchez, 1974). Prior to introduction of burros this vegetation was available to native wildlife and as soil-stabilizing cover.

Changes in the plant community are occurring. Grasses are the first species to decline on burro ranges because grasses are a preferred diet item of burros (Hansen, 1973). In areas of Death Valley used by native animals (but not by burros), native grasses, chiefly Indian ricegrass *Oryzopsis hymenoides*, desert speargrass *Stipa speciosa*, and galleta grass *Hilaria jamesii*, are abundant. Native grasses on burro range are overgrazed and locally absent (near springs).

Burros expanded their range onto the floor of Death Valley in 1969. Within 5 years ≈ 80% of the alkali sacaton grass *Sporobolis airoides* at Eagle Borax historic site was cropped to root level by herds of up to 50 burros. A portion of Eagle Borax Spring and nearby Tule Spring was fenced in January 1976. One year after fencing the enclosure, grass clumps not completely killed sprouted and produced seed.

Other indications of burro impact on vegetation can be seen in Wildrose Basin, an area formerly used by 75 to 180 burros. A burro exclosure was built in February 1972 3.2 km east of Wildrose Spring at an elevation of 1,463 m in the goldenhead—spiny hopsage *(Acamptopappus—Grayia)* community. Sampling of vegetation in 1973 and 1974 showed differences in plant density and biomass on transects inside and outside the fenced exclosure (Fisher, 1974).

As expected there was a slight increase in plants within the exclosure. Native grasses remained low inside the exclosure and were absent outside. Outside the exclosure Anderson thornbush *Lycium andersonii* and blackbrush *Coleogyne ramosissima*, not a preferred burro browse species, increased in numbers. Shockley goldenhead accounted for 24% of total plant volume and > 50% of the total number of perennial plants inside the exclosure. Outside the exclosure goldenhead declined from 47% of the total number of plants to 20%. Results indicate changes in plant community composition are occurring with certain shrub species being preferentially removed (Fisher, 1974).

Vegetation changes probably would have been greater if burro use had not been curtailed. During this period burros were removed from Wildrose Basin by 2 methods: (1) burros were trapped and distributed as pets to California permit holders (under this program 161 animals were removed—47 in 1973 and 114 in 1974); and (2) access to water was restricted by closure of a part of Wildrose Spring, causing 50 to 60 burros to disperse out of the basin.

Relict plants may be affected by burros. Trampling may be the cause of low reproduction among bristlecone pines *Pinus longaeva* above 3,000 m on Telescope Peak in the Panamint Mountains (L. Johnson, *personal communication*). Concern has been expressed about the survival of other relict or rare species of plants which inhabit burro ranges. In Death Valley National Monument alone, there are 20 endemic plant species; 12 of these have very limited distribution and 6 of these occur within burro range.

There are 51 species of native mammals within the Monument. Four species or subspecies of mammals are endemic and share habitat with burros. These are the Panamint chipmunk *Eutamias panamintinus*, pigmy pocket gopher *Thomomys umbrinus oreocus*, Panamint pocket gopher *Thomomys umbrinus scapterus*, and the Panamint kangaroo rat *Dipodomys panamintinus panamintinus*.

Of the 38 species of native reptiles and amphibians in the Monument, 1, the Panamint alligator lizard *Gerrhonotus panamintinus*, is rare and occurs on burro range. The desert tortoise *Gopherus* *agassizi* occurs in very small numbers. The impacts of burros on these animals have not been studied.

New endemic species continue to be discovered. Aquatic mollusks are an example. Of the 15 species of mollusks known from the Death Valley area, 2 are new genera and 12 are new species, yet undescribed (Landye, 1973). Two new species were discovered in 1975 (J. J. Landye, *personal communication*). To date ≈ 4% of the nearly 300 springs in the Monument have been examined. Only 1 spring used by burros has been studied and it was found to contain an endemic snail. Threats to aquatic invertebrates include changes in water turbidity by trampling, changes in water chemistry by the addition of urine and feces, and alteration of the substrate.

Environmental alteration is severe at and near springs because burros tend to congregate around water holes. Soils are trampled and plants are broken or absent. Ponded springs are polluted with urine and feces. Contamination of water by burros does not preclude use by large animals such as bighorn but does severly limit hikers' and backpackers' use of large areas of Death Valley because drinking this water is unsafe and objectionable.

Burros usurp available water at the expense of native wildlife. Many springs go dry or nearly dry in summer; summer is the time of stress in the desert. One of the main factors attributed to the decline of bighorn in Death Valley is the competition for available water.

Experiments aimed at reducing competition for water between bighorn and burros are underway. The surface flow of Quartz Spring in the northern Cottonwood Mountains ceased more than a decade ago. A collection box, buried pipeline, and storage tank were constructed to store and deliver water to wildlife. Burros began to displace bighorn at the spring and twice severed the pipeline. In 1975 the spring was fenced to exclude burros but allow bighorn to enter the fenced area and drink. Fence rails are spaced to permit bighorn to go under the fence or between the rails. Iron pipes (5.08 cm diameter) are used to prevent burros from riding down the rails. An alternate design, using smooth wires with the same spacing as the rails, is being tested at Eagle Borax site.

In the 1930s, bighorn were regularly seen watering at many springs (Sumner, 1959). Since the proliferation of burros, bighorn have disappeared from some springs in the Cottonwood and Panamint mountains. Bighorn fed and watered in Butte Valley in the early 1930s; by 1935 herds of more than 200 burros displaced the bighorn (Sumner, 1959). Cottonwood Spring and smaller springs in the upper Cottonwood drainage basin are used by at least 203 burros. At least 273 additional burros range northward from the Cottonwood basin, according to a 1975 census. One hundred twenty-five bighorn also share this space but in recent decades have not been using Cottonwood Spring, the largest in the area (Hansen, 1972).

Animals must travel frequently to drink at springs and just as regularly move away to feed and seek shade or shelter from storms.

The results of the two-way traffic are obvious landscape features. Burro trails give hillsides a terraced appearance reminiscent of Oriental rice paddies. Trailing on steep hillsides is accelerating soil loss by water and wind erosion. Thousands of acres in the Panamint and Cottonwood mountains are terraced. Trailing is severe on the Naval Weapons Center southwest of Death Valley and elsewhere in the Southwest.

Entire ecosystems—soils, water, plants, and animals—are being altered. This is occurring in units of the National Park System (Death Valley, Grand Canyon, Lake Mead, Bandelier) which were established to retain representative areas of primitive America and to be sanctuaries for indigenous forms of life.

There are 1,600 burros in Death Valley National Monument which range over 2,070 km^2 [= 512,000 acres or 800 square miles], chiefly on the western side of Death Valley.

Reduction of burros in Death Valley began in 1939. At that time the population was 1,500 animals and their range included mountainous areas on both sides of Death Valley. By 1942 all burros were removed from the east side of the valley and the remaining population was 700. Burro removal continued with variable intensity until 1968. Between 1939 and 1968, 3,578 burros were removed from the Monument and may have been as high as 4,130 if unrecorded trapper reports are added (Hansen, 1973). By 1972 burro numbers had again risen to 1,500 with most of the animals concentrated on the western side of the valley. Live trapping of burros resumed in 1973 as an interim control measure and to date (March 1977) 199 burros have been removed.

The U.S. National Park Service requires each of its parks and monuments to prepare a management plan to perpetuate its natural resources. Prior to Death Valley's plan preparation and in accord with National Environmental Policy Act of 1969 guidelines, an environmental assessment was prepared in 1976 (NPS, 1976). Public workshops were held in 3 cities and about 700 copies of the environmental assessment and companion workbook were distributed. The assessment discussed 38 alternatives pertaining to natural and cultural resources and research. Ten alternatives discussed management of burros. The alternatives listed possible solutions developed by the agency and received from the public at informal discussions, field trips, and letters from 1971 to 1976.

Most of the public interest centered around what to do about burros. The assessment explained National Park Service policies and objectives which serve as the guidelines for management of Death Valley.

Nationwide NPS policy (NPS, 1975) regarding exotic plants and animals is as follows:

> "Natural Zones—Plant and animal species, non-native and exotic to a park, may not be introduced into natural zones.

> "Historic Zones—In historic zones, exotics that are a desirable part of the historic scene may be introduced and maintained.
>
> "Control of Noxious or Exotic Species—Control or eradication of noxious or exotic plant and animal species will be undertaken when they are undesirable in terms of public health, recreational use and enjoyment, or when their presence threatens the faithful presentation of the historic scene or the perpetuation of significant scientific features, ecological communities, and native species, or where they are significantly harmful to the interests of adjacent landowners. Care should be taken that control programs do not result in significant damage to native species."

Death Valley National Monument is classified as a natural zone containing local historic sites.

Death Valley resources management objectives are as follows:

1) To maintain, preserve, and perpetuate the aesthetic setting and the natural and cultural resources of Death Valley National Monument

2) To restore conditions conducive to the perpetuation of the natural processes as they functioned before disruption by technological man or competition from non-native plants and animals

3) To restore native plants and animals to their original range

4) To restore to natural appearance the land surfaces disturbed by man, recognizing that significant cultural values must be preserved

5) To ensure perpetuation of rare and endangered plants and animals and those species endemic to Death Valley National Monument

6) To perpetuate the Devils Hole pupfish in the detached Devils Hole section of the Monument

7) To minimize the adverse effects of mining and prospecting that conflict with the preservation and public appreciation of natural and cultural values

8) To develop and execute continuing research programs for natural and cultural resources.

Environmental workbook public responses (n=241) generally agreed with the stated natural resources objectives (Table 1).

TABLE 1. Public responses to Death Valley resources management objectives (percent of 241 responses checking workbook boxes)

Management objective*	Fully agree	Partially agree	Disagree	Not concerned	Not checked
Aesthetic setting	85.9	13.7	0.0	0.0	0.41
Natural processes	63.9	28.6	6.2	0.0	1.20
Restore nature	65.6	31.1	2.5	0.0	0.83
Disturbed surface	61.4	31.9	5.8	0.0	0.83
Rare plants and animals	84.2	13.7	0.41	0.0	1.70
Devils Hole	83.8	7.4	3.3	2.5	2.90
Mining effects	78.8	14.1	5.4	0.0	2.50
Research	79.3	15.7	2.1	0.83	2.50

*See text for full statement of objective.

Burro management alternatives discussed in the environmental assessment (NPS, 1976) are:

1. No action. Nothing will be done to manage burro populations.
2. Control the feral burro population. Elimination of feral burros by trapping and relocation of animals in the care of persons willing to care for them as pets or pack animals.
3. Control the feral burro population. Elimination of feral burros by live trapping and killing by professional recommended humane pharmacological agents.
4. Control the feral burro population. Elimination of burros by shooting with rifles by qualified National Park Service personnel.
5. Control the feral burro population. Elimination of burros by shooting with capture gun and immobilizing drugs by qualified National Park Service personnel.
6. Disposal of carcasses. Carcasses will be left to recycle in the natural environment.
7. Exclusion of feral burros. Fence portions of the Monu-

ment boundary to prevent re-entry of burros. Includes internal drift and barrier fences.

8. Retention of managed burro herds. Burro populations would be reduced in number but not eliminated. About 150 burros would be maintained in number but not eliminated. About 150 burros would be maintained throughout areas where they are now present. Increases will be controlled by removal of excess animals on a continuing basis.

9. Retention of managed burro herds. Establish a burro viewing area in Wildrose basin containing a managed herd. Remove and exclude burros from other areas of the Monument.

10. Control of feral burro population. Sterilize burros to eliminate annual population increment and allow natural attrition to reduce burro populations.

Workbook responses (*n*=214) are listed in Table 2.

TABLE 2. Public responses to burro management alternatives (percent of 241 responses checking workbook boxes)

Alternative*	Select	Reject	Undecided	Modify	Not checked
No action	2.1	89.2	1.7	2.5	4.6
Trapping	28.1	39.3	2.1	26.4	4.1
Live trap/ euthanasia	24.1	50.2	4.1	15.4	6.2
Rifles	52.7	25.3	6.2	11.2	4.6
Capture gun	19.1	52.5	7.9	13.2	7.4
Carcass disposal	50.6	15.4	6.2	21.9	5.8
Fencing	42.3	41.5	5.4	7.5	3.3
Retention of managed herd	24.5	59.7	3.7	9.5	2.5
Viewing area	20.6	57.4	13.2	5.8	2.9
Sterilization	13.3	73.8	3.7	3.7	5.4

*See text for full statement of alternative.

Numerous respondents recommended modifications of the listed alternatives. Suggested was a combination of burro reduction methods, specifically, removal by live trapping and shooting the remainder which cannot be trapped.

Grand Canyon National Park announced a plan to eliminate burros in February 1977. Public reactions to the plan were immediate, numerous and largely opposed to removal of burros. On 4 February 1977, three organizations filed jointly for an injunction to stop implementation of the announced plan to shoot burros. (The plan was withdrawn pending completion of additional research and preparation of an environmental impact statement.)

Reasons given for wanting to retain burros in the national parks are (1) the animals are innocent and have a right to live, (2) they are a symbol of the Old West and to some have a religious importance, and (3) they are a vanishing species. The public seems to be unaware of the provisions of the Wild Horse and Burro Act of 1971 (Public Law 92-195), which protects animals on hundreds of thousands of acres of federal lands administered by the Bureau of Land Management and the Forest Service and mandates these agencies to manage herds.

Because national parklands were established for a single purpose, "...which purpose is to conserve the scenery and the natural and historic objects and the wildlife therein..." (NPS Organic Act, 1916) the National Park Service was not included in the text of P.L. 92-195. Inclusion would make difficult if not impossible the Congressional mandate "...to provide for the enjoyment of the (parks) in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." (NPS Organic Act.)

It is the impairment of natural ecosystems that concerns park managers and some of the public. There are many factors, all directly or indirectly man-caused, which have been or are degrading the integrity of national parks and monuments. The uncontrolled impacts of feral animals is but one factor. The concept of preservation of a total environment, opposed to protection of an individual feature or species, is a distinguishing feature of national park management.

The search for a viable alternative, ecologically beneficial and publicly acceptable, continues. An environmental impact statement is being prepared. To wait it out and let the problem solve itself—by starvation—is unsatisfactory from any viewpoint.

If the animals were feral cows, proposed solutions might be similar but public responses to the alternatives would undoubtedly be different. Facing reality, the fundamental problem is that burros, not cows, have been introduced into a desert ecosystem operating since the Pleistocene without them. In a region of low plant productivity and where water resources are at best limited, the system is unable to absorb the addition of a large herbivore without large scale adjustments.

Overpopulations of large animals have occurred in the United States before and humane control techniques are well known. There are few technical difficulties involved in controlling burro populations. The only real barriers to burro control are sociopolitical ones.

George Laycock, in his book "The Alien Animals", wrote "Too often we ask whether or not the foreign species can live in this country, and too seldom question whether or not native species can live with them." (Laycock, 1970). Until this question is answered by weighing the ecological trade offs required when exotic species are introduced into a natural system, we may find that both the foreign and our unique native species are in trouble.

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The Desert Tortoise in the Late Pleistocene with Comments about Its Earlier History

Thomas R. Van Devender and Kevin B. Moodie

Gopher tortoises separated from their emydine pond turtle ancestors by the early Eocene, but the desert tortoise *(Gopherus agassizi)* and its relatives may have only differentiated in the middle to late Pleistocene. The desert tortoise presently lives in the Mohave and Sonoran deserts from southern Nevada and southwestern Utah, south to northern Sinaloa, Mexico. In the late Pleistocene its range extended from coastal California to southeastern New Mexico. The oldest fossil records for the desert tortoise are 33,590 ± 1500 B.P. (Dry Cave, New Mexico) and greater than 34,000 B.P. (Hueco Mountains, Texas) and are in the northern Chihuahuan Desert. Plant fossils in early Holocene and late Pleistocene packrat middens containing tortoise bones document that it formerly lived in juniper woodland (Arizona and California) and pinyon—juniper woodland (New Mexico and Texas). It became restricted to the Mohave and Sonoran deserts when the modern desert scrub communities formed 8000 years ago.

The desert tortoise *(Gopherus agassizi)* lives in the Sonoran and Mohave deserts west of the Continental Divide. The evolution of these deserts began about Miocene times and culminated in the middle Pliocene (Axelrod, 1950). However, the desert tortoise and its relatives may have evolved as recently as middle to late Pleistocene and are recent invaders of the deserts.

Evolution of gopher tortoises. Gopher tortoises evolved from pond turtles (Emydidae) by the early Eocene (Bramble, 1971). The living gopher tortoises are divided into 2 groups of closely related species. The *Gopherus polyphemus* group includes the Bolson tortoise *(G. flavomarginatus)* of north-central Mexico and the gopher tortoise *(G. polyphemus)* of the southeastern United States. The *G. agassizi* group includes the Texas tortoise *(G. berlandieri)* of south Texas and adjacent Mexico, the desert tortoise *(G. agassizi)* of the southwestern United States and northwestern Mexico, and Auffenberg's tortoise *(G. auffenbergi)* from the late Pleistocene of Aguascaliente, Mexico (Mooser, 1972). Bramble (1971) placed the *G. agassizi* group into the genus *Scaptochelys*, but Auffenberg (1974, 1976) and Van Devender et al. (1976) have not followed him. The criteria for the separation of *Scaptochelys* from *Gopherus* have not been formally published; we will use *Gopherus* in the present paper.

The fossil history of the desert tortoise and closely related species has been interpreted in 2 very different ways. Bramble (1971) derives his *Scaptochelys* in the late Eocene with species present in the middle Oligocene *(Gopherus laticunae)*, Miocene *(G. mohavense = G. mohavetus* in Auffenberg 1974 and Des Lauriers 1965) and middle to late Pleistocene *(G. hexagonata)*. Auffenberg (1974 and earlier) and Williams (1950) view these species as not being in the lineage leading to *G. agassizi* and would derive the desert tortoise group from an unknown middle Pleistocene tortoise. The desert tortoise itself is a late Pleistocene form that appeared long after the deserts it inhabits.

Late Pleistocene desert tortoises. Fossils of desert tortoises have been found in Ice Age [also termed late Pleistocene, Rancholabrean Land Mammal Age, Wisconsinan Glacial Epoch] deposits from as far east as Dry Cave, 24 km west of Carlsbad, New Mexico (Van Devender et al., 1976; Harris, 1970), to as far west as the McKittrick tar pits (L. Miller, 1942) and the Los Angeles Basin (W. Miller, 1971), California. The fossils have been preserved in tar pits, dry caves (Gypsum Cave, Nevada: Brattstrom, 1954; Rampart Cave, Arizona: Wilson, 1942; Van Devender et al., 1977; Schuiling Cave, California: Downs et al., 1959); wet caves (Robledo Cave, Shelter Cave, Conkling Cavern and Dry Cave, New Mexico: Brattstrom, 1961, 1964; Van Devender et al., 1976; Harris, 1970) sedimentary deposits (Los Angeles area, California: W. Miller, 1971), and indurated packrat middens (Arizona, California, New Mexico and Texas: Van Devender et al., 1977; Van Devender and Mead, *in press*; T. R. Van Devender and K. B. Moodie, *personal observations*.) The oldest radiocarbon dates associated with fossil desert tortoise bones are 33,590 ± 1500 B.P. (Tx-1773 on bone carbonates) from Dry Cave, New Mexico (Van Devender et al., 1976) and greater than 34,000 years ago (A-1644 on *Juniperus*) from Navar Ranch No. 1 packrat midden, Hueco Mountains, Texas (T. R. Van Devender and K. B. Moodie, *personal observations*).

Paleoecology. The desert tortoise presently lives in the Sonoran and Mohave deserts from southern Nevada and southwestern Utah, south through Arizona, California and Sonora into northern Sinaloa. The eastern limits of its present range in Arizona are between Tucson and Benson and are coincident with those of several characteristic Sonoran Desert plants including the saguaro *(Cereus giganteus)* and foothills paloverde *(Cercidium microphyllum)*. Western range limits of Chihuahuan forms such as the Texas horned lizard *(Phrynosoma cornutum)* and tarbush *(Flourensia cernua)* are in the same area. The Sonoran Desert generally has mild winters and the eastern limit of the saguaro, foothills paloverde and desert tortoise are probably controlled by winter minimum temperatures. Increases in summer rainfall and decreases in winter precipitation also occur to the east but a similar gradient to the south in Sonora does not limit them.

The late Pleistocene distribution of the desert tortoise extended from farther west in California than it occurs today, eastward to southeastern New Mexico. This includes the present Mohave, Sonoran and northern Chihuahuan deserts and ranges from mostly winter to mostly summer precipitation. The fossil sites for desert tortoises in New Mexico and Texas presently support Chihuahuan desert scrub communities. However, desert tortoise bones, scutes and dung have been found in Ice Age packrat middens with Colorado pinyon *(Pinus edulis)*, juniper (*Juniperus* sp.) and scrub oak *(Quercus pungens)* on Bishop's Cap, New Mexico and in the Hueco Mountains, Texas (T. R. Van Devender and K. B. Moodie, *personal observations*). Only the greater than 34,000 B.P. radiocarbon date previously mentioned is presently available but late glacial ages of ≈ 12,000 B.P. are expected. Plant macrofossils preserved in indurated packrat middens and cave fill deposits in the northern Chihuahuan Desert record a pinyon—juniper woodland at 600-1495 m elevation prior to 11,000 years ago and a juniper—oak woodland until 8000 years ago (Wells, 1966; Van Devender and Everitt, 1977; Van Devender, 1976, 1977).

Today the desert tortoise is restricted to desert scrub habitats in the Mohave and northern Sonoran deserts and thorn scrub in central and southern Sonora and is rarely found in woodland habitats. In north-central Sonora, junipers and oaks enter the desert and grow with saguaros, paloverdes, organpipe cactus *(Lamairocereus thurberi)* and palms because mountains to the north block winter frontal storms and ameliorate winter temperatures. Desert tortoises are common in this "mixed" community and absent from the northern Chihuahuan Desert with its cold winters. Ice Age winters in southeastern New Mexico and Trans-Pecos Texas must have been milder than today without occasional, extremely low temperatures during "blue northers". Bryson and Wendland (1967) suggested that mild winters can be explained as a result of the Arctic air mass being trapped north of the continental glacier. If so, the desert tortoise was probably extirpated from the northern Chihuahuan Desert as the continental glacier melted and allowed Arctic air to move southward.

In Arizona, California and Nevada, fossil packrat middens again record juniper woodlands in areas that are now desert scrub as late as 8000 years ago. As in the Chihuahuan Desert, late Pleistocene and early Holocene desert tortoises were living in xeric woodland habitats. They became restricted to desert scrub habitats in the Mohave and Sonoran deserts as the present desert scrub communities formed 8000 years ago (Van Devender, 1977).

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Status of the Desert Tortoise in the Colorado Desert

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INTRODUCTION

The desert tortoise *(Gopherus agassizii)* is declining throughout its range as a result of habitat deterioration and its popularity as a pet; the species is fully protected by the California Department of Fish and Game. The Bureau of Land Management contracted for a tortoise survey in part of the Colorado Desert as part of the Environmental Impact Statement for the Sundesert Nuclear Project.

METHODS

The survey was conducted during June 1976. Eighty-one transects were distributed mainly around the northern, eastern, and southern perimeter of the Colorado Desert (Fig. 1). Each transect was 2.4 km long and ≈ 15 m wide. Transects were located in presumed suitable tortoise habitat—washes and well vegetated bajadas. Each transect was walked once and all tortoise signs were recorded: live animals, shells, scats, tracks, burrows, and courtship rings.

RESULTS AND DISCUSSION

There are small populations of tortoises scattered throughout the Colorado Desert north and east of the Salton trough (Fig. 1; Table 1). Because transects were deliberately located in suitable-appearing habitat, average densities are probably lower than the figures indicate. Individual transect results are given in Table 2.

The greatest concentrations of tortoises were in the southern bajadas of the Cottonwood Mountains and Chuckwalla Bench. These 2 areas appear to have populations comparable to those in the moderate to good habitats in the Mojave Desert.

Translation of number of burrows into number of tortoises is impossible because little research has been done into the number and depths of permanent burrows that are dug by Colorado Desert tortoises. The Mojave Desert ratio is 1 "deep burrow" (>1.5 m) per tortoise (Kristin Berry, *personal communication*); but in the warmer Colorado Desert it has not been established what constitutes a "deep burrow". Because tortoise activity nearly ceased by June, direct counts were impractical.

Based on this study and numerous incidental observations, the only good tortoise habitat in the Colorado Desert is well-vegetated bajadas, principally those that are dissected by washes. Broad washes appear to be suitable as well. However, tortoises have been found in other habitats, including the edge of the Algodones Dunes and on steep, rocky slopes in the Chuckwalla mountains.

No tortoises were found south and west of the Salton trough; there is no evidence that they have ever occurred there naturally. A number of captives were released in Anza-Borrego Desert State Park, mainly in the early 1970s. No evidence of tortoises was found in the release areas during this survey. The Park has records of several sightings dating back to the 1950s; it is suspected that they were all released animals (Paul R. Johnson, *personal communication*).

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This survey was conducted as part of the Environmental Analysis of the proposed Sundesert Nuclear Project of San Diego Gas and Electric Company. The survey was performed by Marshall Yacoe.

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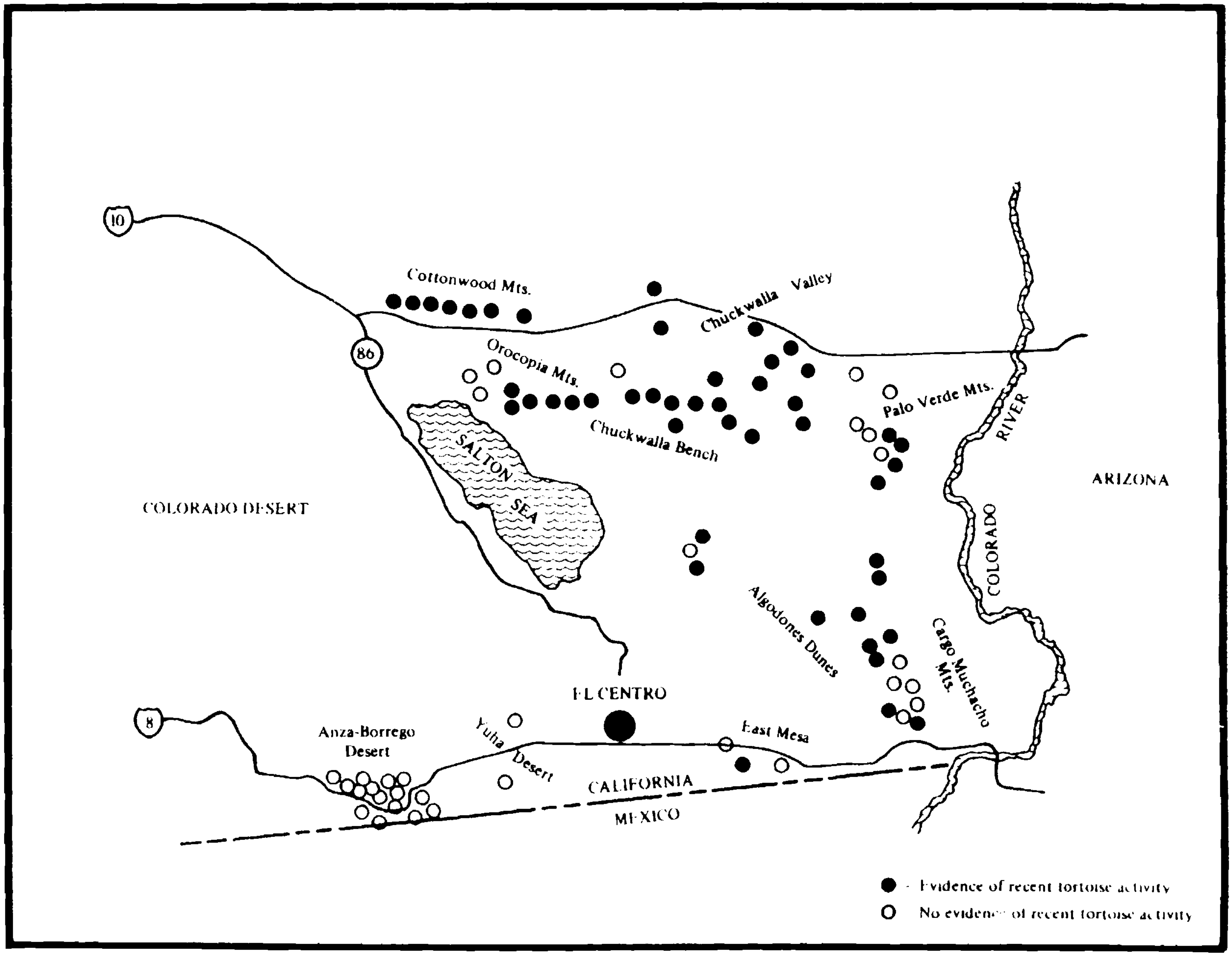

Fig. 1. Locations of tortoise transects in the June 1976 survey.

Table 1. Density of tortoise burrows in selected areas of Colorado Desert. Values are mean number/square kilometre followed by mean no./mi^2 in parentheses.

		Active burrows			Old burrows		
Location	Transects	Total	Deep (> 75 cm)	Shallow	Total	Deep (> 75 cm)	Shallow
Cottonwood Mts.	7	93(241)	50(131)	43(111)	39(101)	12(30)	27(70)
Chuckwalla Valley	9	54(141)	36(94)	18(47)	27(70)	6(16)	21(55)
Orocopia Mts.	5	20(53)	7(18)	14(35)	7(18)	0	7(18)
Chuckwalla Bench	15	82(211)	43(113)	38(99)	34(89)	11(28)	24(61)
Palo Verde Mts./ Milpitas Wash	7	24(60)	16(40)	8(20)	19(50)	0	19(50)
Algodones Dunes	4	20(53)	14(35)	7(18)	0	0	0
Cargo Muchacho Mts.	10	22(56)	11(28)	11(28)	0	0	0
East Mesa	3	0	0	0	0	0	0
Yuha/Anza-Borrego Desert	17	0	0	0	0	0	0

Table 2. Tortoise burrows and live tortoises per transect

			Active burrows			Old burrows			
Transect	Location	Landform	Total	Deep	Shallow	Total	Deep	Shallow	Live tortoises
1	Cottonwood Mts.	B	4	0	4	0	0	0	
2		W	1	0	1	0	0	0	
3		W	1	0	1	3	0	3	
4		B	2	1	1	1	1	0	
5		B	6	5	1	1	1	0	2
6		B	7	5	2	4	1	3	
7		B	3	2	1	1	0	1	
8	Chuckwalla Valley	V	4	3	1	1	0	1	
9		V	1	0	1	1	0	1	
10		V	2	2	0	1	1	0	
11		V	0	0	0	0	0	0	
12		W	1	1	0	1	0	1	
13		V	2	1	1	2	0	2	
14		B	3	3	0	0	0	0	2
15		B	2	0	2	1	1	0	
16		B	3	2	1	2	0	2	1
17	Orcopia Mts.	B	2	0	2	0	0	0	
18		W	0	0	0	1	0	1	
19		W	0	0	0	0	0	0	
20		B	0	0	0	0	0	0	
21		B	1	1	0	0	0	0	

22	Chuckwalla Bench	W	0	0	0	0	0	0	
23		W	2	1	1	0	0	0	
24		B	2	2	0	2	0	2	
25		B	5	4	1	1	0	1	
26		B	9	4	5	2	0	2	3
27		B	4	3	1	2	1	1	
28		B	3	1	2	1	0	1	
29		B	4	1	3	4	2	2	
30		B	3	1	2	1	0	1	
31		W	3	1	2	3	1	2	
32		W	0	0	0	3	1	2	
33		B	2	1	1	1	1	0	
34		B	5	2	3	0	0	0	
35		B	0	0	0	0	0	0	
36		B	3	3	0	0	0	0	1
37	Palo Verde Mts./ Milpitas Wash	B	2	1	1	1	0	1	
38		B	0	0	0	0	0	0	
39		W	0	0	0	0	0	0	
40		W	0	0	0	0	0	0	
41		W	0	0	0	0	0	0	
42		W	2	1	1	1	0	1	
43		B	2	2	0	3	0	3	1
44	Smoke Tree Valley	V	3	3	0	0	0	0	
45	Chocolate Mts.	H	3	1	2	0	0	0	
46		B	1	1	0	2	0	2	

Table .. (Continued)

Transect	Location	Landform	Active burrows Total	Active burrows Deep	Active burrows Shallow	Old burrows Total	Old burrows Deep	Old burrows Shallow	Live tortoises
47	Algodones Dunes	S	1	1	0	0	0	0	
48		S	2	1	1	0	0	0	
49		S	0	0	0	0	0	0	
50		S	0	0	0	0	0	0	
51	Cargo Muchacho Mts.	B	0	0	0	0	0	0	
52		M	1	1	0	0	0	0	
53		W	2	1	1	0	0	0	
54		W	0	0	0	0	0	0	
55		W	0	0	0	0	0	0	
56		W	0	0	0	0	0	0	
57		B	3	1	2	0	0	0	1
58		B	0	0	0	0	0	0	
59		B	2	1	1	0	0	0	
60		B	0	0	0	0	0	0	
61	East Mesa	V	0	0	0	0	0	0	
62		V	0	0	0	0	0	0	
63		V	1	1	0	0	0	0	
64	Yuha/Anza-Borrego Desert	V	0	0	0	0	0	0	
65		B	0	0	0	0	0	0	
66		B	0	0	0	0	0	0	
67		W	0	0	0	0	0	0	
68		C	0	0	0	0	0	0	

69	B	0	0	0	0	0	0
70	H	0	0	0	0	0	0
71	C	0	0	0	0	0	0
72	H	0	0	0	0	0	0
73	H	0	0	0	0	0	0
74	V	0	0	0	0	0	0
75	B	0	0	0	0	0	0
76	B	0	0	0	0	0	0
77	B	0	0	0	0	0	0
78	W	0	0	0	0	0	0
79	B	0	0	0	0	0	0
80	B	0	0	0	0	0	0
81	B	0	0	0	0	0	0

Key to landform abbreviations:

B = bajada, including alluvial fans
C = canyon
H = hills
M = mesa
S = sandy flats
V = valley bottom
W = wash

Preliminary Investigations of the Desert Tortoise on the Beaver Dam Slope in Arizona

Judy P. Hohman

In the past, several studies of the desert tortoise, *Gopherus agassizii,* have been conducted at Beaver Dam Slope in Washington County, Utah, by Woodbury and Hardy (1948) and Coombs (1974). In the winter of 1976-1977 a study of the desert tortoise was begun on the Beaver Dam Slope, Mohave County, Arizona, in an area south of the Woodbury and Hardy study site. This current study is being funded by the Bureau of Land Management.

The terrain of the Slope consists of a broad alluvial fan which ranges in elevation from 580 m at the Virgin River to > 853 m at the Arizona—Utah border. The area is bisected by the Beaver Dam Wash and is crossed by other major washes which drain to the southeast into the Virgin River. Dominant perennials of the Slope include creosote bush, *Larrea divaricata,* and bursage, *Ambrosia dumosa,* with Joshua trees, *Yucca brevifolia,* appearing above 610 m. Economic use of the land is limited to cattle grazing with agriculture concentrated around the mouth of the Beaver Dam Wash.

Because the study was initiated in winter (the dormant period of the tortoise) any evidence of tortoise activity was limited to tortoise sign, that is, tortoise scats, tracks, dens, and shell remains. The locality of known tortoise sign indicates that tortoise activity mainly occurs in areas in and near major washes on the Slope in Arizona. Of 18 tortoise shells discovered, 11 were located within major washes, 5 were < 0.4 km from a major wash, and 1, an adult male, was 3.2 km from the nearest major wash. The location of one of the shells is unknown. Of these 18 shells, 12 are adults (9 ♂♂ + 3 ♀♀), 1 is a subadult, 4 are young tortoises, and 1 is a hatchling. The remains of the 4 young and 1 hatchling are evidence that reproduction has occurred on the Slope in recent years. Half of the 18 shells show some sign of predation either in the form of tooth marks or chewing. Potential predators of the desert tortoise on the Slope include the coyote, kit fox, and feral dog.

Desert tortoise dens, both permanent and ephemeral, were primarily constructed within or near established washes. A few ephemeral dens were found in good condition and were usually < 0.8 km from a major wash. Permanent dens were limited to the banks of major washes and were often excavated just under an exposed layer of caliche and rock. These bank dens were of 2 types: those with the familiar shallow dome-shaped opening, and those with larger cave-like openings similar to those discovered in the Woodbury and Hardy study (1948). These bank dens ranged in depth from 0.6 to > 4 metres.

All tortoise scats found were either in or near the entrance to permanent dens. The numbers, sizes, ages, and locations of tortoise scats along 2 of the washes suggest that in the past, several tortoises have shared the same winter hibernaculum in this area.

Tortoise tracks have only been seen at the entrances to 2 permanent dens.

Field studies for spring and summer 1977 on the Beaver Dam Slope in Arizona will focus on attempting to answer 2 questions about the desert tortoise: (1) what are the demographic properties of this tortoise population, and (2) is competition for food occurring between the tortoise and cattle? To determine the demographic properties of this Arizona population the age, sex, weight, shell measurements, and general condition of each tortoise encountered will be recorded. Any anomalies or evidence of predation will be noted. Each tortoise will carry an epoxy covered number on its carapace along with notched marginal scutes and branded carapace scutes as additional identifying marks. The location of each encounter with a tortoise will be mapped eventually yielding an approximate home range for each tortoise. Ten healthy adults, 5 males and 5 females, will be equipped with transmitters. Because these 10 animals can be easily located, any reproductive activity undertaken by them can be more readily observed.

To answer the second question of whether competition for food is occurring between tortoises and cattle, 2 study areas will be established each with a high density of tortoises. Study area No. 1 will be fenced thus creating an exclosure for cattle. This fenced area will enclose just under 2.5 km^2, is adjacent to the Arizona—Utah border, and includes the Arizona extension of Woodbury and Hardy's "Big Wash". Study area No. 2 will be similar in size to the exclosure. Cattle will be free to graze in this area according to the Bureau of Land Management's seasonal grazing schedule. Monthly fecal samples will be collected from tortoises in both study areas and from cattle in study area No. 2. The samples will be analyzed for species composition, abundance in diet, and (when possible) the plant part consumed. Also, the observed feeding bouts for both tortoises and cattle will be recorded and dated. Analysis of fecal information and feeding bout observations of the cattle and tortoises should yield a temporal record of the food habits of both of these species on the Slope in Arizona. Multiple temporal comparisons of the food habits of these animals will reveal competition for food on an interspecific basis if it is present, as well as the extent of any dietary overlap.

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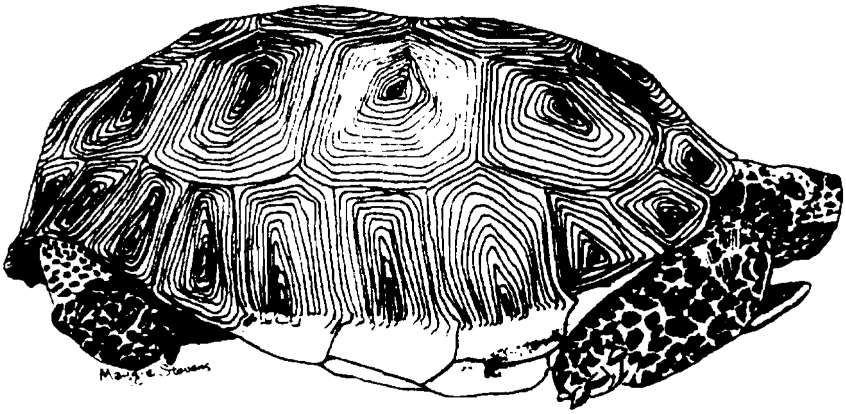

Radiolocating Free-ranging Desert Tortoises (*Gopherus agassizii*): Maximizing Transmitter Range and Longevity

James L. Schwartzmann and Robert D. Ohmart

This paper discusses a proven and efficient method of instrumenting free-ranging desert tortoises with radios. Recent interest in field studies concerning the desert tortoise have increasingly shown definite problems in relocation of marked individuals using nonbiotelemetry techniques. Relocation problems can be minimized or alleviated by the use of radio transmitters.

This study was initiated in August 1975 in Pinal County, Arizona, to determine the movements and behavior of native desert tortoises. The use of radio equipment for location of the animals was essential due to the rough, rocky terrain and the natural camouflaging color of tortoises.

METHODS

The basic system consists of a transmitter, battery, and antenna with ground plane. There were 2 variations, one for males and one for females. Both variations included a 26-g transmitter (35 X 27 X 10 mm), either a 40-g or 85-g lithium sulfate battery, and a transmitting antenna system. The 40-g lithium sulfate battery is equivalent in size to a standard "C" cell flashlight battery and has a life expectancy of 12 months. The 80-g battery is equivalent in size to a standard "D" cell flashlight battery and has a life expectancy of 36 months. The transmitting antenna system consists of a wire formed into a helical configuration and a copper sheet (ground plane) attached to the negative pole to provide a differential between the 2 components resulting in increased signal range.

The transmitter and battery used on males was enclosed in a hermetically sealed metal can with the antenna wire extending from it. This is the simplest variation to apply and is cemented (epoxy glue) to the posterior portion of the carapace. It is essential to position the unit so that its top is no higher than the highest portion of the carapace, thus insuring no interference in movement into and out of former burrows, and to position the unit so that copulatory activity will not be inhibited. The antenna wire is glued along the left marginal scutes to the nuchal scute and then along the vertebral scutes to the center of the carapace. The ground plane (copper foil) is glued to the right marginal scutes. A short wire must be soldered to the ground plane and to the can itself.

In instrumented females, the canned transmitter and battery are not enclosed in a second metal can. The transmitter and battery are glued to the anterior marginal scutes, one on each side of the nuchal scute, insuring no mechanical interference during copulation. As with the male, no portion of the attached units should be higher than the highest part of the carapace. The antenna wire is glued over the left marginal scutes to the pygal scute then continues to the third vertebral scute. The ground plane is then glued over the right marginal scutes and portions of the second and third costal scutes on the same side.

In both cases (male and female) the antenna wire must be at least 46 cm long and at least 4 cm from the copper foil. The copper foil should be ≈ 2 cm wide and 7.5 cm long. Any good 5-minute drying epoxy glue can be used but should be mixed for 2-3 minutes before application to insure rapid hardening and minimal runoff. All components should be covered with at least a 2-mm layer of hard epoxy for protection from mechanical damage. Natural scute coloration is maintained by either adding a colored compound to the epoxy during mixing or by spray pointing the glued components. The former method has been more desirable due to increased permanence and decreased potential toxic effects. Removal of the glued components is easily accomplished with no damage to the scute material of the tortoise. A groove is filed in the epoxy to the scute material and carefully pried off with a screwdriver. The range of this system has been from 1.6 to 6.5 km on the ground and up to 19 km from the air.

The receiver system consists of a 4-element yagi directional antenna and a multichannel receiver (up to 100 channels available). All equipment necessary to instrument the animals is available through Telonics, 1048 East Norwood, Mesa, Arizona 85203. This method has been used successfully since August 1975 in collecting data on movements and behavior of 11 desert tortoises. To date there have been no instances of damage or injury to animals using this method.

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Daily and Seasonal Behavior, and Areas Utilized by the Desert Tortoise *Gopherus agassizi* in Southern Nevada

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From May 1974 through October 1975 changes in daily and seasonal incidence of activity, distances travelled, and sizes of areas used by free-living tortoises were determined from captures of 116 marked tortoises (without transmitters) of various sizes, by radio tracking 10 adults, and by monitering cover site use. Tortoises remained in burrows from November to February. The latest emergence from hibernation was on 20 April. By the 2nd week in May most epigean activity was limited to early morning and late afternoon. The option to emerge during the 1 or 2 activity periods available was not always utilized by an individual, hence these periods were referred to as potential activity periods (PAP). Following the period of initial emergence from hibernation, 20% of the observed PAP of transmitter-bearing adults indicated no-egress. No-egress periods > 2 consecutive PAP were infrequent. Mean distance travelled during a PAP was ≈ 150 m (23-434), nearly equal for ♂♂ and ♀♀. Short and long trips were made each month but a greater number of long trips were observed from July to September. Mean home range size of ♂♂ was 32 ha (11-65); of ♀♀, 14 ha (6-27). Adults used < 5-90% of their home range each month. Activity levels, movements, and sizes of areas used suggested the influence of ambient temperatures, availability of green forage, and periods of sexual interaction.

Available data on daily and seasonal behavior of free-living *Gopherus agassizi* are few. Aspects of seasonal changes in the daily activity patterns of *G. agassizi* have been reported by Berry 1972, 1974*a*, 1974*b*), Brattstrom (1961), McGinnis and Voigt (1971), Voigt (1972, 1975) and Woodbury and Hardy (1948) whose comprehensive work includes home range estimates. In California, Berry has reported on several populations with special emphasis upon feeding habits, population structure and condition in response to the impact of man. Some of Berry's work (1972, 1974*a*, 1974*b*, 1975*a*, 1975*b*, 1976) dealt with the behavior of transplanted free-living, released captive, as well as resident free-living tortoises. Comparable studies of free-living desert tortoises in Nevada have not been reported with the exception of feeding habits and population characteristics (Burge and Bradley, 1976).

From May 1974 through October 1975 numerous aspects of population and individual characteristics were studied (Burge, 1977). The present paper deals with some of those factors: seasonal changes in the general level of activity; changes in the incidence of specific activities (feeding, reproduction); the sizes of the areas used by individuals at different times of the year; and the relationship of size and use of these areas to general activity levels, sex, weather factors, availability of forage, and location of hibernation sites.

The Arden Study Area (elevation 820 m) is ≈ 304 ha of typical Creosote Bush Community of Southern Nevada (Bradley and Deacon, 1967). The area is located on an alluvial fan sloping eastward 2-4% from near the base of the Spring Mts. ≈ 15 km SW of Las Vegas, Clark County, Nevada.

The following climatological data are from U.S. Weather Bureau records, 1937 through 1974 recorded at McCarran International Airport (elevation 658.5 m) at Las Vegas. Mean minimum and maximum temperatures of 0.3°C and 39.9°C occur in January and July respectively. Snow is rare. Mean annual precipitation, 98.5 mm, occurs mainly between July and March. Comparisons of ambient temperatures (T_a) as departures from normal were based upon averages since 1937.

METHODS

As the study area was methodically and repeatedly searched on foot for tortoises and discrete cover sites a map was drawn by pacing and unaided triangulation of salient topographic features. Comparison with aerial photographs and ongoing use and correction of the map to plot and relocate cover sites showed the pacing distances to be accurate within 5-10%.

Fieldwork usually began at dawn (later during winter) and continued for 5-7 hours; 18 visits began early afternoon and ended at dark.

Data recorded at each sighting of a tortoise included: time of day (Pacific standard time); ground surface temperature (T_{gs}); ambient temperature (T_a) ≈ 1 m above the substrate using a Schultheis rapid-registering mercury thermometer (unshaded). The tortoise's location was plotted and its specific situation and behavior described. At initial capture, each tortoise was marked, measured, and if possible, sexed. Transmitters were affixed to 5 adult males and 5 adult females, 220-286 mm carapace lengths. Locations of transmitter-bearing tortoises were determined 1 or more times per day every 1-3 days between mid-September 1974 and the end of October 1975.

Primarily diurnal, the desert tortoise avoids lethal epigean temperatures by intermittent use of cover which includes burrows of different lengths and depths.

The effects of seasonal T_a change in creating 1 or 2 daily periods that are conducive to activity have been observed in the behavior of *G. agassizi* by Berry (1972), Brattstrom (1961) and others. Auffenburg and Weaver (1969) and Rose and Judd (1975) observed the pattern in *Gopherus berlandieri* in Texas, and Gourley (1974) observed the pattern in *Gopher polyphemus* in southeastern U.S. Other petterns include the difference among individuals regarding the time of onset and duration of activity within the same active period and the intermittent tendency for individuals to remain in cover throughout an activity period. Implied in these behavioral variations are important physiological patterns not within the scope of this study.

Activity. To compare activity parameters over the year, utilization of time was plotted against the smallest functional unit of time available during which ambient conditions were potentially suitable for activity or at least not prohibitive—1 or 2 per day depending upon the season. These periods were referred to as potential activity periods (PAP).

The seasonal changes in the number and duration of daily PAP were measured by noting the number of individuals active between 0500 and 1900. When known, each hour of an individual's continuous activity was included.

To compare the monthly change in number of active individuals each tortoise was counted only once during a PAP. Observations of transmitter-free tortoises only were included because of the larger number of individuals represented and the opportunity to observe them was available throughout the PAP unlike the more nonrandom relocations of transmitter-bearing tortoises.

A tortoise was considered active when it was out of cover. Basking was not included, neither was emerging from nor retreating to cover unless activity other than basking was observed. Cover included shade, overhanging branches of shrubs, superficial depressions under shrubs or boulders as well as completely subterranean burrows.

Relative level of activity was indicated by (1) measuring the frequency of egress *versus* no-egress from cover, and (2) the frequency of change to another cover site, both being determined from transmitter-bearing adults, and (3) the number of cover sites indicating recent use.

To indicate activity at a cover site, half-lengths (7.5 cm) of commercial applicator sticks were inserted vertically across the floor of each cover site opening. Sticks were easily pushed flat as a tortoise passed through. Sticks that remained upright at an occupied burrow throughout 1 or more PAP definitely indicated no-egress. Cover sites were examined at a rate of 9-15 per hour. Most sites were checked at irregular intervals from twice daily to twice monthly. About 25% of the sites checked during a field day were checked each field day; 50% were checked twice per week. Toppled sticks and the natural erosion of tracks and plastral impressions indicated (1) use by a tortoise and (2) approximate elapsed time since use. Use within 5 days prior to a check was considered "recent". Following a check, toppled sticks were reinserted.

The distance traversed during a PAP was referred to as a single trip distance (STD). This term applied whether or not the tortoise changed cover sites. To determine the distance traversed, observation throughout a single complete PAP was required, i. e., location in cover before the trip began, during the trip, and in cover following the trip. Unless directly observed, actual paths during activity could not be traced because tracks were rarely evident.

Home Range and Activity Areas. The principal method for determining the size of areas used by transmitter-bearing adults was by frequent direct observation. Convex polygons were drawn from plotted recapture points and the areas within measured with a planimeter. To compare area size, and manner of utilization throughout the year among transmitter-bearing adults, the imposed time frame—a calendar month—was used.

Home range size was determined for several transmitter-free adults ($>$214 mm carapace length). The areas of their convex polygons were adjusted, using the Jennrich and Turner (1969) correction factor based upon the number of captures. Their method accommodates noncircular home ranges; also, the correction factor attempts to eliminate sample size bias. In this context, the home range is the area of the smallest region which accounts for 95% of the animal's utilization of its habitat and assumes that utilization is expressed by a bivariate normal distribution.

Tests for significance were at the 5% level using Student's t-test or else a chi-square test with Yates correction.

RESULTS AND DISCUSSION

Excluding repeated sightings during hibernation, data were obtained from 116 transmitter-free tortoises (38-286 mm carapace length) captured 666 times and from 10 transmitter-bearing adults captured 1252 times. Four of the transmitter-bearing adults were monitored for only 2-9 months. About 64% of the relocations of transmitter-bearing adults were made within 1-PAP intervals; 24%, within $>$1-4 PAP intervals.

Activity. Activity over a year showed 2 major divisions: (1) an active season in spring, summer, and early fall with varying levels of activity; and (2) an inactive season in winter during which tortoises exhibited virtually no activity.

Beginning during the 3rd week of October 1974, a decisive change from frequent egress to 100% no-egress occurred within less than 2 weeks. Immediately prior to this change, males were emerging more often than females (Fig. 1). In 1975, the increase in no-egress of 2 females occurred during the last 2 weeks of September. The percent no-egress recaptures of males was higher during this period in 1975 than in 1974. A sudden decrease in daily T_a to highs $< 20^{\circ}C$ and lows $< 10^{\circ}C$ occurred during the last week in October 1974 and during the first week in October 1975.

No definite dates were available for the beginning of hibernation in the fall 1975 because transmitters had been removed intentionally before tortoises became inactive and out of reach in dens. Dens were burrows usually > 300 cm in length with capacities for several tortoises. After the 1st week in October, transmitters remained on 2 females only.

In 1974, the onset of hibernation, known for 16 tortoises, began over a period of 17 days between 26 October and 11 November; for 13 of the 16, between 26 October and 3 November. Between early November 1974 and 1 March 1975 tortoises remained in their burrows without egress. None of the burrows mapped or checked during that period indicated recent use and no tortoise was observed aboveground.

The total length of the hibernation period, i.e., the time interval between the earliest date after which a tortoise showed no further sign of activity and the latest date of emergence, was 168 days. Individual periods ranged from 121 to 168 days ($\bar{x} = 137$).

Hibernation ended or initial spring emergence occurred for 26 tortoises between 1 March and 20 April (51 days); 7 individuals during the 1st week in March; 5 during the 2nd; 2 during the 1st week in April; and 12 between 12 and 20 April. Occupants of the same den made their emergence on widely separated dates that showed no correlation with sex or size. Individuals that emerged prior to 12 April had subsequent periods of 6 to 34 consecutive PAP without egress and basking comprised most of the activity observed. For some individuals, hibernation was apparently resumed.

For certain populations in California, hibernation usually begins from mid- to late October and ends during the last week in February or early March (Berry, 1972, 1974*a*, 1974*b*). In southwestern Utah, tortoises moved into winter dens during October. During April, tortoises left dens and moved to areas where "summer holes" were located (Woodbury and Hardy, 1948).

Between 24 February and 3 March T_a lows increased from 1° to $11^{\circ}C$; highs from 19° to $27^{\circ}C$; however, after 3 March temperatures decreased and between 10 March and 12 April, 26 of the 33 days averaged below normal, on 11 days by 6 or more degrees Celsius. Highs on 28 of the 33 days never exceeded $21^{\circ}C$. During the second half of April, daily highs seldom reached $24^{\circ}C$ and daily means remained as much as $7^{\circ}C$ below normal until the beginning of the 2nd week of May.

From the last initial emergence from hibernations (20 April) through September, only 20% of recaptures of transmitter-bearing adults indicated no-egress (Fig. 1). The semimonthly mean percentages for males and females were similar; however, the frequency of occurrence and the duration of periods of no-egress through the active season varied considerably with the individual.

The last post-emergence period of 2 or more consecutive PAP of no-egress before activity became more or less sustained was of 9 PAP ending 7 May (Fig. 2). In June, all observed periods of 2 or more consecutive PAP of no-egress occurred during the last half of the month. The longest periods of no-egress that neither immediately preceded nor followed hibernation and were not the apparent response to injury were 2 periods of 6 and 7 PAP involving 1 male and 1 female during the last half of August and the first half of September. For transmitter-free tortoises there was no indication of extended periods of no-egress with the exception of early spring.

Upon emergence from cover, a tortoise usually basked. Durations of basking were not observed in most instances but basking was observed in every month of the active season. After basking, a tortoise might (1) return to cover without further activity, (2) travel varying distances and return to the same cover site, or (3) travel and end activity at another cover site. Although the difference between the first 2 alternatives is biologically significant, the relative frequency of each alternative was not determined; however, basking followed by retreat occurred each month and between changes to another cover site, egress occurred during more than half of the intervening PAP. A transmitter-bearing adult generally used a given cover site for < 1 to 6 PAP between changes.

The frequency of cover site change by transmitter-bearing adults (Fig. 3) forms plotted curves that are nearly the reciprocal of no-egress curves (Fig. 1). Not until mid-April did the frequency of change equal that of prehibernation. Except for a drop to ≈ 20% in the second half of June for both sexes, the frequency of change remained between 40% and 70% for males through September and for females through the second week in August. The greatest frequency of change of each of the 3 females was in July. During other months, the frequency varied considerably among individuals of the same sex. For example, during the last half of September, 2 females showed a 48% frequency of change, the third, 14%. In August the frequency of change of 2 males ranged from 85 to 100%, the third ranged from 0 to 25%.

From mid-September 1974 through October 1975, 700 cover sites were checked 7000 times for use. In 1974, the decrease in use during the 3rd and 4th weeks of October was apparent, day to day (Fig. 4). In 1975, use decreased from 47% on 28 September to 10% during the 1st week of October. There were decided increases on 3 May and 16 July. The peak of 64% on 28 July was followed by continued high level of use through September. During the last week of July and the first half of August there were 13 days during which T_a reached maxima for the season—38.0°C to 45.0°C and daily lows were between 24.0°C and 29.0°C. The frequent but discontinuous use of burrows during this period was not indicative of a general tendency for aestivation.

The number and duration of daily PAP changed through the season (Fig. 5). The distribution of hours when tortoises were active was similar for transmitter-bearing and transmitter-free adults ($>$ 214 mm carapace length). About half the observations were from each group and their data were combined. The number of adults per hour calculations were adjusted to accommodate slight differences in the duration of field visits.

From the 2nd week in May through the 3rd week in September between 1130 h and 1500 h only 2 active tortoises were seen. Both sightings were on 22 May between 1200 h and 1300 h; T_a was 23.4°C; cloud cover 50%.

The morning PAP in each month (May-September) were ≈ 6 hours duration; the afternoon PAP, ≈ 4 hours. Visits from 1500 until dark comprised only 10% of the field hours and those afternoon PAP during June, August and September were less well represented.

Tortoises were observed moving into cover within the last few minutes before darkness prevented further observation. I did not remain on the study area after dark; however, location checks on the morning following evening observations never indicated that egress had occurred during the night.

The dates during which the number of PAP/day changed in the spring and fall were estimated from the individual records of 8 transmitter-bearing adults. For each, the seasonal change occurred within less than a week. In fall 1974, the total period of change (8 adults) extended from the last week in September into the 3rd week of October. The period of change, spring 1975, extended from 27 April through 11 May. In fall 1975, 3 females changed on or about 21 September, and the 3 males sometime after 1 October.

The approximate duration of activity for an individual during a PAP was observed on 80 occasions. Most observations were of transmitter-bearing adults during the morning PAP of 2-PAP days. Data from males and females were combined. The frequency distribution within given activity-duration-ranges were as follows: 1 h, 2; 1¼-2 h, 27; 2¼-3 h, 39; and 3¼-4 h, 12. The sample size was too small and the range of durations too wide to determine if monthly differences were significant; however, both long and short durations occurred each month and all observed durations were shorter than the length of the PAP. Voigt (1972) observed that individuals might emerge over a 2½-hour period during a PAP and remain active from < 1 to 4 h during a given period.

During 1-PAP days and the morning of 2-PAP days the monthly mean T_a during which tortoises were active ranged from 17.5°C in March to 30.5°C in July. During the afternoon PAP, means ranged from 28.5°C in May to 35.8°C in July. From May through October the mean T_a when tortoises were observed moving into cover following morning activity was 31.0°C.

The absence of active individuals near midday during most of May through September, and the fact that during those hours all tortoises sighted were in cover, may be due to the prohibitively higher T_a, which during the 1st week in May began to exceed 30.0°C in the sun at 1 m above the ground surface. The effect of high T_a was also suggested by the progressive change in the hours during which most of the active tortoises were observed, i.e., becoming earlier in the morning as spring progressed and later toward fall. The pattern of season change in number of activity periods per day was similar to that described by McGinnis and Voigt (1971) and others.

The number of observations of active individuals each month (Fig. 6) was determined from 55 adults and 25 juveniles and subadults (82-214 mm). The monthly values were adjusted to correct for slight differences in time spent in the field each month.

A greater number of active individuals (all sizes) were observed during May and July. Considering 1975 only and eliminating March values, the number for each month was compared to the expected (the mean, April through October). April and October were significantly less than expected; May and July, significantly greater than expected ($P < .05$). The number of "active" observations was greater in October 1974 than October 1975.

The number of active adult males per month was compared with the number of active adult females. If the sexes were equally active during a given month the number of observations (unadjusted values) for each sex would be expected to be proportionate to the percentage of each sex in the adult population. Of 67 adults marked during the study, 59.7% were males; 40.3%, females. For each month, the numbers of active males and females did not differ significantly from the expected ($P > .05$) although during May 1975 and September and October 1974 the number of active males was proportionately greater than the number of active females.

The 47 observations of individuals < 214 mm carapace length were too few to indicate any more than the major seasonal activity trends. Observations of active tortoises < 180 mm, 40% of the marked population, comprised only 12% of all observations during activity; tortoises < 100 mm, 13% of the marked populations, comprised only 1% of the observations.

Probably the major factor responsible for the differences between total number of large and small tortoises observed is the greater difficulty in detecting small tortoises. Also, structural and possible physiological differences affecting heating and cooling rates among tortoises of different sizes may influence the time and duration aboveground and microhabitats chosen. Among the structural differences of small tortoises is the incompletely ossified shell during the first few years of life. Without the insulative properties of an ossified shell, heat exchange rates may be affected.

Comparing thermal relationships in the laboratory among 7 age-size classes, Naegle (1976) found that smaller (younger) tortoises heat and cool at about the same rate. With increasing size, heating rate decreases but becomes progressively greater than cooling rate. Naegle's findings also indicated that tortoises < 125 mm carapace length and < 500 g had significantly higher preferred body temperatures than larger tortoises and therefore may be active at higher T_a.

Under equal ambient conditions small tortoises with shorter heat exchange cycles may emerge intermittently for shorter periods than larger tortoises and may remain closer to shrub cover during activity. The PAP of juveniles may also differ.

Aspects of feeding including species use frequencies for the 1975 season were previously described for the Arden population (Burge and Bradley, 1976). Briefly, temporal aspects of feeding and forage availability were as follows: Thirty tortoises were observed feeding on 118 occasions; 93% of the feeding observations were from May through September. Peak months were May and July. A slight decrease in the number of observations (mid-June) was coincident with the drying of winter annuals, particularly *Plantago insularis*, which was eaten during 37% of the feeding observations, more frequently than any of the 17 other forage species. Tortoises also ate *Plantago* and other species when the plants were dry. On 3 July, rain and extensive flooding produced a second emergence of winter annuals and renewed growth of many perennials including food species. Green forage was available through most of July, the month with the greatest number of feeding observations.

Observations of courting, combat and associated behavior or its sign are given in Table 1. Recent mating depressions and linear paths which remain on the soil surface following copulation and/or mounting were counted as additional indications when the behavior was not observed. Mating depressions have been described by Berry (1972, 1974*b*) and Woodbury and Hardy (1948).

Male-female interaction was implied when there was simultaneous use of burrows which during most of the season were occupied by only 1 tortoise at a time. Periods of simultaneous use by a pair usually extended over 2-4 PAP during which egress usually occurred and recent mating depressions were sometimes found within a 10- to 20-m radius. Each observation involved 1 male and 1 female except for 4 observations in which 1 female was found with 2 or 3 males. Dens were not included in tabulating these data because both sexes used dens simultaneously year-round.

The few observed agonistic encounters between males began at a cover site and extended over 20-60 m.

Observed simultaneous use of single-tortoise burrows by 2 or more males was repeated to continuous over 2-4 consecutive PAP. Once inside, no agonistic behavior was observed; however, sometimes 2 or 3 head-bobs were seen just prior to passage through the opening which was accomplished without incident more often than not.

No agonistic behavior between females was observed and no females were found together in single-tortoise burrows.

Irregularly shaped areas of disturbed soil with tracks (but none of the distinctive signs of copulation) were obviously the result of energetic interaction. These encounters may have involved a male and a female, but more probably, 2 males. In each instance, this sign was within 1-10 m of a burrow.

Berry (1972, 1974*b*) observed 2 periods of courtship and mating which coincided with periods of peak activity, one in the spring and the other in late summer and/or fall. On the Arden Study Area in 1975, the general level of activity was highest during May and July; however, only 7% of the male-female interactions were observed in May, 9% in July, and 75% in August and September. The low number in May may have been the result of below average T_a with a proportionately greater time spent basking. Berry also observed that several males copulated with the same female and there seemed to be no fixed pairs. Similarly, on the Arden Site sexual relationships were promiscuous. Increased movements would be associated with this type of pairing. Increases in agonistic behavior and other indications of male interaction were coincident with increases in the general level of activity and breeding behavior. It is reasonable to assume that this increase in agonistic behavior was partly the result of an increase in male contact as they sought females.

Sexual activity apparently was not dependent upon opportunity. For example, males and females shared dens simultaneously during every month. Male No. 108 spent much of his time in an area shared by the 3 transmitter-bearing females. One of female No. 96's burrows was within 1 m of one of No. 108's principal burrows, and male No. 108 shared a burrow with another female for several days in June. There was no sign of No. 108 interacting with either female; however, he was sexually active in September and October.

The copulation and sign that was observed only in October 1974 probably reflected the longer period ($>$ 2 weeks) during which T_a remained high enough to support continued activity in contrast to October 1975 (Figs. 1, 3, and 4).

Berry (1972, 1974*b*) observed that males (at the Salt Wells Valley Site) were never seen together in a burrow. Dens were not observed there. Even during hibernation, 1 male with 1 or 2 females was the rule. Grant (1936) observed only single occupants in burrows (California). Woodbury and Hardy (1948) found that at a given time the average number of observable occupants in any 1 of 95 monitored dens was about 3, with the maximum being 17. These dens, in the consolidated gravels of wash banks, were used primarily as hibernacula, apparently by both sexes simultaneously. There were a few instances of simultaneous use of the shorter "summer holes" ($\approx$ 1 m long) by a male and female. Woodbury and Hardy (1948) observed shoving and jousting between males when placed in the sun following temporary removal from dens during hibernation.

One instance of egg laying was observed on 11 June 1975. Few data have been reported regarding nesting behavior of free-living *G. agassizi*. Berry (1974*b*) observed egg laying on 7 June. Laying dates reported for captives extend from 28 May through 28 July, most occurring in June (Booth, 1958; Grant, 1936; Miller, 1955; Nichols, 1957; Stuart, 1954). Laying dates of 10 clutches from captives maintained out-of-doors, year-round at my Las Vegas residence were from 16 May through 20 June (1974-1975). Laying on the Arden Site was apparently a normal representative of the nesting period.

Manner of travel was typified by steady pace on a clearly evident heading. If after several minutes a tortoise's location was sought by following the tortoise's original heading, the tortoise was commonly located in a burrow on that heading. During this kind of travel the tortoise repeatedly circumvented shrubs and boulders and returned to the original heading. During straight-line travel, the tortoise might pause to feed for several seconds to minutes. "Straight line travel" has been described by Berry (1972).

The difference between the distance actually travelled and the straight-line distance (SLD) between 2 cover sites was determined for 20 STD observed for 95 to 100% of their lengths. The STD included deviations imposed by topographic barriers. Nine of the 20 trip distances were equal to the SLD and this included the longest trip observed (434 m). Four were 10% longer than the SLD. The maximum deviation was 38.5%, the mean 9.3%. There was no apparent correlation between the length of the trip and the amount of deviation.

Deviations were associated with feeding, copulation, or movements along a wash bottom or rim prior to a major correction in heading. Sometimes no cause for deviation was observable. Segments of a trip that were deviations were few and were often travelled as a SLD. For the purpose of comparison, each STD between 2 cover sites was expressed as the SLD.

When a tortoise returned to the same cover site from which the trip began, the configuration formed a loop, generally elliptical in outline with lateral deviations often no more than 1 or 2 body lengths. Total travel distance was observed for 7 loop trips which occurred at different times over the season. The maximum distance from the cover site ranged from 42 to 113 m. The mean distance travelled, 148 m, did not differ significantly from the mean STD between 2 cover sites ($P > .05$), consequently, the distances of both types of trips were considered together.

Single trip distances observed for 1 transmitter-free and 10 transmitter-bearing adults included 111 in 1975 and 6 during September and October 1974. Of the 117 STD, 27 were observed for 95 to 100% of their length, 39 for > 50% and 51 for < 50%. Trips observed for < 95% of their lengths were observed over 2 or more discontinuous intervals. Of the 111 STD observed during the active season 1975, trips < 50 m comprised 7%; 50-200 m, 75%; and > 200 m, 18%. Lengths of the 6 STD observed during September and October 1974 approximated this distribution. In each month, trips > 200 m never comprised more than 29%; however, 85% of all trips > 200 m were observed during July, August, and September. Those in July were made by females and comprised 50% of all their trips > 200 m; those in August and September were mostly by males and comprised 90% of their trips > 200 m.

In 1975, STD mean (± 1 SE) of males was 143 ± 12 m (23-381); of females, 147 ± 9 m (49-366) (Fig. 7). The difference between the means is not significant ($P > .05$). The mean of males in July was significantly lower than their seasonal mean. Male mean in September-October 1974 did not differ significantly from the September-October 1975 mean. Of females, only the higher mean in March differed significantly from the season mean. When monthly comparisons were made between males and females, only in July did they differ significantly.

The 111 STD represented 75% of the 1-PAP observations made after travel was known to have occurred (all known trips); but only 30% of all known trips (1975). On a monthly basis STD represented 11-50% of known trips. The significantly higher mean STD of females in March was based upon only 4 STD; however, they represented the highest percentage of known trips for any month (50%). May and the first half of June were the least well represented (11-19% of known trips). During July, August, and September when STD represented 30-41% of known trips, 7 of the 8 STD < 50 m were observed as well as the greater percentage of STD > 200 m. It appears that when sample size was > 30% of known trips during a given month, short and long trips were observed. The significance of differences between monthly means of each sex and between the sexes are very possibly the result of small sample sizes and extreme variations among individuals (suggested by variations in data from other activity parameters).

Areas. Seven transmitter-bearing adults were relocated 135 times between July and hibernation 1974. Only 1 of those sites was outside the area used by that individual during 1975; therefore, 1974 sites were included in total home range data. The mean convex polygon areas of 3 males and 3 females monitored for a full active season did not differ significantly ($P > .05$) (Table 2).

For each individual total home range area was also calculated by taking random samples of recapture loci. These subsamples were plotted and the areas measured. Using the Jennrich and Turner (1969) method the projected areas were larger than those observed; however, the difference between the observed and adjusted means was not significant for either sex ($P > .05$). From observations of movements relative to peripheral cover sites and observed home range boundaries, the home range sizes, as observed, were considered to be more representative.

There were periods of 1-4 weeks during which an individual utilized a more or less discrete area and expressed a relatively consistent level of activity; however, these periods varied in distinctness throughout the season and showed no consistent relationship to the periods of other individuals. Gaps in data collecting were sufficient to create or augment these ambiguities; hence, the use of the calendar month for comparisons. If naturally occurring periods were correlated with sex, ambient conditions, or other factors, more 1-PAP observations would be needed from a greater number of individuals.

The monthly activity areas were more or less discrete but not always mutually exclusive (Figs. 8A, B, C). During a few months, frequent successive sightings and observed trips resulted in plotted points that formed a linear configuration the area of which could not be measured precisely. Due to transmitter failures (1975) contact was lost with male No. 161, 10 June-9 July; with male No. 108 from 22-25 April and 17-20 September; and with female No. 94 from 12-20 April.

The percentages of home range area used by each adult during each month were averaged for each sex (Fig. 9). In 1975 the greatest percent used by each of the 3 females was during June and July, when the range of the maxima was 65-90%. Among the 3 males, the months were May and August and/or September when the range of the maxima was 40-85%. The smallest activity areas (< 5-20%) were used during October, March, and April by both sexes and in August by 2 females and 1 male. The other 3 adults ranged widely during August. A mid-month reduction in size of area occurred in June for 4 of the 5 tortoises that could be relocated. As a rule, the actual number of hectares used during a given month also varied widely among individuals. For example, the individual maximum of females ranged from 8 to 24 ha, that of males, 11 to 27 ha.

There were no obvious differences among the areas in the availability of forage, cover sites, or potential mates. Mean tortoise density was 1 per 2.3 ha.

During August, September, and October 1975, 5 of the transmitter-bearing tortoises were observed using cover sites or discrete areas that had not been used by them since approximately the same dates during the previous year. There were 8 such instances. Two (by males) involved widespread movements and several burrows and included returns to hibernation sites. Five (3 by females) involved the use of 1 burrow for 1-12 days. Except for the 1, 1-day use the burrows were used simultaneously by a male and female or by 2 males for most of the period. Recaptures during these periods increased home range areas 0-10%. Male No. 160's area was increased 165%.

The relationship of the location of the hibernation site to area used during the active season was known for 26 tortoises. Hibernation sites of 24 were well within their respective active-season areas; 2 tortoises used a site that was 1100 m from the closest boundary of their respective active-season areas. Eighteen (of the 24) used their hibernation sites during the active season.

The relationship of hibernation sites to widespread periodic movements into infrequently used areas is exemplified by 2 transmitter-bearing males.

Male No. 108's hibernation den was used by other tortoises throughout the active season and by some, also during hibernation. In 1974 and 1975 use by No. 108 began in September, 3-4 weeks prior to hibernation. During these periods No. 108's use of the area was not confined to that near the den; he moved to the den and back across his home range covering wide areas. Use of the den became continual only after 30 September 1974 and 23 September 1975. Following emergence from hibernation No. 108 moved directly away from the den, and (until the 3rd week in September) was captured no closer than 300 m from it. Including the hibernation den in his home range, the area increased by ~ 3 ha (= 7%).

In contrast, male No. 160's hibernation den was also his principal cover site, used during every month. Most of the active season 1975, No. 160 used the same 30-40% (7-8 ha) of his home range. Beginning 22 August, trips were made to areas and burrows used during September 1974 but not again until 1975 (Fig. 8A). During both years, trips included several returns to the area of the hibernation den and use of the den.

Seasonal movements relative to hibernation dens described by Woodbury and Hardy (1948) were short migrations to dens in the gravel banks of washes during late September through early October and a return to the shorter soil burrows on the flat areas between the washes during March and early April. These tortoises usually utilized dens in their area but varied from year to year in the degree of repeated use of a given den. The time of movement, the tendency for repeated use, and the relationship to home range were similar to my findings—most dens were cavities in the consolidated gravels of wash banks; however, these dens were few and 15 of the 30 tortoises observed during hibernation used single-tortoise burrows in soil in scattered locations over the flats. The limited availability of dens; the scattered locations of other hibernation sites; and the utilization of dens year-round help to explain the observed differences in movements relative to hibernation sites.

The fact that most hibernation sites observed were within the area used by the individual during the active season and most were used year-round suggests that the larger areas used and the longer trips taken during the fall were not related entirely to hibernation.

The disproportionately large areas that were sometimes included in the home range as a result of periodically used and often peripheral sites were considered no less representative of home range area despite the low level of utilization. The rationale for including these areas was the possible significance of these trips to reproduction.

Agonistic behavior did not appear to result in changes of activity areas. Within 24 hours following combat the males might share the same cover site and may have done so during the weeks prior to the encounter.

Unlike many lizards, territorial behavior does not seem to be a major factor determining population densities of turtles in general which appear to respond more directly to availability of habitat requirements (Cagle, 1944, 1950). On the Arden Site, combat (territoriality) occurred between males at or near cover sites; however, in effect, it appeared that the mutual need for cover dominated aggressive tendencies.

Nesting requirements or related behavior of the nesting female might influence the size of the activity area. Stickel (1950) observed that female *Terrapene carolina* often travelled outside their home ranges at nesting time, travelling distances that were 1-6 times greater than the home range diameter and apparently these trips were not the result of unsuitable nesting sites in the home range.

The nesting site used, 11 June, was near the center of the female's home range, 45 m from her nearest burrow. The site appeared to be of a widely available combination of soil, vegetation, and exposure. The only other indications of nest sites were old nest cavities and/or eggshell fragments within a few centimetres of the opening of 25 burrows; however, the relationship of these nests to particular females was not known. The possibility remains that the relatively large areas used by females during early June may have been associated with nesting behavior.

Because of the monthly differences in percentages of total home range used by transmitter-bearing adults, home range area was determined for those transmitter-free adults who not only were recaptured most frequently but whose individual monthly representation was most complete. The areas of the convex polygons based upon all capture sites were measured for 6 males and 5 females captured 10-56 times. The areas delineated by capture sites during 1974 were essentially the same as those in 1975 and were included. The monthly capture frequencies and areas of convex polygons are given in Table 3.

The table of correction factors (Jennrich and Turner, 1969) accommodates capture numbers from 3 through 25. Correction factors (C_n) for 3 transmitter-free males captured 26-56 times were determined by extrapolation. Fitted to the best logarithmic curve by regression analysis $C_n = \ln N(0.254) - 0.301$, correlation coefficient = .9988.

When the observed home range areas of the 3 transmitter-bearing males were averaged with the adjusted home range areas of 6 transmitter-free males, the mean (±1 SE) was 32.3 ± 6 ha (11-65). This differs significantly from the mean of the 8 females whose values were treated in the same manner, 14.8 ± 2.6 ha (6.4-27) ($P < .05$).

Home range estimate of 4-40 ha ($\bar{x} = \approx 20$) for adults was reported by Woodbury and Hardy (1948) for a portion of a population in southwest Utah. Berry (1974*b*) estimated home range size for adults at the Salt Wells Valley site, San Bernardino County, California, to be 130-259 ha for males; females, ½ to ¼ that of males. The absolute values (in hectares) differ between the Arden Site and those reported by Berry; however, the area size relationship between males and females was similar. Reliable comparisons between the 3 areas were not possible from the data available. The effect of density and distribution of forage upon movements and area sizes is suggested in the following.

The relationship of trip distance to distribution of forage was examined. The annual, *Plantago insularis* and the suffrutescent perennial *Sphaeralcea ambigua* were the major food species (61% of the use-frequency). Both species were distributed widely over the study area and within 20 m of a cover site, both were available; however, after feeding near its cover site, > 50% of the remainder of a trip to the next cover site was often travelled without pauses to feed upon available forage. Also, distances travelled prior to feeding often exceeded the distance to the nearest available source of the species ultimately eaten.

Berry (1974*b*) observed that during spring 1972, annuals (the principal food) were few and their distribution patchy. Winter rain was below average and drying of annuals occurred 45 days earlier thar usual. Distances of 470 to 823 m (per day) were common and trips of 1000 m were observed. Tortoises appeared to seek out and remain near areas with patches of wildflowers, sometimes for days or weeks, utilizing a burrow 55-274 m away and moving on when the particular food source was gone.

During the present study, STD did not exceed 434 m and mean monthly recapture distance (after 2 or more PAP following a cover site change, when spring forage was utilized [April to mid-June]) ranged from 165-265 m (males) and 101-211 m (females). Concentrations of a diversity of species occurred only in the major washes, yet foraging was seen there proportionately less often than on the flats between the washes, very possibly because of the tortoises' preference for *Plantago*, which was widespread rather than localized, and comprised a greater percentage of the winter annuals on the flats. This may explain the lack of obvious forage-site utilization relative to cover sites and shorter trip distances than those observed by Berry.

With the exception of courting and combat, the parameters indicating activity levels and area size showed the same trends (Figs. 1, 2, 3, 4, 5, 6, 8, 9). Data were similar from transmitter-bearing and transmitter-free adults. Males were somewhat more active than females in May and early fall. The factors influencing the observed trends are suggested in part by the following: The dates of decline of activity and size of areas used differed in October 1974 from October 1975; however, both were coincident with the major seasonal T_a drop.

The physiological as well as behavioral aspects of tortoise hibernation are not well known. Although T_a is a limiting factor it is doubtful that it functions alone to initiate fall movements that include pre-hibernation use of hibernation sites, or that it alone initiates spring emergence. Other factors may include photoperiod, endogenous rhythms with different degrees of flexibility, energy reserve, and reproductive cycles (Case, 1976; Cloudsley-Thompson, 1971; Jackson et al., 1976; Licht, 1972; Mayhew, 1965).

Following emergence from hibernation the rate of increase in activity was coincident with the slow increase in T_a which was below normal most of the time until 8 May, when the change from 1 to 2 PAP per day occurred for most adults.

The sudden reduction in activity mid-June was coincident with moderate T_a, traces of precipitation, and (probably most influential) the drying of the few remaining winter annuals. The reduction in activity, including feeding, suggested the tortoises' strategy relative to the cost of foraging.

Activity areas tended to be larger when forage was relatively abundant. Small activity areas between 1 March and mid-April when forage was available were apparently the result of T_a too low to sustain activity. The increase in available forage following the rain and flooding 3 July, probably supported the high level of activity which included maximum feeding observations for any month. Apparently, the T_a peak in July was not prohibitive to epigean activity when green forage was available. Implied is that the cost of pulmocutaneous waterloss during foraging was compensated.

The second emergence of green forage was eaten or had dried by the end of July; however, activity levels remained high through September. This may have been the result of the relatively well hydrated condition of the tortoises, a condition which continued to the period of increased sexual activity during August and September.

Berry (1974*b*) observed low activity levels during July and August when emergence occurred once or twice a week, if at all. Activity increased during August or early September; however, some individuals remained in their burrows and hibernated without having emerged. Summer activity level was estimated at ≈ 10% of that of spring.

United States Weather Bureau records over the past 20 to 40 years show that at most areas in the northwestern Mojave Desert, precipitation falls mainly from October through February or March. Late spring and summer are typically very dry. In southern Nevada, rain commonly occurs in July and August; however, the extensive flooding, 3 July 1975, may have supported an amount of forage and subsequent activity that were considerably greater than usual for that time of year.

At a given site, annual species composition and abundance vary greatly from year to year depending upon precipitation and temperature patterns (Beatley, 1969). In 38 Mojave Desert Communities (*Larrea* and closely related types) in southern Nevada, site means of winter annual biomass at reproductive peak averaged 60, 19, and 160 kg/ha in 3 successive years. At a given site a $>$ 20-fold difference from year to year was not uncommon (Beatley, 1969). Where rainfall is erratic spatially and temporally such as in local deserts, it is reasonable to assume that availability of forage would be a major factor influencing tortoise behavior, particularly movements relative to available forage. Year to year changes in the size and shape of the individual's home range may also result.

The home range data presented suggest a high degree of fidelity of an individual to an area. This is further supported by my preliminary observations of fidelity to particular burrow sites. How the individual's movements reflect its year to year water and energy budgets remains a question. Answering this question may affect our interpretations of home range size and possibly population density indices: both have management implications for a species in marginal habitat.

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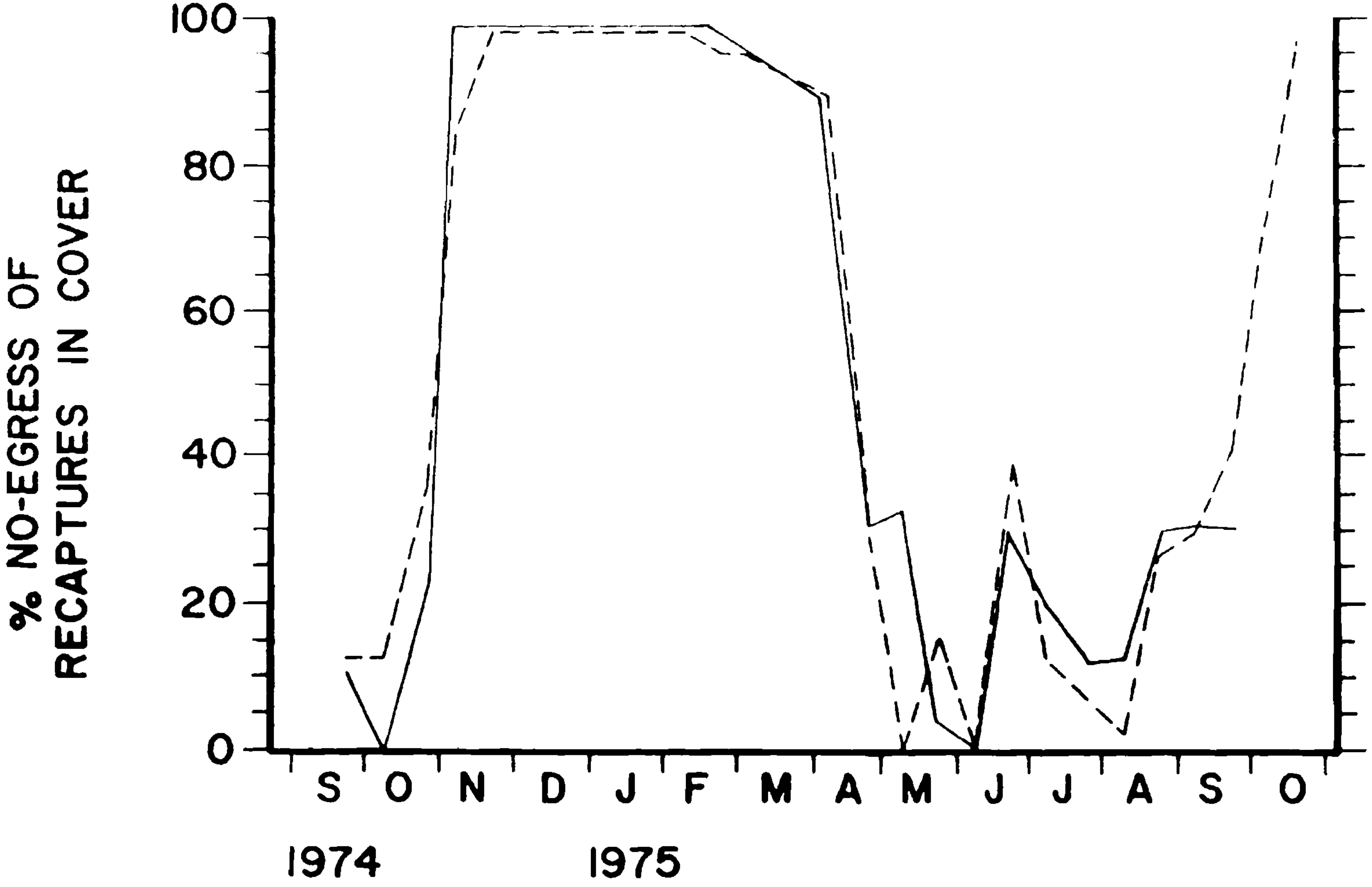


Fig. 1. Semimonthly percent no-egress PAP of recaptures in cover (6-10 transmitter-bearing adults).
Solid lines are ♂♂; broken lines are ♀♀.

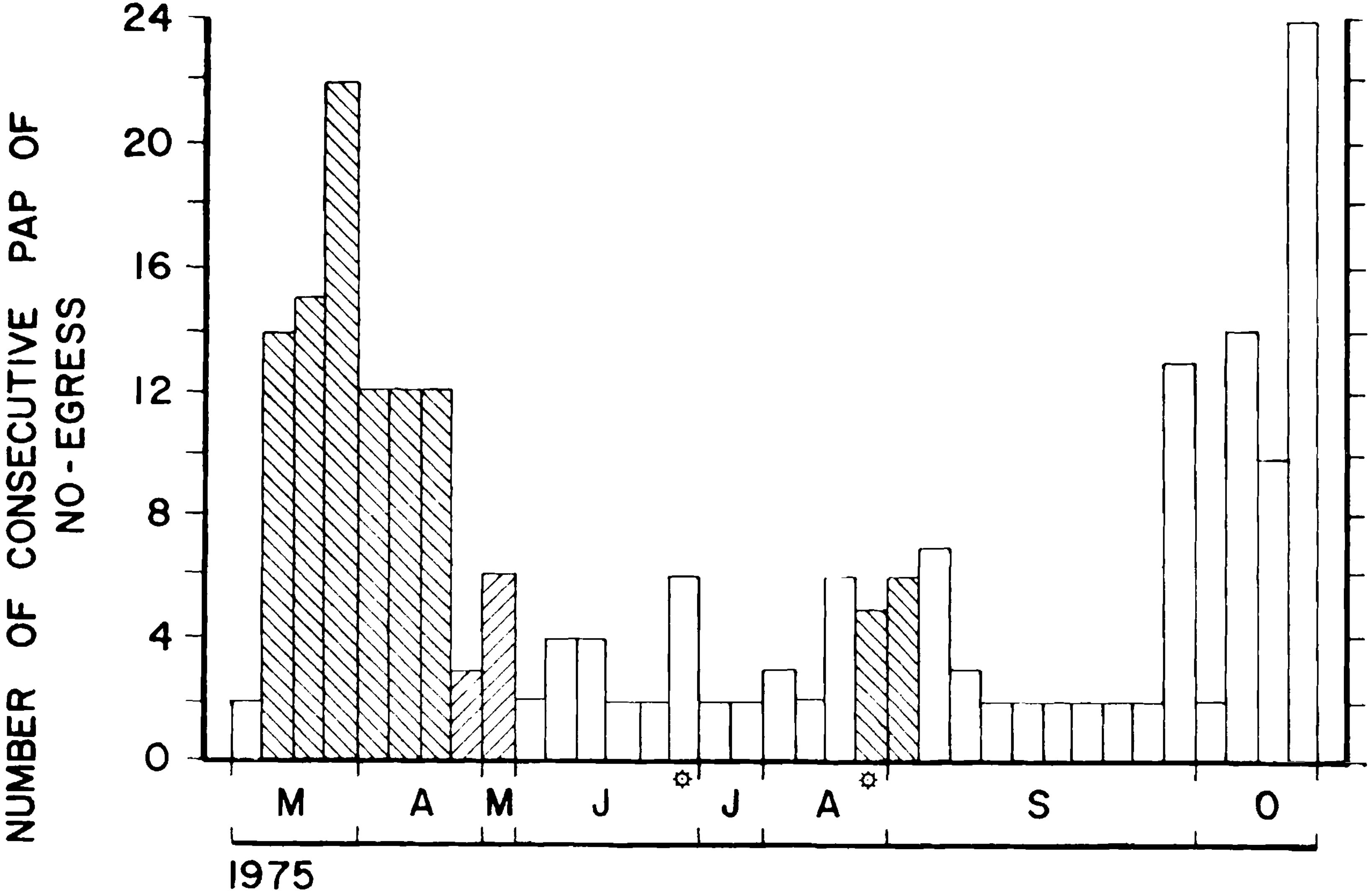


Fig. 2. Duration of known periods of 2 or more consecutive PAP with no-egress of 3 transmitter-bearing ♂♂ and 3 transmitter-bearing ♀♀ following each tortoise's initial emergence from hibernation. Periods that continued across monthly divisions are represented by bars with continuous diagonal lines. Those in March and April were from 3 adults each with 26- to 34-PAP periods. Periods during other months are in chronological order. ☼ = periods immediately following injury.

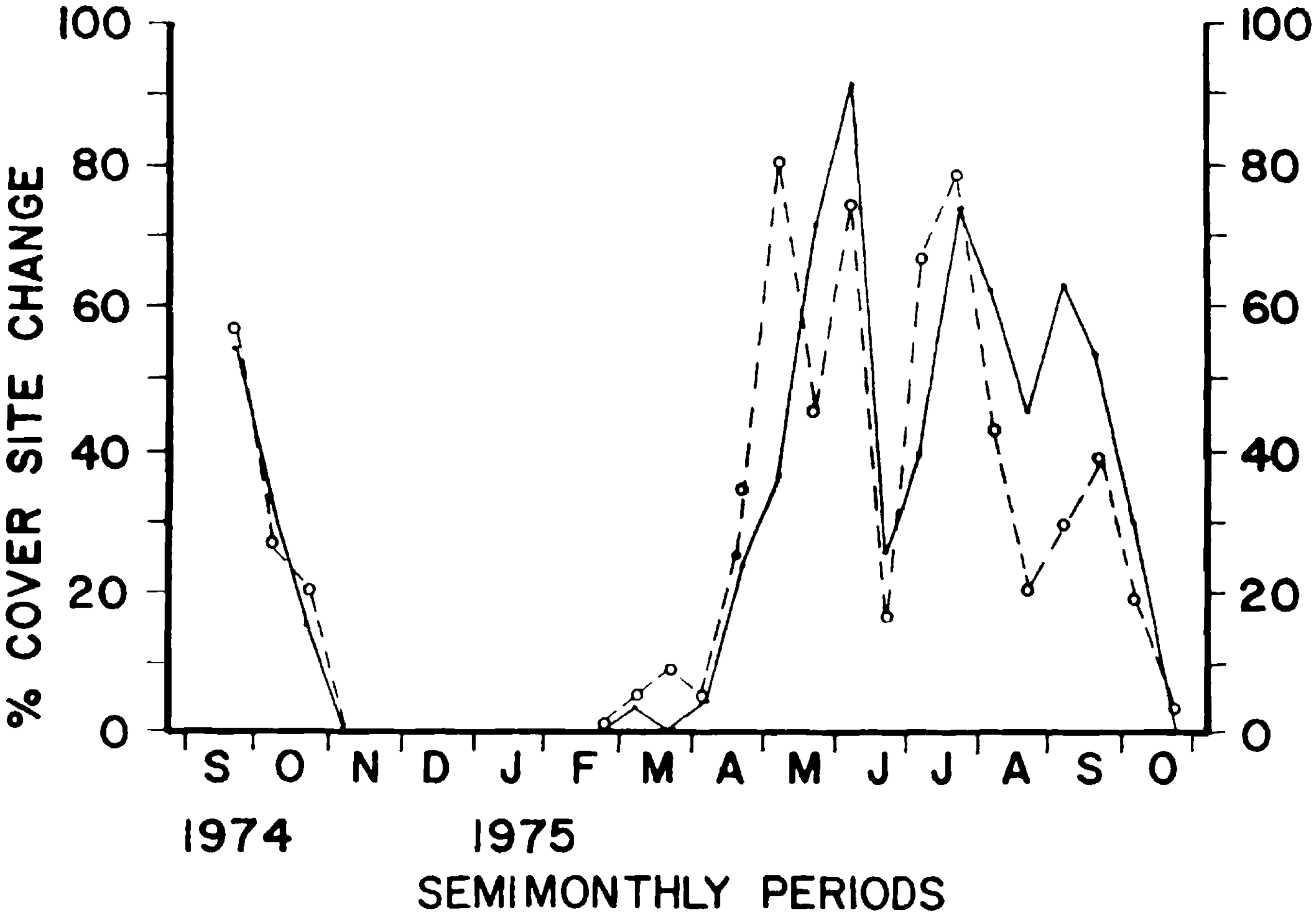


Fig. 3. Semimonthly percent of recaptures in cover that indicated that tortoises changed cover sites (6-10 transmitter-bearing adults).

Solid lines are ♂♂; broken lines are ♀♀.

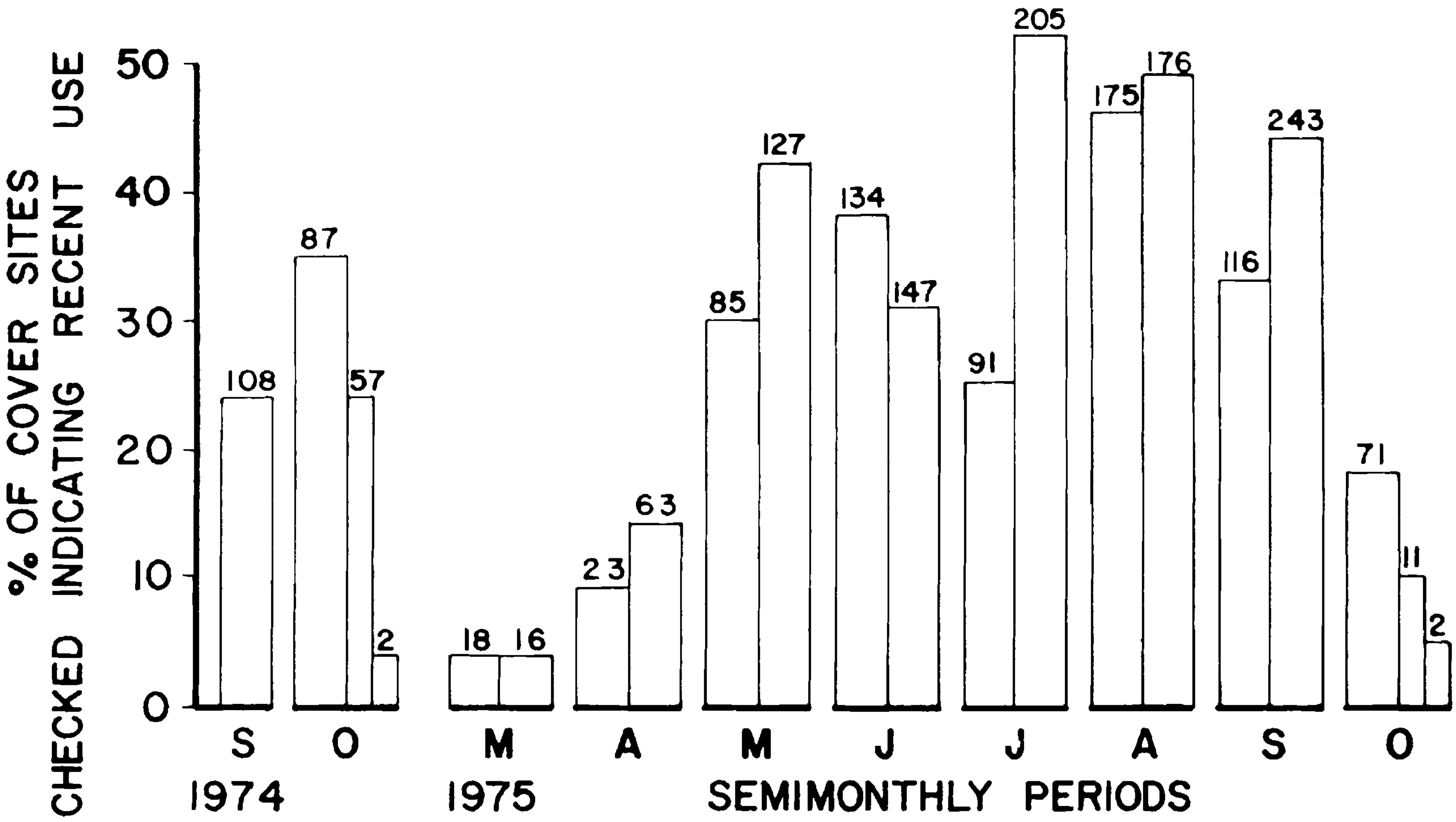


Fig. 4. Percent of cover sites checked that indicated "recent" use during each semimonthly period in which tortoises were active between mid-September 1974 and the end of October 1975. The last half of October in both years is divided in half to show the continuing trend. The number of recently used cover sites is given above each bar.

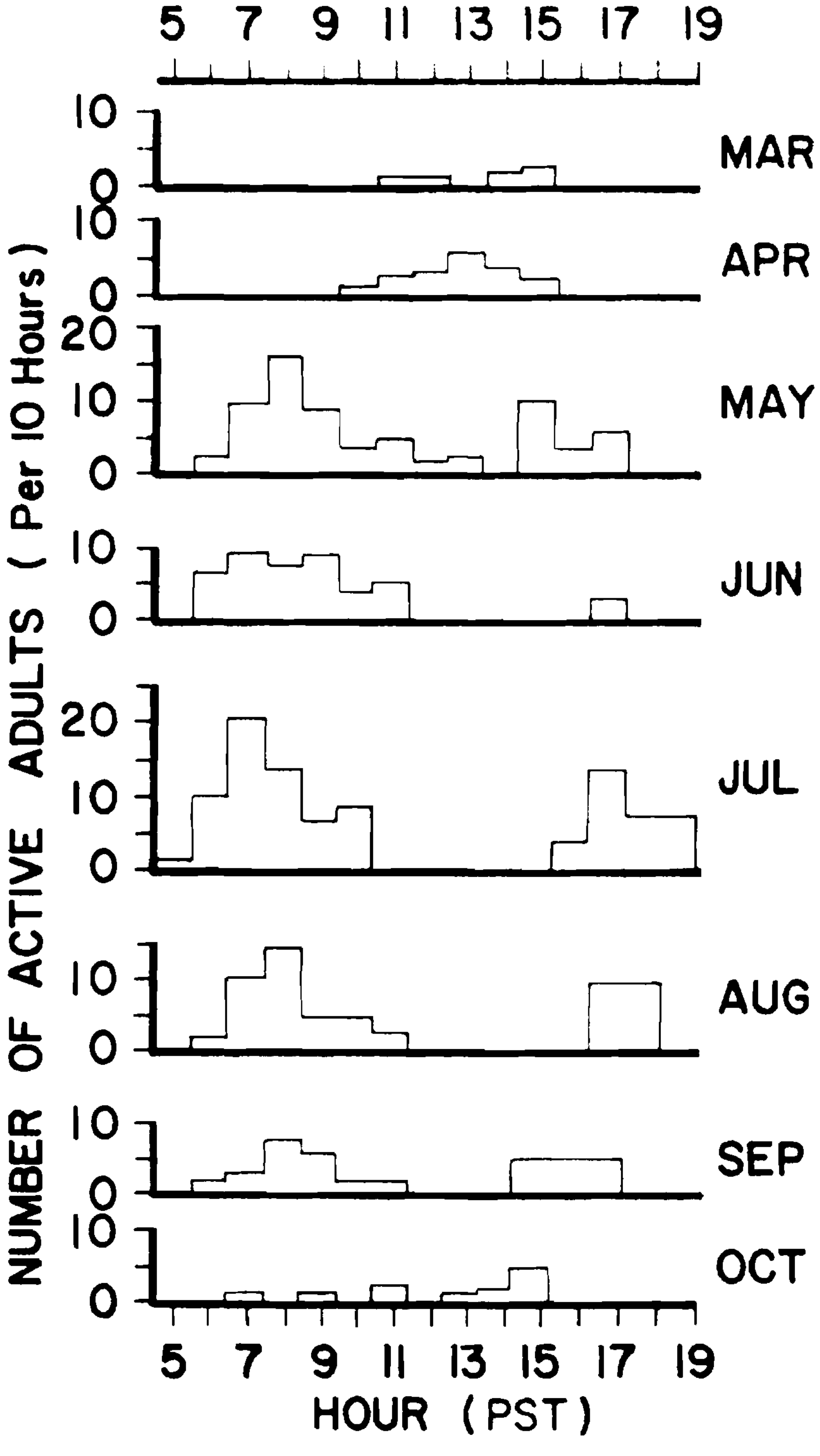


Fig. 5. Number and duration of the daily PAP indicated by the hours in which adults were observed engaged in epigean activity.

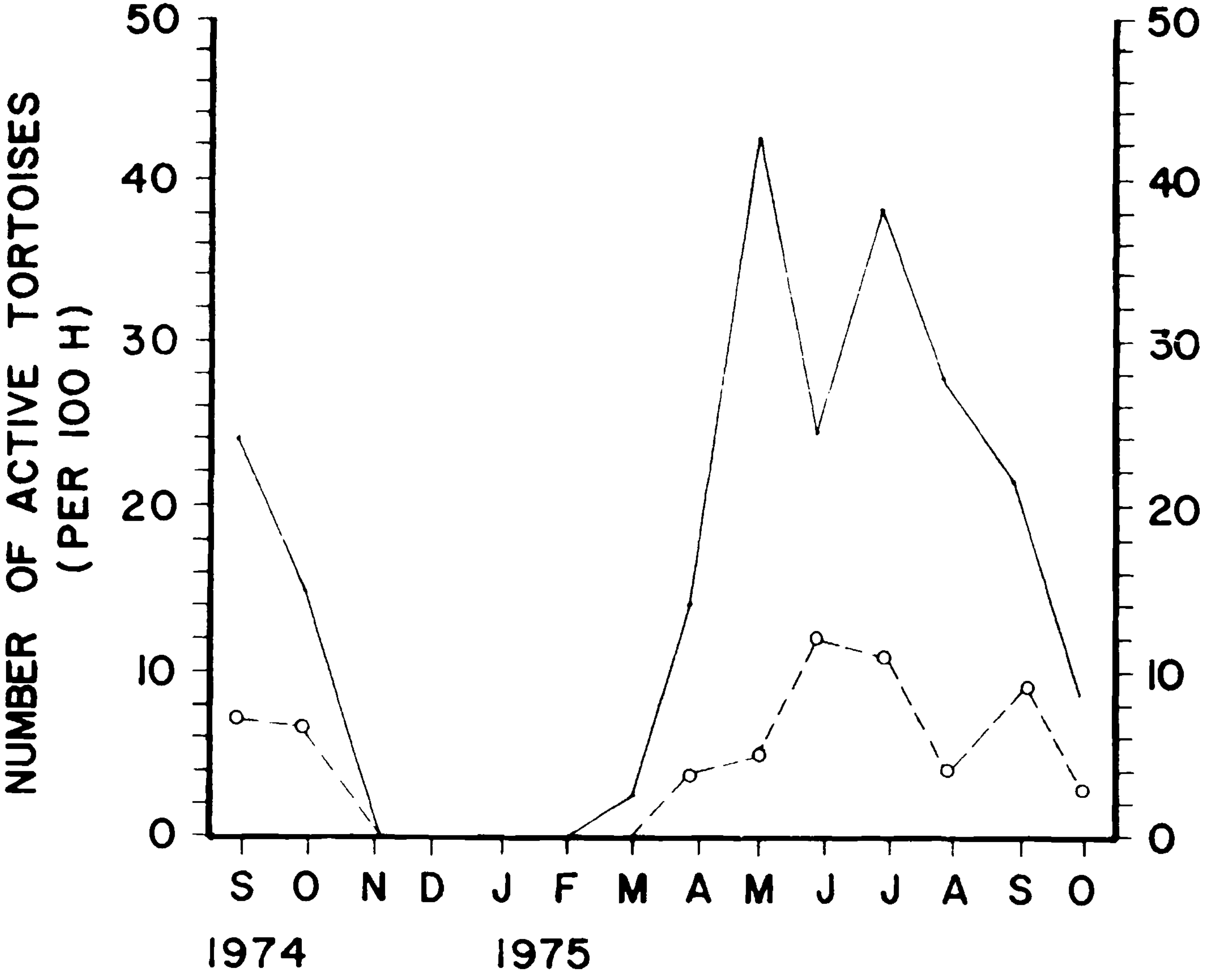


Fig. 6. Number of observations of transmitter-free tortoises engaged in epigean activity. Solid lines represent 55 tortoises 215-286 mm carapace length (*N* = 163); broken lines represent 25 individuals 82-214 mm carapace length (*N* = 47).

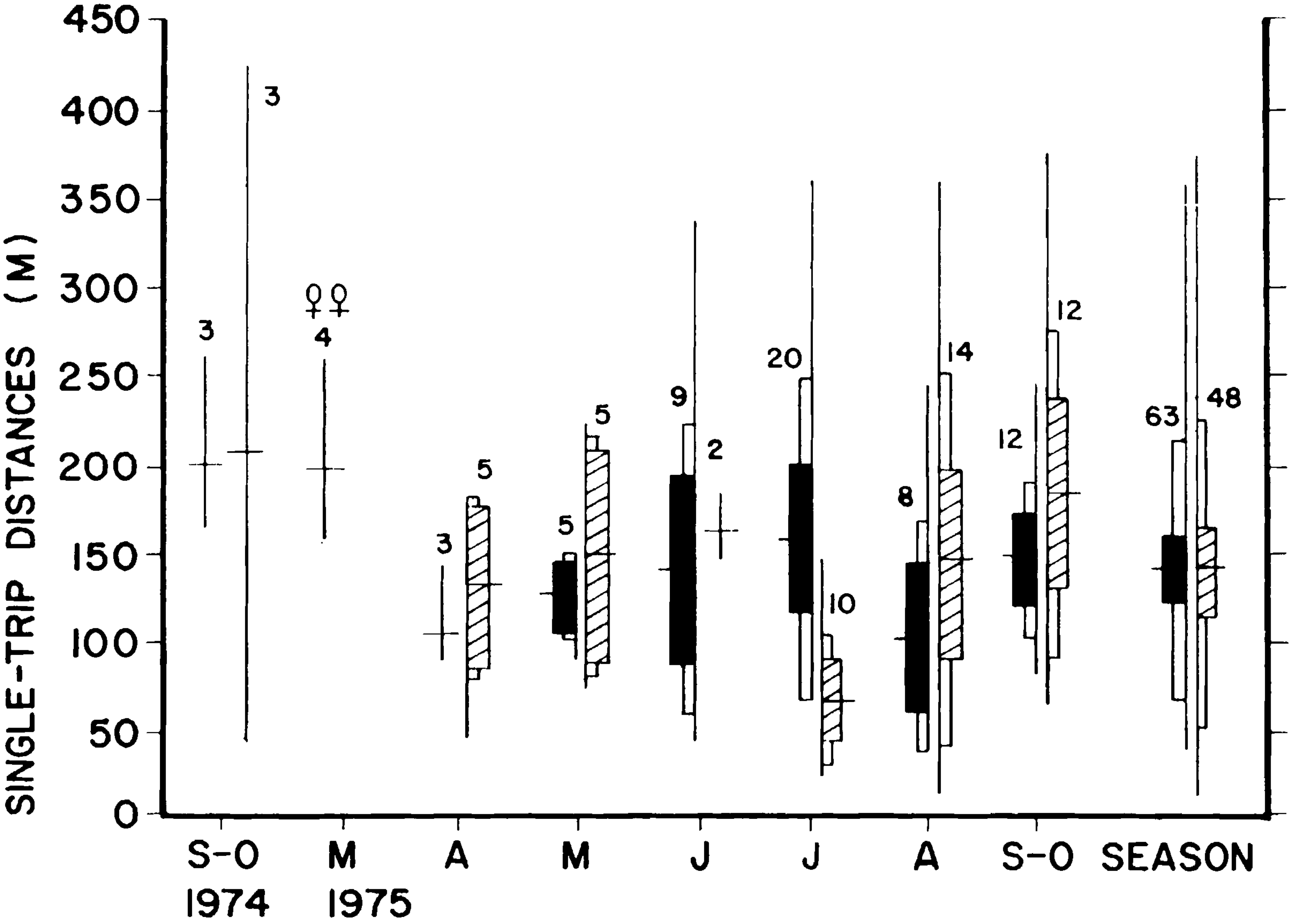


Fig. 7. Monthly values of 117 STD-SLD of 6 ♂♂ and 5 ♀♀; mid-September 1974 through mid-October 1975. Vertical and horizontal lines represent the range and $\bar{x}$; open rectangles = 1 standard deviation; solid rectangles = 2 standard errors (♀♀); diagonally-lined rectangles = 2 standard errors (♂♂). Numbers at the top of each bar indicate sample size. Standard deviation and SE not shown for samples $N \leq 4$.

Figs. 8A (Nos. 160 and 161),
8B (Nos. 108 and 96), and
8C (Nos. 94 and 203), on pages 88, 89, and 90, respectively.

Monthly activity areas of 6 transmitter-bearing adults shown in relation to home range. March, May, July, and September are delineated by continuous lines; recapture sites are indicated by filled circles for 1 recapture and the number for >1. April, June, August, and October are delineated by broken lines; single recaptures by open circles; and multiple recaptures by the number encircled. Filled squares indicate hibernation sites not used during the 2-month period; open squares indicate hibernation sites, if used, and the number indicated as in the manner of other recaptures. Home range boundaries cover monthly areas along the perimeter. The date of the last sighting in October is given with arrows indicating the individual. September 1974 sites are plotted from the 15th.

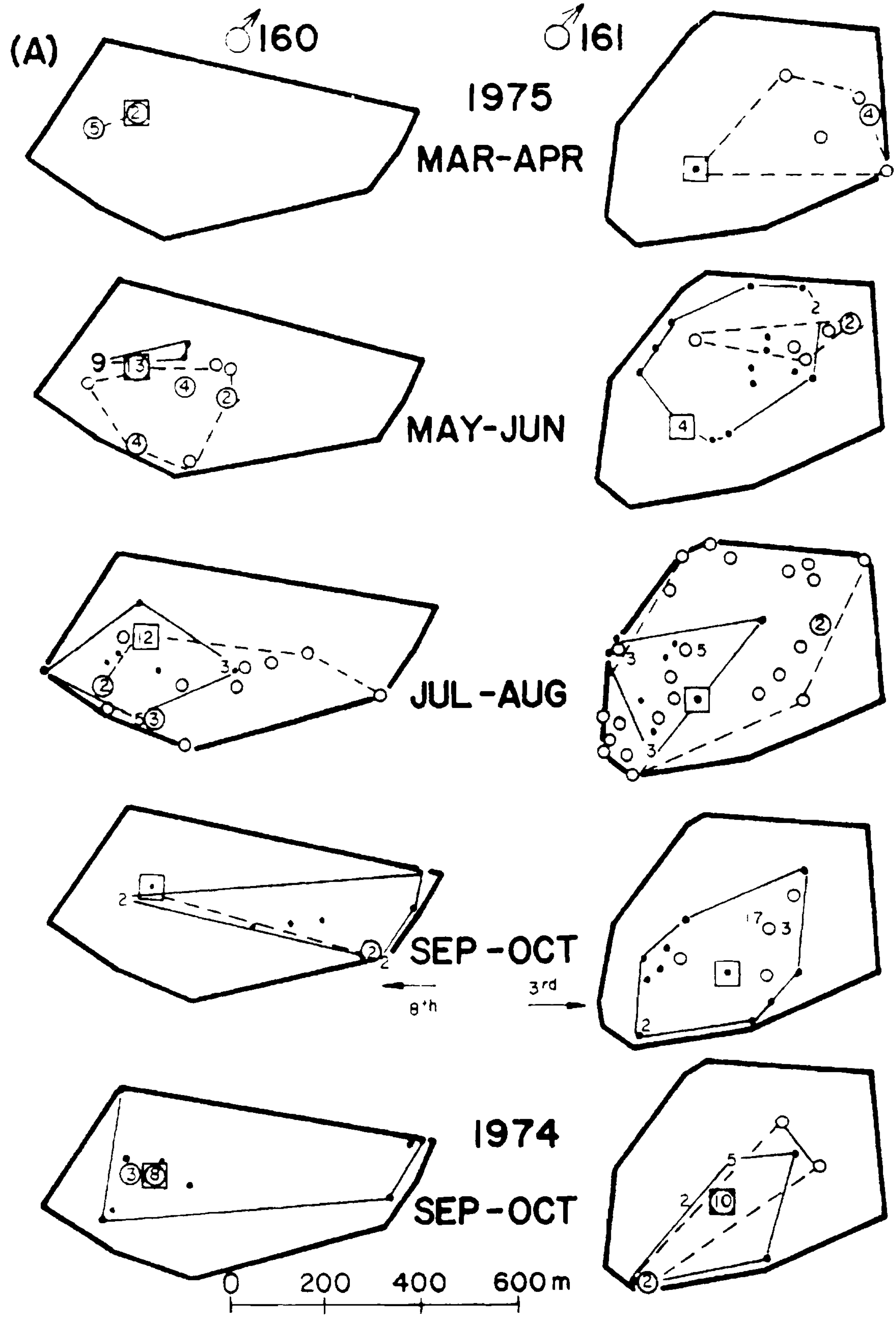


Fig. 8A. Monthly activity areas of tortoises No. 160 and No. 161 in relation to home range. Complete legend on page 87.

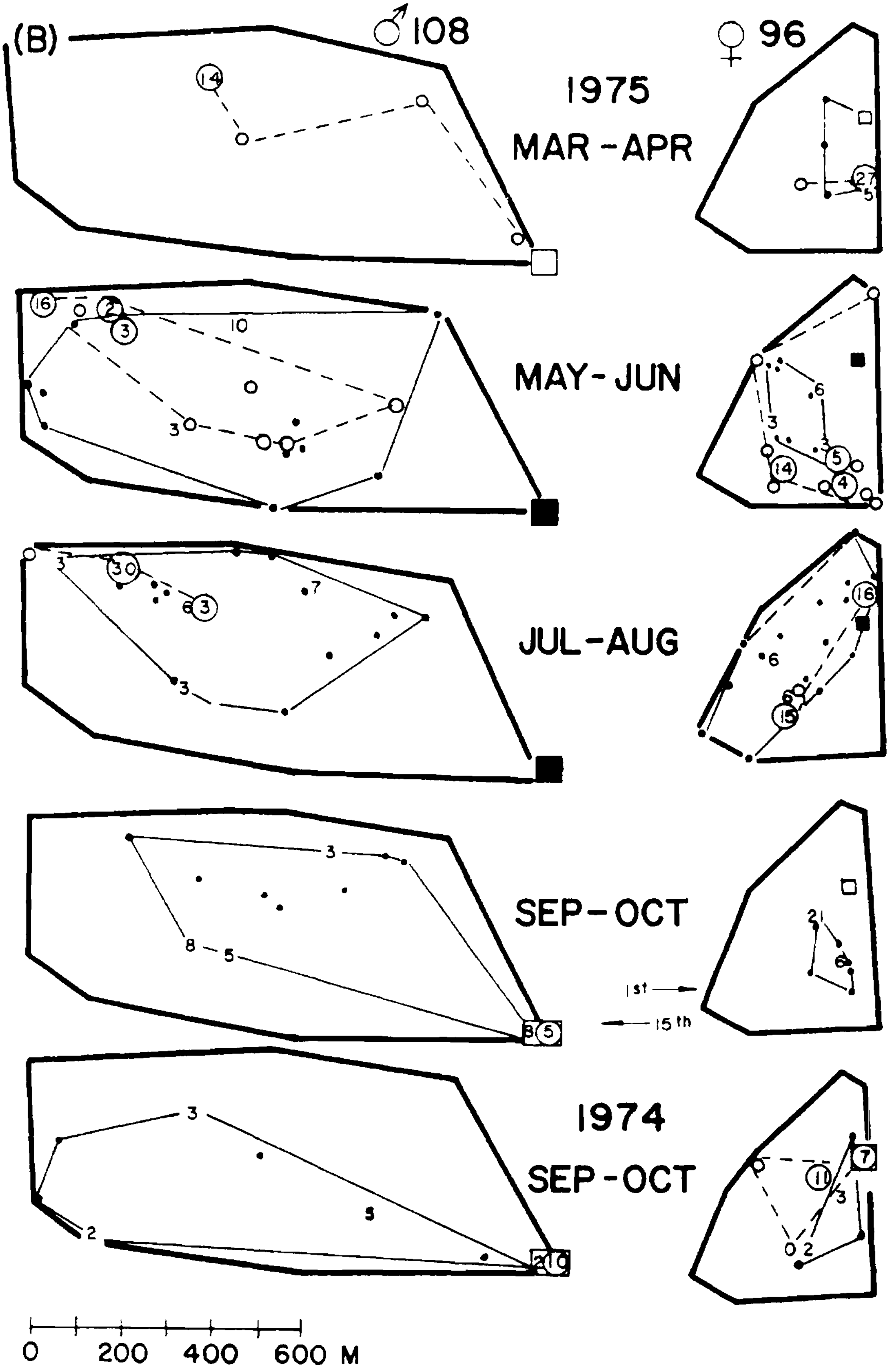


Fig. 8B. Monthly activity areas of tortoises No. 108 and No. 96 in relation to home range. Complete legend on page 87.

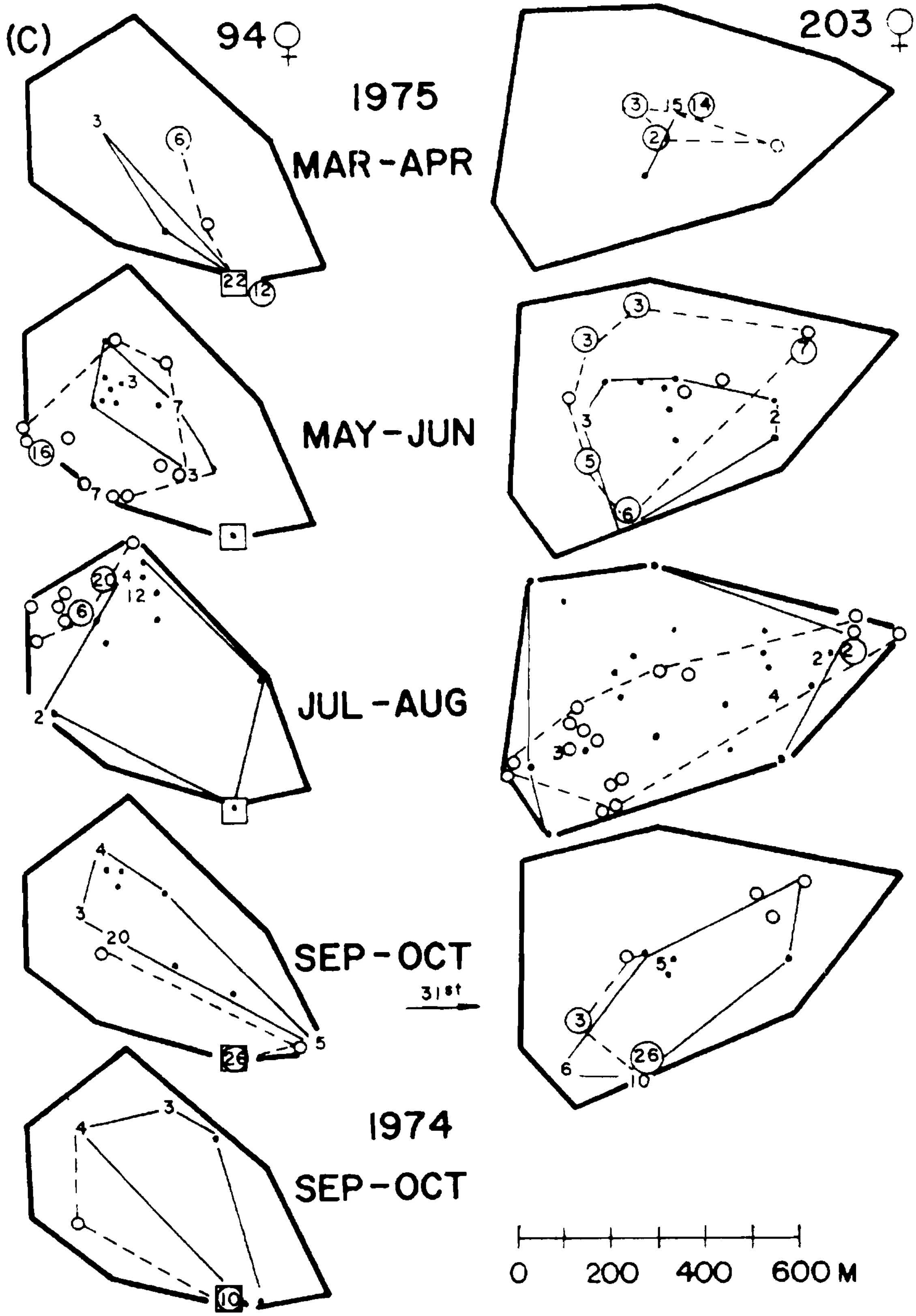


Fig. 8C. Monthly activity areas of tortoises No. 94 and No. 203 in relation to home range. Complete legend on page 87.

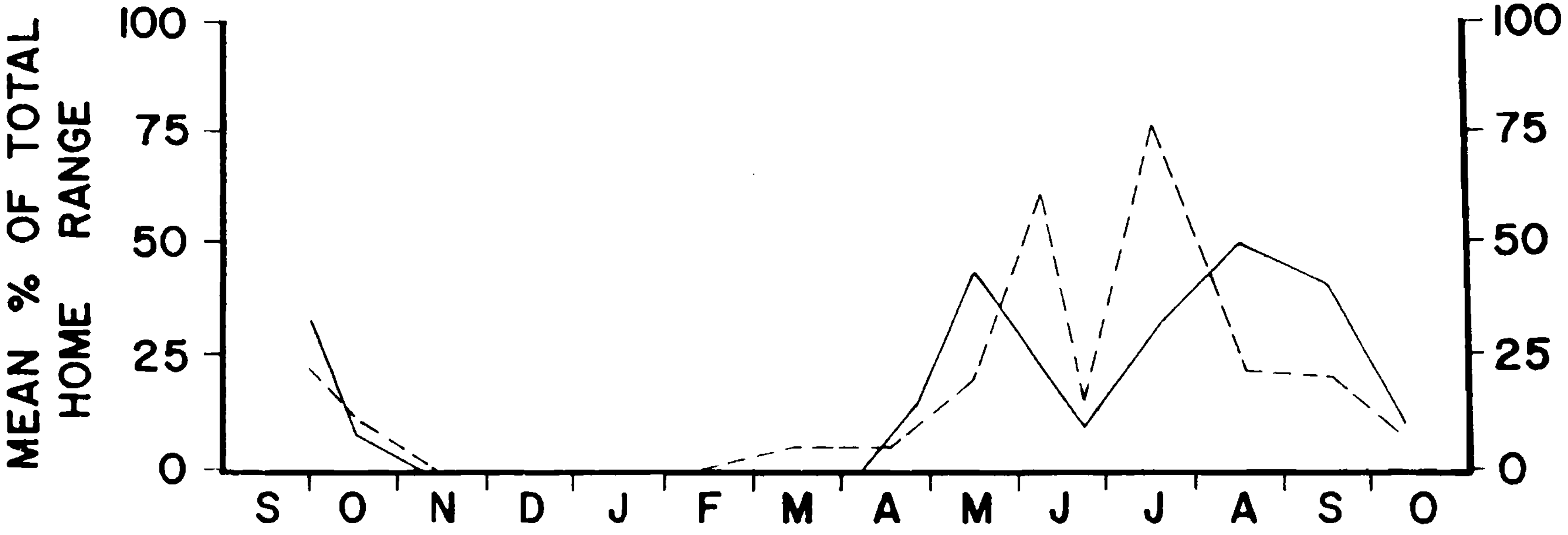


Fig. 9. Mean percent of home range area used each month by 3 ♂♂ and 3 ♀♀ from mid-September 1974 until transmitters were removed in October 1975. Solid lines are ♂♂; broken lines are ♀♀.

Table 1. Observations of behavior or sign of reproductive or possible territorial nature that occurred from July 1974 through October 1975; years combined except where noted. Sign not included if behavior observed.

Type of behavior or sign	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Total
Copulation						3	1	2*	6
Mating depressions		1	3	2		2	8	2*	18
Simultaneous use of burrows (♂ and ♀)	1	1	1	3	2	10	16		34
Agonistic behavior		1			3	2	3	2*	11
Simultaneous use of burrows (♂ ♂)						3	8	8	19
Sign of interaction type, not known			3				6	6	15
Total	1	3	7	5	5	20	42	20	103

*1974 only.

Table 2. Area of convex polygon delineated by all recaptures, mid-July 1974 through October 1975 of 6 transmitter-bearing adults monitored for at least the full active season, 1975. Recaptures during hibernation not included.

Tortoise	Captures and recaptures (N)		Area of convex polygon (home range) (ha)
♂♂			
No. 160	103		20
No. 161	136		20
No. 108	175		38
		$\bar{x}$ (± 1 SE)	26 ± 6.0
♀♀			
No. 96	215		11.3
No. 94	241		18.7
No. 203	203		27.0
		$\bar{x}$ (± 1 SE)	19 ± 4.5

Table 3. Monthly distribution of captures, area of convex polygon, and adjusted home range area of 11 transmitter-free adults, from initial capture through October 1975. Repeated captures during hibernation (H) not included.

Tortoise	Carapace Length (mm)	1974							1975								Total captures (*N*)	Area of convex polygon (ha)	Adjusted area* (ha)
		M	J	J	A	S	O		M	A	M	J	J	A	S	O			
♂♂																			
No. 194	240						1	H	H	1	3	1	8	2	1		17	8	19.1
No. 105	248			1	1	1	1	H				3	2	6	2		17	14	33.5
No. 162	255					1		H			5	3	4	1	3		17	4.5	10.8
No. 98	255			1		3	1	H	H	1	3	2	3	4	7	4	29	36.5	65.2
No. 48	280	1		2	1	2	3	H	5	6	1		3		4	4	32	26.2	54.5
No. 66	272	1		1		4	2	H	H	2	6	6	7	14	13		56	21.0	29.6
♀♀																			
No. 79	225	1	1					H	H	1	2	7	7	4	1	1	25	7.6	14.7
No. 47	230	1			1	1	1	H	1	3	5	3	2		3	1	22	3.1	6.4
No. 169	230					1	1	H			2		5	4	3		16	5.0	12.7
No. 101	226				2			H		1		1	3	1	2	1	11	2.0	6.6
No. 236	246							H			1	4	1	3	1		10	6.0	21.1

*Jennrich and Turner (1969).

Status of the Desert Tortoise, *Gopherus agassizii*, In the State of Utah

Eric M. Coombs

The desert tortoise, *Gopherus agassizii*, is a protected nongame species in the State of Utah. This status is a result of the concern for the animal and its habitat, both of which have experienced various disturbances over the years. This report is a brief summary of a final report that I recently completed on the desert tortoise in Utah (Coombs, 1977*b*).

The desert tortoise naturally inhabits ≈ 180 km^2 of the extreme southwestern corner of Washington County, Utah, on the slope of the Beaver Dam Mountains and the Beaver Dam Wash. There are an additional 26 km^2 now inhabitated by introduced tortoise populations north of St. George, Utah. There are ≈ 800 tortoises presently inhabiting the state. An estimated 350 tortoises are native to the Beaver Dam Slope, with an additional 70 captives that were introduced. There are about 150 tortoises in the Paradise Canyon Study Area, and about 200 in the St. George Hills population (Fig. 1). Woodbury and Hardy (1948) forewarned of the conflicts that were affecting desert tortoise populations in Utah. In May 1971, the Utah Division of Wildlife Resources placed the desert tortoise, along with the venomous Gila monster, *Heloderma suspectum*, on the state protected wildlife list. There are > 400 known winter dens on Beaver Dam Slope, and (estimating an average of 5 tortoises/den) the state may have once sustained more than 2,000 tortoises.

The tortoise habitat on the Slope is ≈ 900 metres in elevation. The area is a gravelly floodplain with *Larrea tridentata, Ambrosia dumosa, Yucca brevefolia, Krameria perviflora, Dalea freemontii, Eurotia lanata, Thamnosma montana,* and *Ephedra nevadensis* being the dominant species. Few tortoises are found above the blackbrush, *Coleogyne ramosissima,* zone.

The St. George areas are characterized by Navajo Sandstone with scattered extrusions of basaltic lava flows. The vegetation is similar to that of the Beaver Dam Slope, except that *Yucca brevefolia* and *Thamnosma montana* are missing.

Tortoises were located by walking, driving, searching their excavations, and with the aid of a well-trained dog. Tortoises that were captured were observed, marked with a notching system, and various data taken and recorded on special data sheets. Tor-

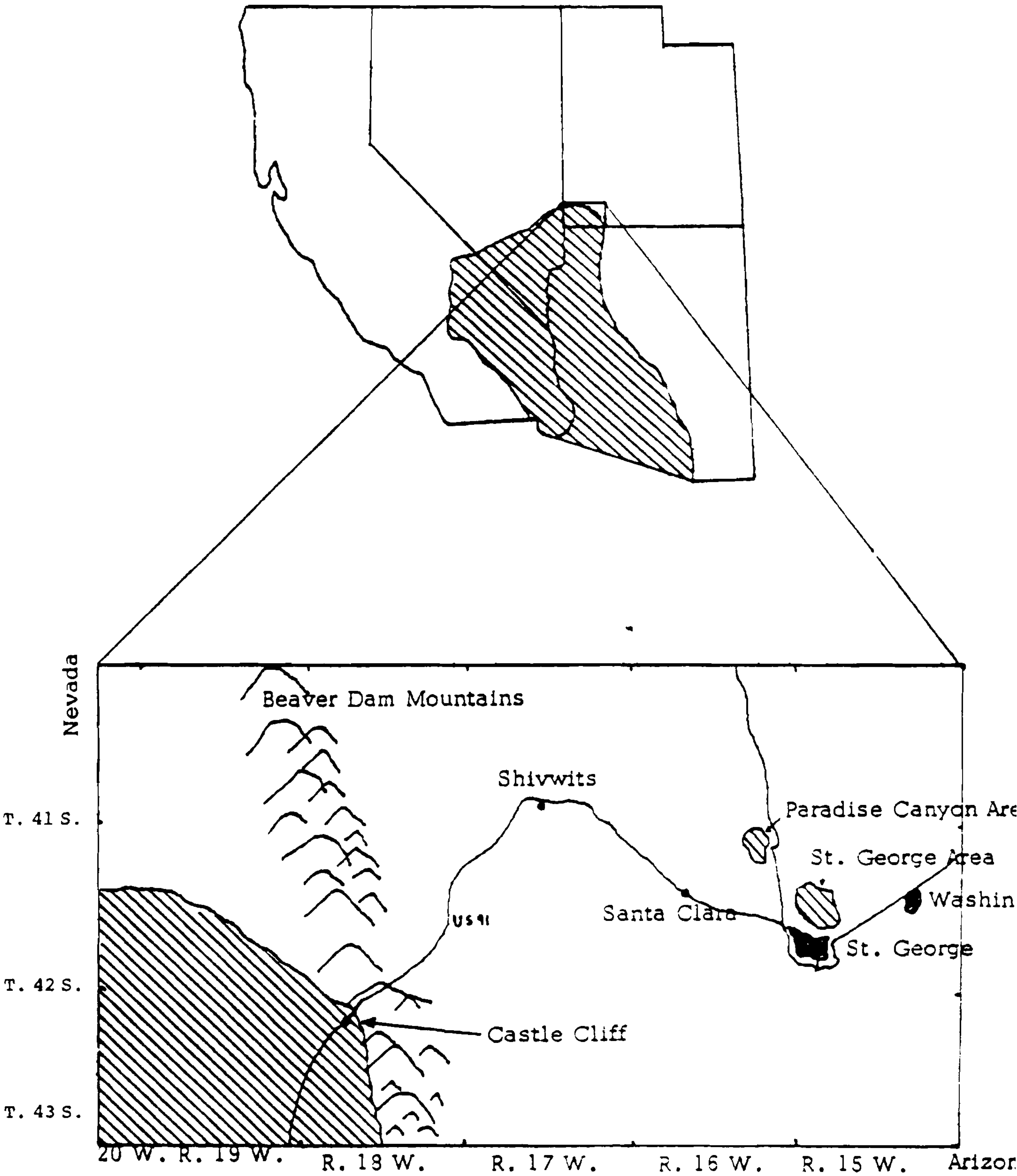


Fig. 1. Distribution of *Gopherus agassizii* in southwestern Utah.

toises that were unobtainable in certain dens were recorded as to their presence and estimated size. Scats, if found in the dens, were also collected for future analysis.

Winter den locations were mapped and recorded if they were active or inactive. Over 400 dens were discovered, and more certainly remain undetected. The location and structure of these dens are critical and a limiting factor to tortoises in Utah, and govern their distribution within the state. Tortoises often dig their own dens under exposed layers of caliche, where washes have eroded through.

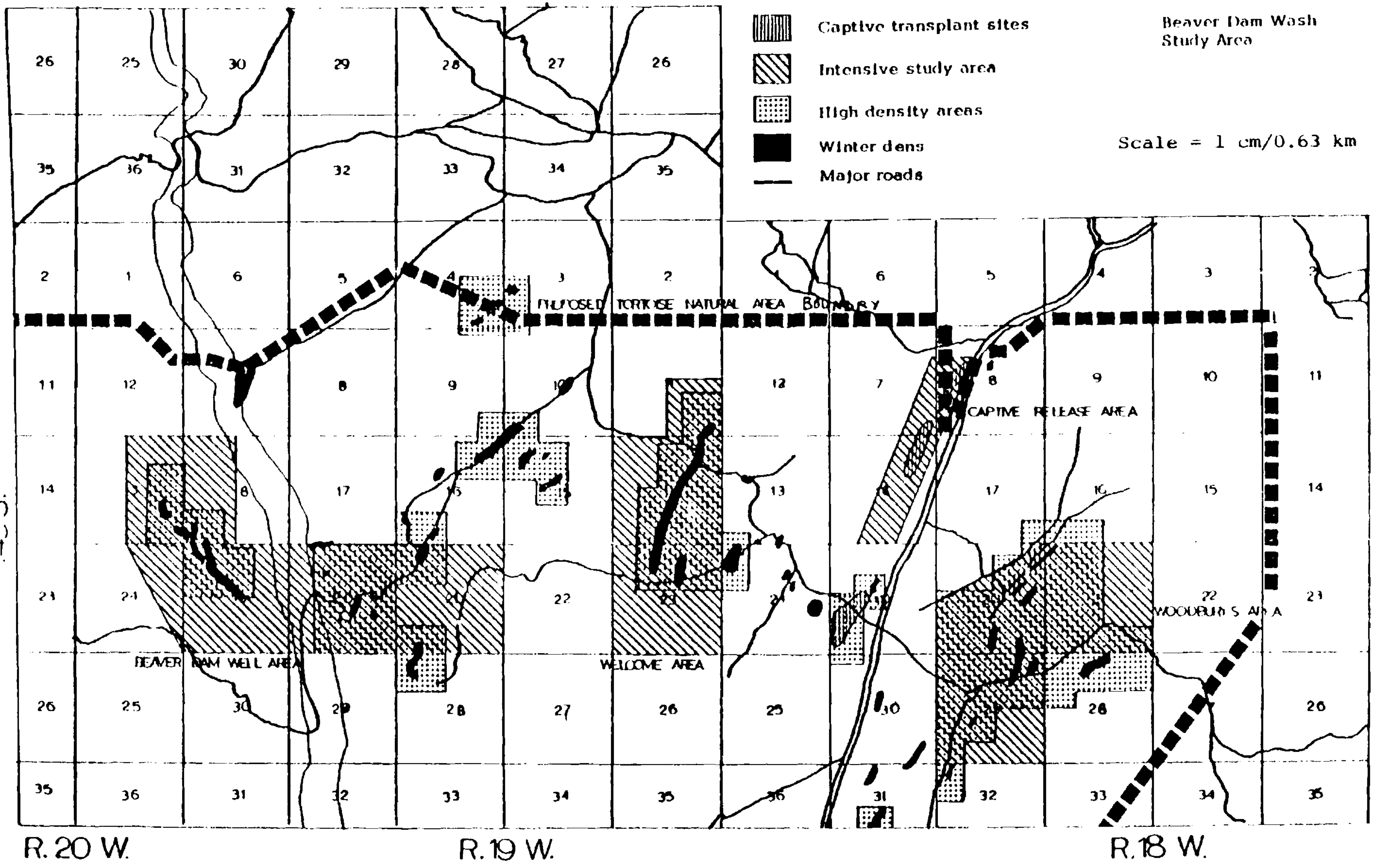
Summer holes, the temporary excavations about 0.6-1.2 metres deep, are used during the active part of the year, April through October, with tortoises digging an average of 2-4 holes per year. During years of lush plant growth and above average rainfall, tortoises may construct more summer holes. The holes are seldom used more than 1 active season, and are rarely shared with other tortoises. The holes cave in annually from rodents, weathering, and from livestock trampling.

As previously mentioned, I estimated the population of the Slope to have been around 2,000 tortoises. Since the 1860s, the Slope has sustained a long history of heavy grazing by cattle and sheep, and road development. Tortoises were faced with competition for food and space, and were heavily collected for the pet trade.

During the Woodbury and Hardy study (1948) the desert tortoise population was estimated to be 36% male and 64% female. The population is now 70% male and 30% female, more than a complete reversal. This change was directly attributed to collecting for the pet trade, as females were easier to find near the winter dens, while the males had mostly dispersed out into the flats to establish their summer home ranges.

There are 33.7 km^2 of habitat on Beaver Dam Slope that contain the majority of the tortoise population and winter dens (Fig. 2). Since the disturbance of the population, the density has changed from $59.5/km^2$ to $10.4/km^2$, a figure 5.7 X lower than it once was. The Paradise Canyon study area has $\approx$ 57.9 tortoises/km^2, and the population is $<$ 80 years old. Hardy (1945) further substantiated and documented that tortoises were being released and becoming established in the areas north of St. George. About 30% of the known Utah tortoise population has been marked since 1970. The population percentages of the Beaver Dam Slope are estimated to be 72.0 adult, 18.0 subadult, 9.0 juvenile, 1.0 hatchling, with Paradise Canyon being 42.0 adult, 20.0 subadult, 28.0 juvenile, and 10.0 hatchling.

Woodbury and Hardy (1948) stated that a tortoise population should have an annual increase of at least 5% in order to maintain itself. The natality rate of the Beaver Dam Slope has only been 1.57%, in contrast to 4.4% in the Paradise Canyon population.


Beaver Dam Wash
Study Area
Captive transplant sites
Intensive study area
High density areas
Winter dens
Major roads
Scale = 1 cm/0.63 km
PROPOSED TORTOISE NATURAL AREA BOUNDARY
CAPTIVE RELEASE AREA
BEAVER DAM WELL AREA
WELCOME AREA
WOODBURY'S AREA
T.43S.
R. 20 W.
R. 19 W.
R. 18 W.

There were 32 young/100 females on the Slope, and 47 young/100 females in Paradise Canyon.

Mortality plays an important role in governing the trend of the Utah tortoise populations. Woodbury and Hardy (1948) found only 30 dead tortoises in a 10-year period. I found 73 in 6 years. The mortality rate of the Beaver Dam Slope's population was estimated at 6.86%/year. Added to this is a 2.2% depletion due to human removal of tortoises as pets, and mortality related to vehicles which yields a total loss rate of 9.06% of the population. This rate, less the 1.57% natality rate, is an annual loss of 7.49% of the population. If human removal is curtailed, it would still leave a net population loss of 5.29%/year. If this rate of decline continues as a percentage, there will be only 10 tortoises in 85 years. At a 7.49% rate of decline, there will be 10 tortoises in 55 years. However, as populations decline, the mortality rate increases. The mortality rate of the Paradise Canyon population is 1.07%.

Predation accounts for 35% of the observed losses. The primary predators are the desert kit fox (*Vulpes macrotis*) and the coyote (*Canis latrans*). Kit foxes often inhabit tortoise dens, thus increasing the chances of tortoise predation. Juveniles, because of their small home ranges, were found to be 2.1 X more likely than adults to be recaptured; thus this phenomenon may also increase the predation rate by kit foxes that concentrate around tortoise dens.

Food habits were also observed and were found to vary with each area, depending on elevation, soil type and vegetation. The main food items observed were *Bromus rubens* and *Erodium cicutarium*. Woodbury and Hardy (1948) observed that *Muhlenbergia porteri* and *Bromus rubens* were the chief foods. Most feeding occurs in April, May, and September. The diet was found to change with the availabilities of plants throughout each season. A total of 39 food species were observed. The major foods were *Bromus rubens, Erodium cicutarium, Chorizanthe rigida, Eriogonum inflatum, Cryptantha circumcissa, Tridens pulchellus, Tridens pilosus, Euphorbia albomarginata,* and *Plantego insularus*.

A total of 25 scats from tortoises and cattle were sent from 3 different locations from the Beaver Dam Slope to Colorado State University, Range Department, for analysis. The computed dietary similarity indices were: tortoises-tortoises 0.61, cattle-cattle 0.72, and tortoise-cattle 0.37. Many items used in Utah for food were not important in other states (Berry, 1976; Burge and Bradley, 1976). The present population of 350 tortoises on the Slope may utilize ≈ 3 metric tons of vegetation per year of activity.

The diet of Utah tortoises has changed since Woodbury and Hardy's (1948) study in that perennial grasses are much less abundant on the range and in the diet. These grasses are important as they would provide the major source of food and moisture after annuals dry up in mid-May to mid-June. Previously, (Coombs, 1977*b*), I stated my belief that because of the change of the water, nutrients, and electrolytes in the diet from perennials to annuals, the change in density, sex ratios, disruptions of social behavior, and competition from livestock that the Utah population is in imminent danger if one or more of these factors are not corrected. Tortoises have often been observed feeding on unpaved roads where easy access is provided to the abundant annuals. Behavior modeled to this type of utilization increases the danger of predation, collection, and mortality related to motor vehicles.

Tortoises have been observed drinking water from various collecting places after summer rains. Some tortoises exhibited a distinct familiarity of such places, and made use of them after rains. After drinking, urine was spontaneously eliminated.

The home ranges were found to average ≈ 0.8 hectares, with some as large as 7.3 ha. Daily movements of tortoises averaged: hatchlings (15-46 m/day), juveniles and subadults (152-366 m/day), and adults (152-457 m/day), depending on the season and weather. Factors involving tortoise movement included feeding, comfort seeking, social interactions, breeding, and establishing and maintaining territories.

Grazing has, without a doubt, been a very important factor governing the tortoise and its habitat in southwestern Utah. Woodbury and Hardy (1948) observed the overgrazing that occurred and speculated on the possible effects on the desert tortoise. Hardy (1976) mentioned the reduction of the once-abundant perennial grasses. The Slope has not received a year's rest in > 100 years of livestock grazing. Not only grazing, but the presence of man, throughout all of the tortoise habitat, has influenced the downward trend of the Slope's population. Part of the underlying problem may deal with the nutrients, water, and electrolyte balance in the foods that remain, as a result of grazing pressures, certainly not in the amount or bulk that is left (Coombs, 1977*b*). The history of poorly-managed livestock practices has had a severe impact on one of Utah's most unique, fragile, and limited habitats. Many changes in the populations and the habitat occurred within the lifetime of many of the presently remaining individuals. The ability of a species to adapt genetically to a changing environment belongs to populations, not individuals, especially in this case of a *K*-selected species, the desert tortoise.

I feel that the long history of overgrazing on Beaver Dam Slope cannot be undone with any grazing systems because the area is too fragile and rainfall too low. The damage took over 100 years to occur; it will take many more to heal. Only the complete elimination of grazing on the Beaver Dam Slope may prove effective in reestablishing the vegetation in tortoise habitat to sustain and produce a viable population. If conditions continue as they have, the Beaver Dam Slope population faces inevitable elimination.

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Adaptive Responses in the Water and Electrolyte Budgets of Native and Captive Desert Tortoises, *Gopherus agassizi*, to Chronic Drought

John E. Minnich

Water turnover was measured using tritiated water (HTO) in a free-living population of desert tortoises *(Gopherus agassizi)* near Barstow, California, during summer 1970. The release of captive animals at the study site permitted comparison of their H_2O budgets with those of established tortoises. During July and early August 1970, conditions at the study site were very dry. Under these conditions H_2O intake rates of all tortoises (0.27 ml$[100\ g]^{-1}$day^{-1}) were very low, approximating rates of metabolic H_2O production (0.22 ml$[100\ g]^{-1}$day^{-1}). Tortoises lost H_2O more rapidly (0.46 ml $[100\ g]^{-1}$day^{-1}), lost body weight slowly (0.28 g $[100\ g]^{-1}$day^{-1}), mostly through evaporation, remained in their burrows and did not feed or void urine. Cessation of feeding protects tortoises from accumulating toxic levels of dietary potassium at a time when insufficient water is available to excrete it. Most excess K was stored in the urinary bladder as precipitated potassium urate salts.

Rain fell at the study site on 12 August 1970, causing all animals to become active. Established animals drank rainwater, voided urinary wastes and stored the rainwater in their bladders as a dilute urine. They also resumed daily activity and feeding during the period following the rain. Although dietary plants still contained little H_2O but high K concentrations, tortoises were capable of excreting the K load because the dilute bladder urine was apparently utilized as a H_2O reserve. In contrast to the established tortoises, captive animals that had been recently released did not drink rainwater and, although active after the rain, did not eat.

One of the most challenging physiological problems faced by desert organisms is the procurement and conservation of water. A closely related problem is the excretion of dietary electrolytes with a small loss of water. This is important because (1) concentrations of electrolytes in the food of many desert animals are very high and (2) some water is lost in ion-free form through evaporation. Moreover, most animals cannot balance evaporation through the production of "metabolic water", created by oxidation of foodstuffs (Schmidt-Nielson, 1964). Because drinking water is generally not available on a regular basis, most desert animals obtain needed water from their food and excrete excess dietary electrolytes with little water loss. Desert reptiles excrete most ingested electrolytes in the urine as precipitated urate salts (Minnich, 1972) and, in many species, via the salt gland (Dunson, 1969, 1976).

One dietary electrolyte of particular interest is potassium. This electrolyte, found in high concentrations in many desert plants of North America (Minnich and Shoemaker, 1970, 1972; Nagy, 1972), is regulated very precisely in both intracellular and extracellular fluids of almost all animals (Burton, 1968; Schmidt-Nielsen, 1975; Minnich, 1977). Elevation of intracellular K concentrations disrupts such basic cellular processes as DNA replication, RNA synthesis and the activity of many enzyme systems (Bygrave, 1967; Lubin, 1964). Elevation of extracellular K disrupts tissue excitability, heart rhythms and nerve impulse conduction (reviewed by Steinbach, 1962). Consequently, desert animals which ingest considerable dietary potassium most excrete the potassium load.

Desert tortoises (*Gopherus agassizi*) are especially interesting for studies on water and electrolyte metabolism, being exclusively herbivorous and thus potentially able to ingest considerable quantities of potassium with little accompanying water. Unlike most herbivorous desert reptiles, desert tortoises lack a functional salt gland (Schmidt-Nielsen, 1964; Minnich, 1977). Consequently, the only routes by which they can excrete potassium are through the feces and urine. Tortoises also possess a large urinary bladder which may be utilized for storage of water and urinary wastes. Finally, preliminary observations suggest that during chronic summer drought tortoises do not consume any preformed water. Is the cessation of feeding at these times a device which protects tortoises from accumulating toxic levels of potassium at a time when they are unable to obtain sufficient water to excrete the potassium load?

The objectives of this study are to (1) quantify water intake and loss in free-living desert tortoises during summer drought, (2) assess the handling of potassium by free-living tortoises, (3) investigate possible functions of the urinary bladder under natural conditions and (4) compare the water and electrolyte metabolism of native tortoises to that of captive animals released for a short period at the study site.

METHODS

Study Site. Field studies on desert tortoises were conducted during the summers of 1970 and 1971 at Stoddard Valley (elevation = 900 m), ≈ 10 km south of Barstow, San Bernardino County, California (Minnich, 1971, 1973, 1976a). The study site contained sparse vegetation characteristic of much of the Mojave Desert (mostly *Larrea tridentata, Ambrosia dumosa* and dried grass). There were 2 principal divisions to the study site. The northern site was in the bottom of Stoddard Valley and contained sandy soil. The southern site, located 2 km SSW of the northern site was located near a range of hills (elevation = 1000 m) and contained a more gravelly soil. A few tortoises were also studied at a site 0.5 km south of the range of hills. In addition to examining established wild tortoises, a number of captive animals that had been released at the study site were also monitored to see if they fared as well as the established animals.

Water Turnover. Water turnover was quantified by measuring the rate of disappearance of tritiated water (HTO) injected intraperitoneally at a dose of 1 ml/kg body weight of 0.1 mCi/ml in 0.9% NaCl. After sufficient time for equilibration of the isotope with the body water (12-24 h), an initial sample of bladder urine was obtained. During equilibration, animals were held in cages at room temperature (20°-25°C) without access to food or water. Tritium activity in the initial urine sample was used to estimate body water volume. The stock solution of HTO used for injection was standardized by injecting a measured volume into a known volume of distilled H_2O and determining the resulting tritium activity. Body water content was calculated from the equation,

$$W = \frac{V_s \, CPM_s \, \frac{a}{s}}{CPM_a} - a,$$

where W = body water content (ml),

V_s = volume of standard solution (ml),

s = volume of stock solution injected into standard solution (ml),

a = volume of stock solution injected into animal (ml),

CPM_s = tritium activity of standard solution,

CPM_a = tritium activity of bladder urine of animal.

After injection of HTO and collection of the initial urine sample, tortoises were weighed and released at the site of capture. At intervals of 7-10 days, tortoises were recaptured by hand, weighed and a sample of bladder urine obtained to assess the rate of HTO disappearance. From information on weight changes, body water content and rate of HTO disappearance, rates of water intake and loss were calculated from the equations,

$$I = \frac{100\ KW_i}{BW_i},$$

$$L = I + \frac{100\ (BW_iW_i - BW_fW_f)}{BW_iT},$$

where I = water intake rate (ml $[100\ g]^{-1} day^{-1}$),

L = water loss rate (ml $[100\ g]^{-1} day^{-1}$),

K = fractional turnover rate,

W_i = initial body water content (ml/g),

W_f = final body water content (ml/g),

BW_i = initial body weight (g),

BW_f = final body weight (g),

T = elapsed time (days).

Body weight changes were corrected for weight losses in captivity and for any weight loss in the field caused by handling of the animal (defecation, bladder urine release). The fractional turnover rate (K) was calculated from the equation,

$$K = \frac{\ln i - \ln f}{T} - 1.53 \times 10^{-4}/day,$$

where i = initial tritium activity of bladder urine,

f = final tritium activity of bladder urine.

The constant, 1.53×10^{-4}/day, corrects for the radioactive decay rate of tritium. These equations yield estimates of water intake and loss that are identical to those used by Nagy (1972).

Metabolic water production was estimated using HTO in 6 tortoises held without food or water in outdoor cages at the University of California, Riverside. The techniques used were the same as those employed on free-living tortoises.

Rainfall. Rainfall during the study was monitored at both the northern and southern portions of the study site using coffee cans containing a thin layer of mineral oil. Records were compared to those of the U.S. Weather Bureau station at Barstow, California (U.S. Weather Bureau, 1970, 1971).

Collection of Samples. Samples of blood, urine and feces were collected from tortoises during the study. Blood samples were obtained by heart puncture using a heparinized 5 ml tuberculin syringe and a 22-gauge 38 mm hypodermic needle. To permit entry of the needle into the heart, a tiny hole was made in the plastron below the heart using a 1/16-inch [= 1.59 mm] bit attached to a hand drill. The hole was later sealed with epoxy glue and masking tape to prevent infection. Recapture of tortoises a year later revealed that the hole had healed properly. Blood samples were certrifuged at 500 X *g* for 10 min, the cells discarded and the plasma stored frozen until analyzed.

Fecal samples were collected from wild-caught tortoises by placing them in large, 1-inch [= 2.54 cm] wire mesh cages at room temperature (20°-25°C). Samples used for electrolyte analysis were collected on a sheet of Parafilm® placed below the cage. Those used for measurement of water content were collected over a pan of mineral oil. Oil-free water content of these samples was estimated using the methods described by Minnich and Shoemaker (1972). Some bladder urine was released by those tortoises. Liquid samples were aspirated from the mineral oil using a Pasteur pipette and used for solute analysis. Urinary precipitates were also collected from some animals. They were used for water and electrolyte analysis in the same manner as fecal samples. Any fecal or urine samples that were mixed together were not used for estimation of water and electrolyte content. Samples of feces and precipitated urine were stored dried until analyzed.

Body Fluid Volumes. Body water content was measured by HTO dilution, as described in the "Water Turnover" section above. Extracellular fluid volume was measured by cardiac injection of 1-2 ml of 10% sodium thiocyanate, as described by Minnich (1970).

Analysis of Samples. Tritium activity was measured by scintillation counting as described by Minnich and Shoemaker (1970, 1972) on 10 microlitres of each sample of bladder urine. Samples were counted to 1% error and corrected for background. Because of variability in quenching, all samples were corrected by external standardization to the same counting efficiency (≈ 20%).

Osmotic concentrations of undiluted samples of plasma and bladder urine were measured on a Mechrolab® vapor pressure osmometer. They were prepared for electrolyte analysis by diluting 10 microlitres in 5 ml of distilled H_2O. Samples of dried feces and precipitated urine were prepared for electrolyte analysis as described by Minnich and Shoemaker (1970, 1972) and Minnich (1972). Concentrations of sodium and potassium were measured with a flame photometer, and chloride determinations were performed on a Buchler-Cotlove® chloridometer. Ammonia and urea concentrations were measured on 50-microlitre samples of plasma and 10-microlitre samples of bladder urine using the Conway microdiffusion technique (Conway, 1933) and urate concentrations were determined on 50-microlitre samples of plasma or bladder urine using the ultraviolet—uricase technique (Praetorius and Poulsen, 1953).

Statistical Tests. Comparisons between samples were done using Student's two-sample *t*-test (Steel and Torrie, 1960). In cases where variances were not homogeneous the modified *t*'-test of Cochran and Cox (1957) was employed. Fecal H_2O and electrolytes were compared using the Wilcoxon two-sample test. Equations for straight lines were calculated by the method of least squares and the slope was tested for a significant difference from zero using a *t*-test. In all cases the level of significance used was $P = .05$. Variation is expressed in this paper as the standard error (SE).

RESULTS AND DISCUSSIONS

Water Turnover. During the dry period between 16 July and 12 August 1970, water turnover (intake) rates of desert tortoises were very low (0.27 ± 0.029 ml$[100\ g]^{-1}$day^{-1}, $N = 9$) (Fig. 1) and were not statistically different from rates of metabolic water production (0.22 ± 0.027 ml$[100\ g]^{-1}$day^{-1}, $N = 6$). During this period tortoises were consuming very little, if any, preformed water in food or through drinking. The animals were inactive, only occasionally emerging for short periods from their burrows, and were not observed to eat. The stomach and small intestine of 1 tortoise captured in August 1971, when conditions were also very dry, contained no food. Under these conditions tortoises lost body weight slowly, at a rate of 0.28 ± 0.049 g$[100\ g]^{-1}$day^{-1} ($N = 9$) (Fig. 2), and were in negative water balance. Rates of total water loss averaged 0.46 ± 0.058 ml$[100\ g]^{-1}$day^{-1} ($N = 9$), or about 1.7 X the water intake rate. Most of this water loss appears to be from evaporation, as tortoises did not void urine and they voided only small amounts of feces because they did not eat. Fecal water content was also quite low, averaging 0.63 ± 0.20 ml H_2O/g dry weight in 4 animals at the northern site. An evaporation rate of approximately 0.4 ml$[100\ g]^{-1}$day^{-1} appears reasonable, as Schmidt-Nielsen and Bentley (1966) observed evaporation rates of 0.34 ml$[100\ g]^{-1}$day^{-1} from resting, laboratory-maintained tortoises at 35°C.

In tortoises that were hydrated from an earlier rain (on 9 July 1970) at the southern site, osmotic concentrations in bladder urine increased gradually until they became equal to those of the plasma (Fig. 3). At the northern site, which received very little rain on 9 July, tortoises exhibited signs of dehydration. Osmotic concentrations of the plasma were significantly elevated (from a normal value of about 260-300 mosm/l to about 320-360 mosm/l—see Fig. 4) and those of the bladder urine equaled those of the plasma (Fig. 4). Osmotic concentrations of the bladder urine remained fairly constant throughout the period (Fig. 3). The bladder urine of these animals was dark brown and contained large quantities of gelatinous urate precipitates.

On 12 August 1970 a brief, but heavy rain fell at the study site. Approximately 12 mm fell at the southern site and 4.7 mm at the northern site. Dramatic changes were observed in most of the tortoises. First, almost all animals became active. Second, all established animals at the southern site exhibited a sharp decline in HTO activity (Fig. 1), dramatic increases in body weight (Fig. 2, and abrupt decreases in the osmotic concentrations of the bladder urine (Fig. 3). The color of the bladder urine changed from dark brown to colorless and the precipitated urate disappeared. There was also a slight, but not statistically significant, increase in fecal water content (from 0.63 ± 0.20 in 4 animals to 0.97 ± 0.16 ml/g dry weight in 6 animals). Except for increased activity, these changes did not occur in animals at the northern site or in the released captive tortoises at either site. The above data suggest that established tortoises at the southern site drank rainwater and stored most of it in their urinary bladders. Kristin Berry (*personal communication*) stated that established tortoises utilize specific drinking sites within their home ranges after rains of sufficient magnitude. Established tortoises have also been observed digging drinking sites just before a rain (K. A. Nagy and P. A. Medica, *personal communication*). The absence of such changes in tortoises at the northern site suggests that insufficient rain fell there for the animals to drink. Released captives did not drink, apparently because they had not been present at the study site for a sufficiently long period to establish and utilize a drinking site (they had been released only 19 days before the rain).

From Fig. 1, the amounts of rainwater drunk were calculated from the sharp decline in urinary HTO activity. The calculations assume that the rate of HTO decline in individual tortoises between 3-4 August (the last recapture prior to the rain) and 12 August (immediately prior to the rain) were the same as those before 3-4 August. The average amount drunk by 13 established tortoises at the southern site was 17 ± 1.9 ml/100 g body weight. The increase in body weight that occurred following the storm (17 ± 2.2 g/100 g, *N* = 9—see Fig. 2) almost equaled the amounts of rainwater drunk. This suggests that the rainwater is not only retained in the body, but also that most of the weight change is due to drinking. However, drinking is not the only phenomenon which affected body weight subsequent to the storm. After the rain, several animals were observed eating dried vegetation. The stomach of 1 animal that had been hit by a car after the storm was filled with dried grass. Feeding, of course, results in further weight gain. However, this gain was canceled, not only because of defecation, but also because of the release of the bladder urine that had been stored before the rain. As mentioned above, bladder urine of dehydrated tortoises is dark brown, contains abundant urate precipitates, and has a high osmotic concentration. After the storm, bladder urine was colorless, contained no precipitate, and had a very low osmotic concentration (Fig. 3). These observations suggest that the rainwater consumed was being stored in the urinary bladder.

During the period following the rain (13-25 August 1970) the water turnover of desert tortoises increased slightly, especially after 18-21 August (Fig. 1). During the period 13-18 August, water turnover of 7 tortoises increased only slightly but not significantly, from 0.27 ± 0.029 to 0.40 ± 0.10 $ml [100\ g]^{-1} day^{-1}$ (insufficient data were available to calculate water turnover during 18-25 August.) However, tortoises maintained relatively constant body weight during this period (average weight change of 7 tortoises during 13-18 August was + 0.01 ± 0.078 $g [100\ g]^{-1} day^{-1}$). Tortoises remained active and consumed food. The low water turnover during 13-18 August is related to the dryness of dietary items. The diet consisted primarily of dried grass, dried stems of woody perennials and occasional stones. However, after 18 August, many perennial plants developed new, succulent leaves in response to the rain of 12 August. Feeding on these plants would account for the high water turnover observed in some tortoises during 18-25 August (see Fig. 1). The rainfall of 12 August 1970 created favorable conditions for tortoises, especially at the southern site, allowing them (1) to excrete excess wastes that had been stored in the urinary bladder, (2) to store dilute fluid in the bladder, and (3) to resume normal activity and feeding.

In August 1971, 3 tortoises that had been injected with HTO during 1970 were recaptured, 1 at the northern site and 2 at the southern site. Analysis of HTO activity, body weight and body water content permitted calculation of an annual water budget for these animals. Between 1 August 1970 and 31 July 1971, rainfall at Barstow totaled only 69 mm or about 66% of average. All 3 animals exhibited no significant change in body weight or shell (plastron) length during 1970-1971. Body water contents were also essentially constant. Therefore, water loss rates in these animals equaled water turnover (intake) rates. The 2 tortoises at the southern site consumed an average total of 218 ± 8.0 ml water/100 g body weight over a period of exactly 1 year (equivalent to a daily intake rate of (0.60 ± 0.020 $ml [100\ g]^{-1} day^{-1}$). This amounts to turning over the body water pool 3 times during the year. The tortoise at the nothern site turned over water at the even slower rate of 80 ml/100 g for the year (daily rate = 0.22 $ml [100\ g]^{-1} day^{-1}$). This is equivalent to turning over the body water about 1.2 times during the year. Two other published studies on reptiles permit calculation of an annual water turnover rate, that of Green (1972) on a monitor lizard, the sand goanna *(Varanus gouldii)*, at Flinders Chase, Australia, and that of Nagy (1972) on an iguanid lizard, the chuckwalla *(Sauramalus obesus)*, at Black Mountain, near Barstow, California. Between November 1966 and December 1968, *V. gouldii* turned over H_2O at the annual rate of 480 ml/100 g (equal to 1.3 ml 100 $g^{-1} day^{-1}$). Green (1972) states that his figures are from lizards which balanced their H_2O budgets. Between April 1970 and March 1971, *S. obesus* turned over H_2O at an annual rate of about 220 ml/100 g (equal to

0.6 ml [100 g]$^{-1}$day^{-1}). Although this value is similar to that of tortoises at the southern site, H_2O losses in *S. obesus* were much higher. For the year, tortoises maintained body weight while *S. obesus* endured a net weight loss of about 43 g/100 g (daily rate = 0.1 g [100 g]$^{-1}$day^{-1}) (Nagy, 1972).

Unfortunately the maintenance H_2O budget of active, free-living tortoises was not estimated during this study. During much of the summer tortoises were in negative H_2O balance. Estimation of maintenance water budgets is especially important when interspecific comparisons are made. They also permit evaluation of the H_2O required to sustain an animal indefinitely under natural conditions. Minnich (1978) recently surveyed H_2O budgets in free-living xeric habitat lizards and found that maintenance H_2O intake during a warm season was related to body weight by the equation, $R = 21\ W^{0.84}$, where R is H_2O intake (millilitres/day) and W is body weight (kilograms) (Fig. 5). The slope (0.84) is significantly different from 1.0 ($P < .05$, *t*-test), which suggests that small lizards consume H_2O more rapidly per unit body weight than large lizards.

Figure 5 shows that desert tortoises consumed H_2O at a much slower rate than that predicted for lizards of equivalent body size. This is, of course, because tortoises were dormant during the time that the study was conducted and were not consuming preformed water. Although tortoises did approximate balanced water budgets during the period of 13-18 August 1970, and were active, their water intake at this time probably did not approximate a long-term maintenance budget. This is because (1) the time of measurement was too short (5 days), (2) tortoises fed on dry items, and (3) relative humidities were probably above normal because of the rain on 12 August. If tortoises weighing 613 g (the average weight during this study) consume water at the same maintenance level as do xeric habitat lizards of equivalent body size, their water intake rate would be 2.2 ml [100 g]$^{-1}$day^{-1} (see Fig. 5). This figure is significantly below the maintenance value of 3.1 ml [100 g]$^{-1}$day^{-1} in the closely related gopher tortoise (*Gopherus polyphemus*) (Fig. 5). These tortoises, which averaged substantially larger than the desert tortoises in the present study (mean weight of *G. polyphemus* was 3,182 g), were studied during summer 1974 in the humid subtropical woodlands of central Florida (Minnich and Ziegler, 1976) (see paper by Minnich and Ziegler in the proceedings).

Body Water and Solutes. Because the hydration state of tortoises varied considerably during the study, measurements were made on body fluid volumes and on concentrations of solutes in plasma and bladder urine of hydrated and dehydrated animals. Results are summarized in Table 1. "Hydrated" tortoises were established animals with hypoosmotic bladder urine sampled from the southern site during July-August 1970. "Dehydrated" animals were collected throughout the study site on 3-8 August 1971, 4 months after the last measureable rainfall (U.S. Weather Bureau, 1971). Although tortoises drank rainwater and stored it in their bladders, fractional body water content was not significantly different between hydrated and dehydrated tortoises (Table 1). Extracellular fluid volume was not measured in hydrated tortoises in the field, but in 1 hydrated laboratory-maintained animal it was lower than in dehydrated field animals (Table 1).

The osmotic concentrations of both plasma and bladder urine, as expected, were significantly elevated in dehydrated tortoises (Table 1, Fig. 4). Plasma osmotic concentrations in hydrated field tortoises in this study were nearly identical to those observed in hydrated, laboratory-maintained desert tortoises by Dantzler and Schmidt-Nielsen (1966) and in the related tortoise *Testudo hermanni* during summer (Gilles-Baillien and Schoffeniels, 1965). Moreover, plasma concentrations of sodium, potassium and chloride in the latter species during summer were also very similar to those of hydrated desert tortoises (see Table 1 and Gilles-Baillien and Schoffeniels, 1965). Dehydrated desert tortoises in this study, however, exhibited an elevation in plasma osmotic concentration of ≈ 15% over hydrated values (Table 1).

The major solutes which contribute to the elevation of plasma osmotic concentrations of dehydrated tortoises are uncertain, but sodium and chloride both appear to be important. Plasma chloride was significantly higher in dehydrated tortoises and, although not significantly different, plasma sodium was also elevated by ≈ 26% (Table 1). A similar parallel relationship between plasma sodium, chloride and osmotic concentrations has also been observed in *Testudo hermanni* (Gilles-Baillien and Schoffeniels, 1965). Although plasma ammonia, urea and urate were measured in dehydrated tortoises, they were not in hydrated animals (Table 1); consequently the contribution of these solutes to the elevation in plasma osmotic concentrations in dehydrated tortoises cannot be directly assessed. Nevertheless, comparisons can be made with hydrated *G. agassizi* studied by Dantzler and Schmidt-Nielsen (1966) and *Gopherus berlandieri* studied by Baze and Horne (1970). Plasma ammonia in dehydrated *G. agassizi* (Table 1) is similar to that observed by Baze and Horne (1970) in both hydrated and dehydrated *G. berlandieri*. Similarly, plasma urate in dehydrated *G. agassizi* (Table 1) is very low, although not quite as low as in hydrated and dehydrated *G. berlandieri* (Baze and Horne, 1970). Plasma ammonia and urate are generally present in very low levels in reptilian plasma (reviewed by Dessauer, 1970 and Minnich, 1978). The plasma nitrogenous waste which varies greatest is urea. However, plasma urea levels in dehydrated tortoises sampled during this study do not appear to be substantially elevated, as Dantzler and Schmidt-Nielsen (1966) observed plasma urea levels in hydrated, laboratory-maintained desert tortoises that were nearly the same as those of the dehydrated animals in this study (Table 1). Dehydration of tortoises in the laboratory can cause significant elevation of urea. Dehydration of *G. agassizi* for 6 weeks and *G. berlandieri* for 60 days increased plasma urea to ≈ 62 mmole/l (Dantzler and Schmidt-Nielsen, 1966; Base and Horne, 1970). The measured solutes in the present study accounted for about 86% of plasma osmotic concentrations in dehydrated tortoises (see Table 1).

Because desert tortoises appear to tolerate considerable dehydration in the field, preliminary studies were conducted on the effects of long-term dehydration in the laboratory. Three tortoises (*G. agassizi*) were subjected to chronic dehydration at 30°C for 134 days without food or water in a Scherer® environmental chamber. At the end of that period all animals had survived and incurred an average weight loss of 30.1 ± 5.15 g/100 g initial weight. Fractional body water content decreased slightly, but significantly ($P < .01$, compared to hydrated values), to 63.1 ± 0.86 ml/100 g body weight (see Table 1). Furthermore, plasma osmotic concentrations became significantly elevated to values averaging 622 ± 14.3 mosm/l, more than twice hydrated values ($P < .001$) (see Table 1). As expected, both plasma sodium (185 ± 26.1 meq/l) and chloride (163 ± 19.8 meq/l) were substantially elevated compared to hydrated values, but only chloride was significantly different ($P < .01$). However, plasma potassium (6.77 ± 0.34 meq/l) was not significantly changed over hydrated figures (see Table 1). Nevertheless these 3 electrolytes account for only 57% of the observed osmotic concentration. Presumably most of the remaining increase in plasma osmolality is due to an increase in urea levels (see Dantzler and Schmidt-Nielsen, 1966; Baze and Horne, 1970).

The apparent elevation in extracellular fluid volume in dehydrated field tortoises (Table 1) seems to have been at the expense of cell water, as total body water did not change (Table 1). Such a fluid shift may have resulted from retention of sodium and chloride in the extracellular fluid along with leakage of potassium from the cells. Evidence for this idea is seen in (1) the slight elevation in plasma sodium and chloride in dehydrated tortoises and (2) the much higher potassium concentrations in bladder urine of dehydrated animals (Table 1). Such a response is commonly seen in reptiles subjected to chronic dehydration (reviewed by Minnich, 1978). During dehydration the retained sodium and chloride causes a slight osmotic shrinkage of cells; the cells in turn leak potassium, which results in the maintenance of constant intracellular potassium concentrations and enhanced urinary potassium excretion. This is reflected in the high potassium concentrations in the bladder urine of dehydrated tortoises. It also explains, in part, the substantial amounts of potassium that are present in the urate precipitates within the bladder of dehydrated tortoises (see Table 2 and discussion below).

Excretory solutes. Dehydration also has a dramatic effect on the osmolality and solute composition of bladder urine. As mentioned above, bladder urine is hypoosmotic to plasma in hydrated tortoises but is isosmotic to plasma in dehydrated animals (Fig. 4, Table 1). Thus it is not surprising that bladder urine osmolality in hydrated tortoises is significantly lower than that of dehydrated animals (Table 1). One solute which accounts, in part, for this difference is potassium; levels of this cation are > 15 X as concentrated in bladder urine of dehydrated tortoises (Table 1). As mentioned above, this appears to be a result of excretion of potassium that is lost from dehydrating cells. Dietary potassium does not appear to be important, because dehydrated tortoises were not feeding. Urinary sodium and chloride levels do not differ significantly between hydrated and dehydrated tortoises (Table 1).

Unfortunately, urinary nitrogenous wastes were not measured in hydrated tortoises (Table 1). Nevertheless comparisons can be made between urinary nitrogenous wastes of dehydrated desert tortoises (Table 1) and those of hydrated Texas tortoises (*G. berlandieri*) published by Baze and Horne (1970). Urinary ammonia, urea and urate levels in dehydrated, wild-caught desert tortoises were all higher than in hydrated, wild-caught Texas tortoises (Table 1). Ammonia levels were even higher than in Texas tortoises dehydrated in the laboratory. Urea levels however, were of the same order of magnitude as in dehydrated Texas tortoises (Table 1). Assuming that urinary nitrogen is comparable in hydrated individuals of both species, it appears that urinary nitrogen levels increase in dehydrating desert tortoises. This was certainly true of urate in the present study. Because of its low solubility, urate readily precipitates in the urinary bladder. The bladder urine of hydrated tortoises after the rain of 12 August never contained urate precipitates but that of dehydrated tortoises always contained large quantities of gelatinous urate precipitates (Minnich, 1976*a*). Baze and Horne (1970) also observed that dehydration increased the amount of urate precipitates in bladder urine of *G. berlandieri*. Even the liquid fraction of the bladder urine contained high levels of urate in dehydrated desert tortoises (Table 1). The amounts present (13.5 ± 1.0 mmole/l—Table 1) actually exceeded the solubility of urate at the pH of the bladder urine (about 5 mmole/l at pH 5.47); this suggests that some of the urate in the liquid fraction of the bladder urine was present in a colloidal state (Minnich, 1976*a*, *b*). The measured solutes in the bladder urine of dehydrated tortoises accounted for only 50% of the urinary osmotic concentration (see Table 1). The major remaining solutes are unknown but the dark color of the bladder urine suggests that urobilin or urobilinogen (wastes derived from bilirubin) may be important solutes. When hydrated, the bladder urine of tortoises was colorless.

The gelatinous nature of the bladder urate precipitates suggests that a urate-binding urinary protein may be present which stabilizes colloidal urate and permits urate precipitation in a "disordered" gelatinous state (Minnich, 1976*b*). Such a protein may serve to protect the bladder epithelium and duct from damage by crystalline ("ordered") urate precipitates. Occasionally a large stone, about the size of a baseball, may be found in the bladder of a diseased tortoise. Such a condition has been observed in nature (Miller, 1932) and may eventually be lethal to the animal because of damage to the urinary bladder. Holes apparently caused by the presence of hard urate stones have been observed in the bladder of severely dehydrated tortoises (John E. Minnich, *personal observation*). The presence of large bladder stones also limits the amount of liquid urine that can be stored in the bladder.

Because of their gelatinous nature, the bladder urate precipitates contain a relatively large amount of water. Average water content in these precipitates was 2.58 ± 0.35 ml/g dry mass (Table 2), or about 3-10 X as much water as in the hard urate precipitates in desert lizards (see Minnich, 1972; Minnich and Shoemaker, 1972; Nagy, 1972; Braysher, 1976). The ionic content of the urate precipitates of tortoises is presented in Table 2. The sodium and chloride levels are comparable to those of several lizards (Minnich, 1972) and potassium is the predominant cation. The abundant potassium is not surprising, because dehydrated tortoises excrete K lost from cells. The potassium content of the urate precipitates is comparable to that of carnivorous lizards and snakes, but is lower than that of herbivorous lizards (Minnich, 1972). The comparatively low levels in tortoises of this study are due to fasting, because fasting reduces the K content of the urate precipitates (Minnich, 1972). When fed plants, the K levels in the precipitates of desert tortoises are comparable to those of fed herbivorous lizards (Minnich, 1972).

Contents of H_2O and electrolytes in the feces of desert tortoises did not vary substantially with hydration state Table 2). Potassium, as expected, was the most abundant cation in the feces; this probably reflects the high K levels in the desert plants that are a normal part of the tortoise diet (see Minnich and Shoemaker, 1970, 1972; Nagy, 1972). Although K content (expressed as milliequivalents per kilogram dry weight) of the feces did not vary with hydration state, K concentrations (expressed as milliequivalents per litre of fecal water) were significantly higher in dehydrated tortoises (Table 2). This suggests that the cloaca and colon of tortoises may secrete K in response to dehydration. The cloaca of lizards has been shown to secrete potassium (House, 1974); Skadhauge and Duvdevani, 1977; B. Schmidt-Nielsen, *personal communication*). However, such a response of the tortoise cloaca and colon to dehydration needs investigation.

Functions of the Urinary Bladder. The urinary bladder appears to serve at least 2 principal functions in desert tortoises. First, it permits the storage of significant urinary wastes during prolonged dry periods. Kidneys of desert tortoises continue to add urinary wastes to the bladder until plasma osmotic concentrations exceed 400 mosm/l (Dantzler and Schmidt-Nielsen, 1966), a value that was not exceeded by even the most dehydrated field tortoises in this study (Table 1, Fig. 4). Not only does the bladder urine of dehydrated tortoises contain significant amounts of waste nitrogen and electrolytes in the liquid portion (Table 1), but it also contains large quantities of N and K as precipitated potassium urates (Table 2 and Minnich, 1972). The capacity of tortoises to store K as precipitated urates, plus the cessation of feeding during extreme drought, probably account for the lack of elevation in body K in dehydrated tortoises. The prevention of K accumulation is very important, as no reptile can tolerate chronic elevation of intracellular or extracellular potassium (reviewed by Minnich, 1978).

Although data are incomplete at this time, present information strongly suggests that the tortoise urinary bladder may also function as a H_2O reserve. When osmotically dilute water becomes available (either as rainwater or as succulent food low in electrolytes, as may occur in spring after a wet winter), tortoises appear to store it in the urinary bladder. This is evidenced by the sudden decline in osmolality of the bladder urine after a rain (Fig. 3). When water availability again becomes restricted (such as during the period after the rain 12 August 1970), the osmotic concentrations of bladder urine again increase gradually until they become isosmotic to plasma (Fig. 3). This increase is probably due to the addition of urinary wastes by the kidney (and perhaps to secretion of solutes by the bladder itself) but must also be due to water reabsorption from the bladder. Because ureteral urine is always hypotonic (Dantzler and Schmidt-Nielsen, 1966) but bladder urine eventually becomes isotonic (Fig. 3), there must be a gradual increase in bladder water permeability as tortoises dehydrate. Such a change in bladder water permeability is probably under the control of the hormone arginine vasotocin (AVT). Although Bentley (1962) and Gilles-Baillien (1969) observed no effect of AVT on bladder water permeability of summer tortoises this may have been due to their experimental design. Both studies employed isolated bladder preparations and may have incubated them at a temperature too low to demonstrate a response to the hormone. To evaluate these ideas, studies are needed on water and solute exchanges across the bladder of tortoises recently captured in the field, as the bladder of laboratory-maintained animals appears to have different permeability characteristics than that of wild-caught tortoises (see Dantzler and Schmidt-Nielsen, 1966; Minnich, 1976*a*). Nevertheless, the storage of hypotonic urine in the bladder of desert tortoises is exceedingly important in osmoregulation. As long as bladder urine remains hypotonic to plasma, plasma osmolalities remain relatively constant at about 260-300 mosm/l (Fig. 4). The presence of dilute bladder urine was also important in permitting the resumption of feeding after the rain of 12 August 1970. When hydrated, the tortoises are capable of excreting the dietary potassium load. The water storage function of the tortoise bladder is very similar to that of arid-adapted toads (Ruibal, 1962).

SUMMARY AND CONCLUSIONS

During severe drought desert tortoises become inactive, cease feeding and remain in their burrows for long periods. Cessation of feeding protects tortoises from accumulating toxic levels of dietary potassium at a time when insufficient water is available to excrete it. Under these conditions water intake is reduced to the rate of metabolic water production and tortoises slowly dehydrate. Water loss is mostly through evaporation. During dehydration, plasma osmotic concentrations become slightly but significantly elevated and part of this increase is due to elevation of sodium and chloride concentration. This causes body water to shift from cells to extracellular fluid. Cells respond by leaking potassium, which results in maintenance of normal intracellular potassium concentrations and enhanced urinary (and possibly fecal) potassium excretion.

When rains of sufficient magnitude fall during summer, established tortoises drink rainwater, void stored bladder urine, then store the rainwater in the bladder as a dilute urine. Rehydration of tortoises causes a return of body fluids to normal and resumption of feeding. The urinary bladder of tortoises appears to function (1) in storage of urinary wastes, especially during drought and (2) as a water reserve.

In contrast to established tortoises, captive tortoises recently released in the field do not drink rainwater. They do not appear to feed either, even after the rain, until after they have become sufficiently familiar with their surroundings.

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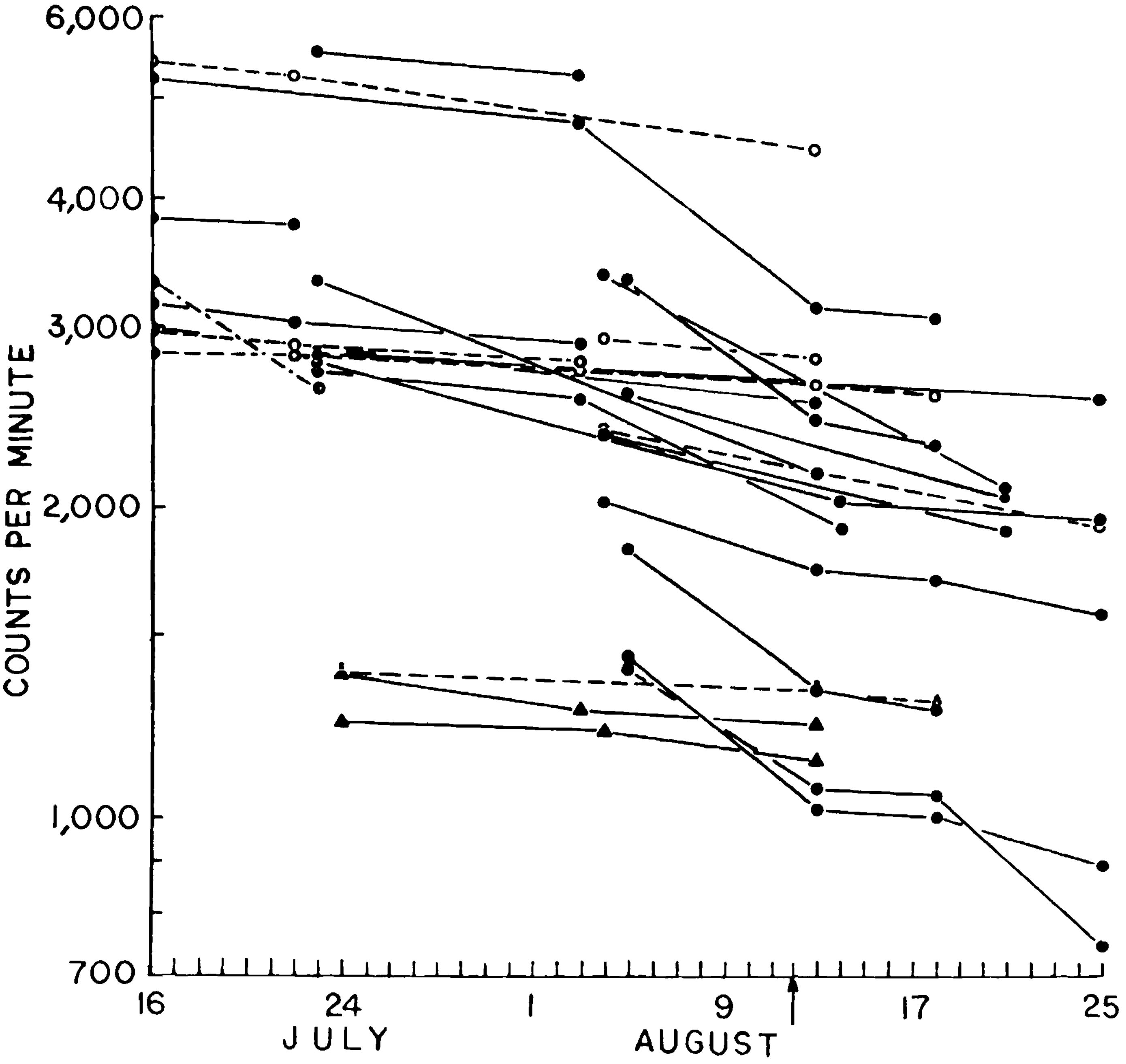
COUNTS PER MINUTE
6,000
4,000
3,000
2,000
1,000
700
16
24
1
9
17
25
JULY
AUGUST

Fig. 1. Changes in tritium activity in bladder urine of desert tortoises near Barstow, California, during summer 1970. Rain fell at the study site on 12 August and is indicated by an arrow on the abscissa. Curves represented by dashed lines and open symbols are from animals at the northern site; those represented by solid lines and closed symbols are from animals at the southern site. Circles represent established animals and triangles represent released captives. The 1 established animal symbolized by a half-closed circle and modified dashed lines was from a wetter location south of the main study site. (*From* Minnich, 1976*a*).

Minnich

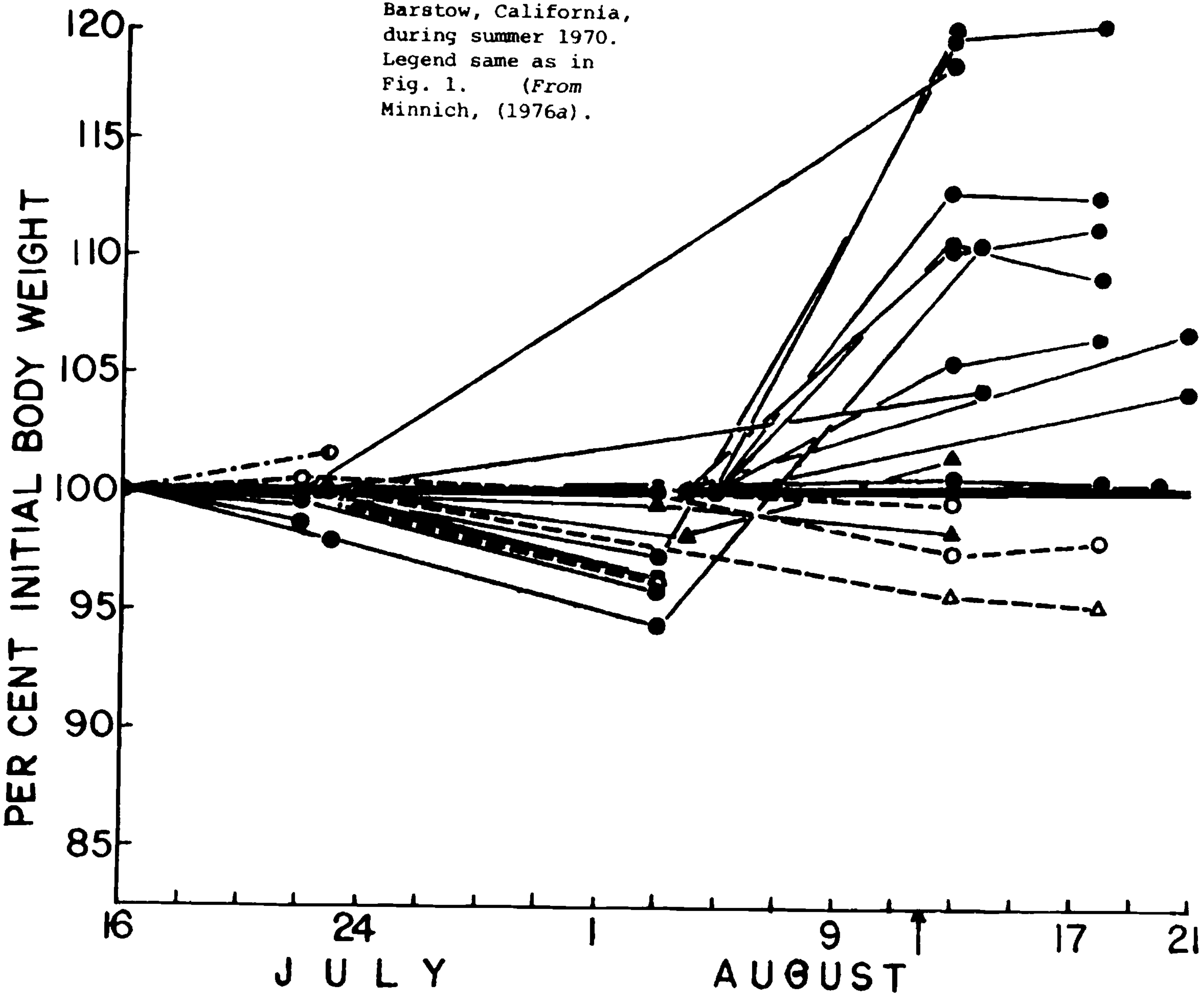

Fig. 2. Changes in body weight of desert tortoises near Barstow, California, during summer 1970. Legend same as in Fig. 1. (*From* Minnich, (1976*a*).

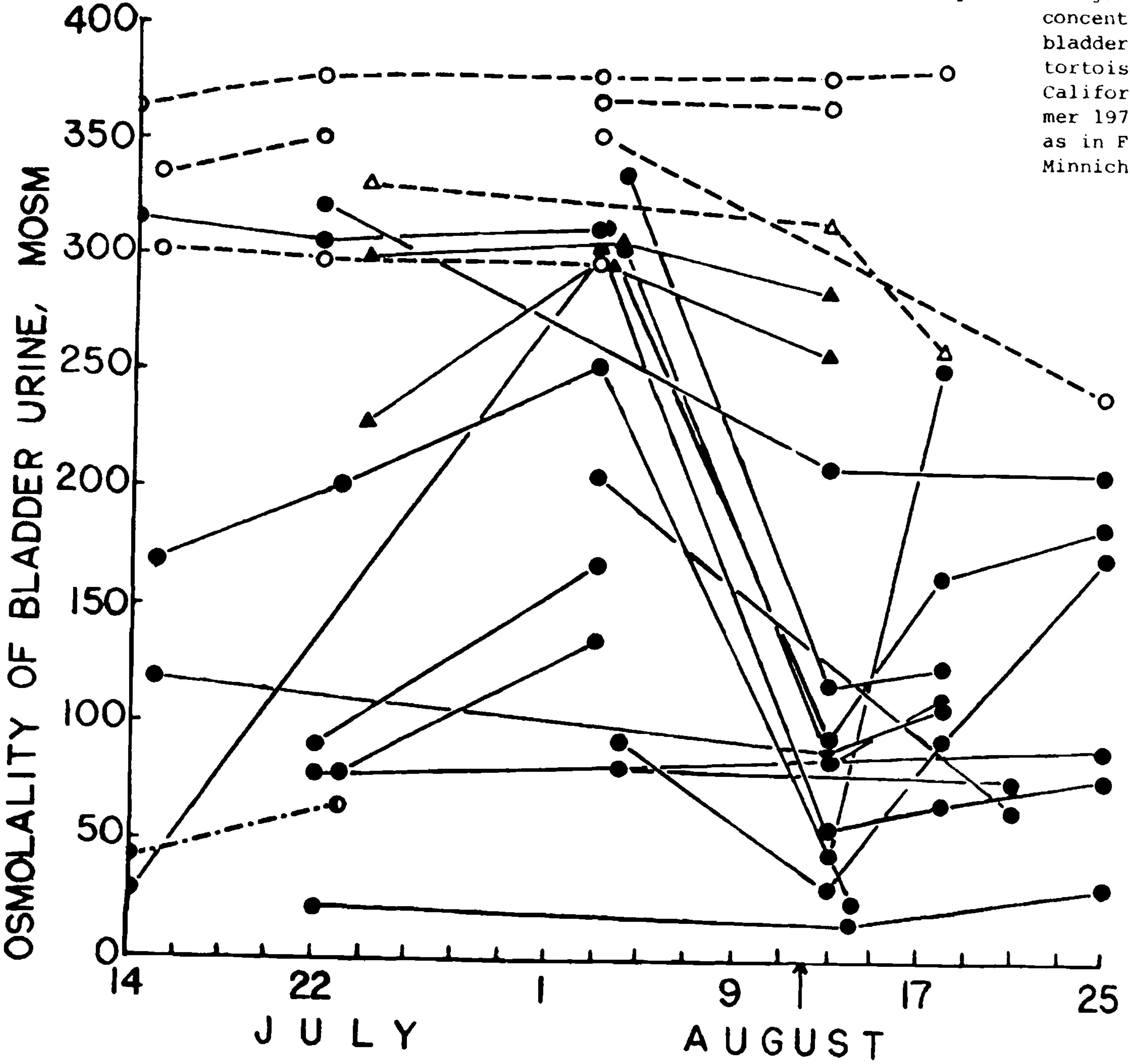

Fig. 3. Changes in the osmotic concentrations of the bladder urine of desert tortoises near Barstow, California, during summer 1970. Legend same as in Fig. 1. (*From* Minnich, 1976*a*).

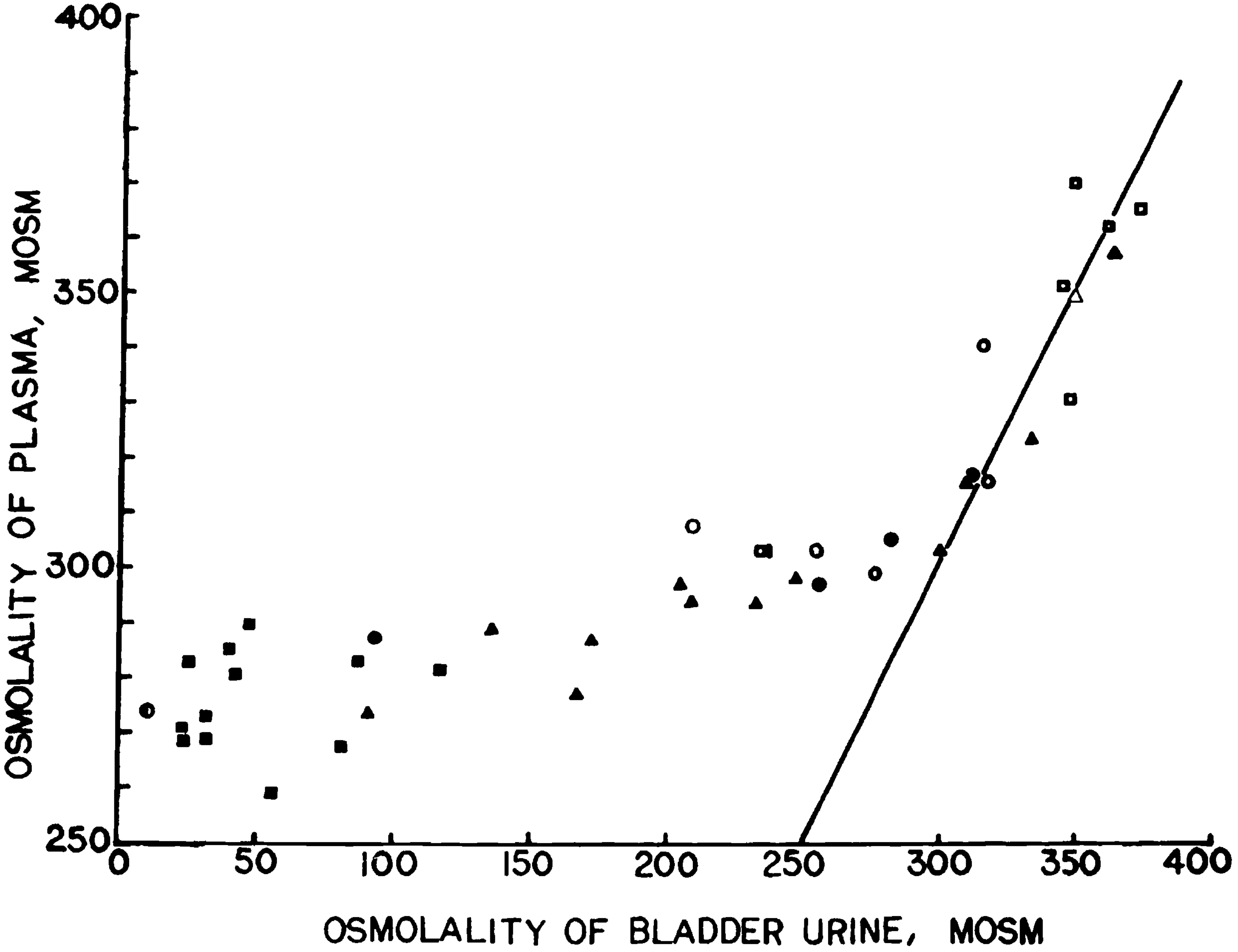
OSMOLALITY OF PLASMA, MOSM
400
350
300
250
0
50
100
150
200
250
300
350
400
OSMOLALITY OF BLADDER URINE, MOSM

Fig. 4. Relation between osmotic concentrations of the blood plasma and bladder urine of desert tortoises. Solid line represents the part of the graph where osmotic concentrations of the plasma and bladder urine are equal. Symbols: open triangle = established animal from northern site, sampled 3-4 August 1970; closed triangle = established animal from southern site, sampled 3-4 August 1970; open square = established animal from northern site, sampled 13-14 August 1970 (after rain of 12 August); closed square = established animal from southern site, sampled 13-14 August 1970; half-closed circle = established animal from south of main study site, sampled 13 August 1970; closed circle = released captive animal, sampled 13-14 August 1970; open circle = captive animal maintained at the University of California, Riverside, sampled 12 August 1970. (*From* Minnich, 1976*a*).

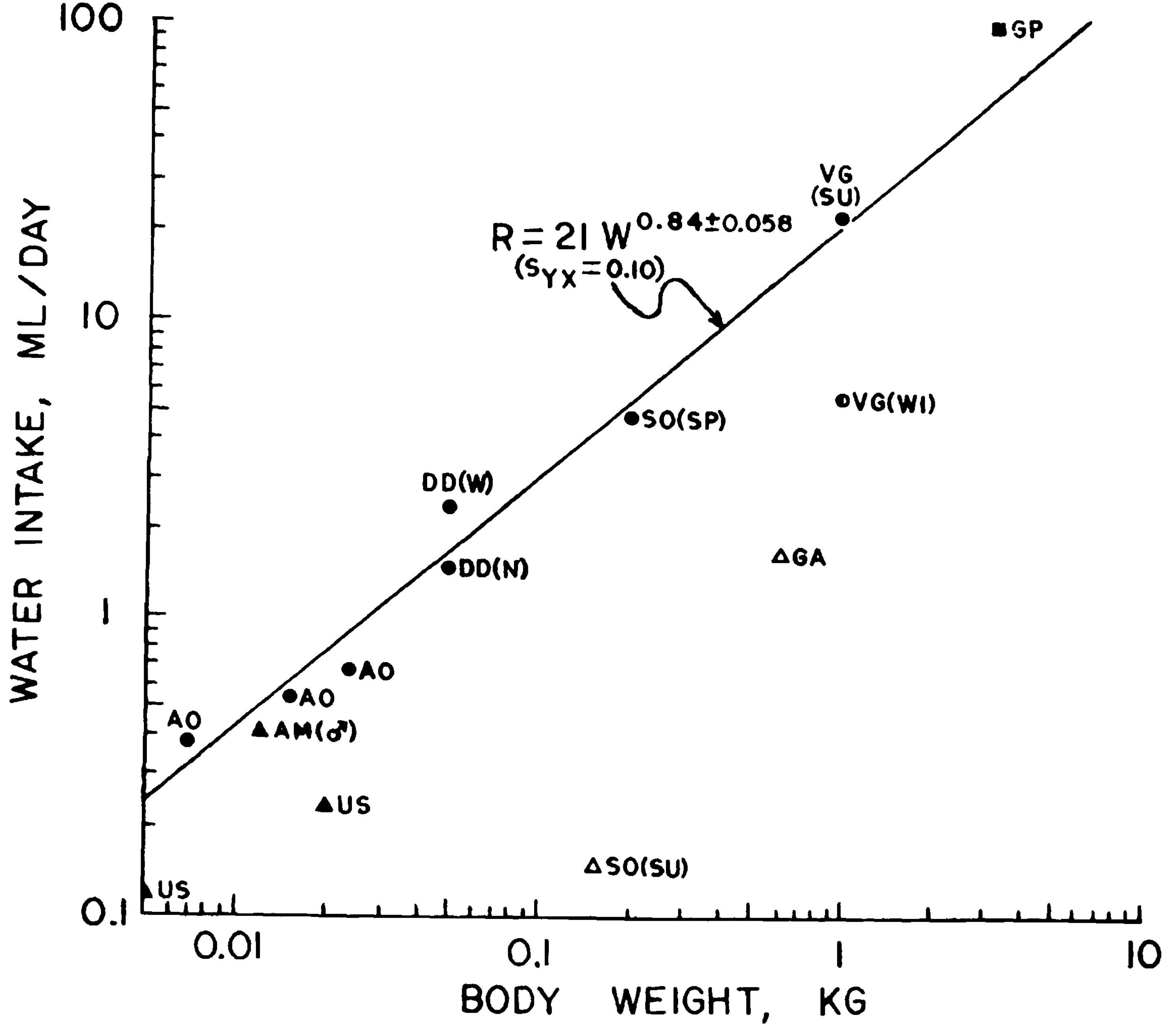
100
10
1
0.1
WATER INTAKE, ML/DAY
0.01
0.1
1
10
BODY WEIGHT, KG
R = 21 W$^{0.84 \pm 0.058}$
(S_{YX} = 0.10)
GP
VG (SU)
VG(WI)
SO(SP)
DD(W)
DD(N)
GA
AO
AO
AO
AM(♂)
US
SO(SU)
US

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Fig. 5. Relation between total H_2O intake, measured in the field using tritiated H_2O, and body weight in terrestrial reptiles. Symbols: closed circle = active lizard maintaining weight; closed square = active tortoise maintaining weight; closed triangle = active or partially active reptile losing weight; open triangle = inactive reptile losing weight; half-closed circle = partially active reptile maintaining weight in winter. Except for the animal represented by the half-closed circle, all reptiles were studied during late spring or summer. Equation for line was calculated by the method of least squares from the data on active lizards maintaining weight (symbolized by closed circles). Abbreviations of animals and sources of data: AM (♂), *Agama mutabilis* (♂♂ only) (Bradshaw et al., 1976); AO, *Amphibolurus ornatus* (Baverstock, 1975), DD (N), *Dipsosaurus dorsalis* (no drinking H_2O) (Minnich, 1970); DD (W), *D. dorsalis* (drinking H_2O available) (Minnich, 1970); GA, *Gopherus agassizi* (Minnich, 1976*a*); GP, *Gopherus polyphemus* (Minnich and Ziegler, 1976); SO (SP), *Sauromalus obesus* (late spring) (Nagy, 1972); SO (SU), *S. obesus* (late summer) (Nagy, 1972); US, *Uma scoparia* (Minnich and Shoemaker, 1972); VG (SU), *Varanus gouldii* (summer) (Green, 1972); VG (WI), *V. gouldii* (winter) (Green, 1972). Data on *Amphibolurus ornatus* were calculated from fractional turnover rates (*K*-values) of Baverstock (1975), assuming a body H_2O content of 73 ml/100 g body weight (see Bradshaw, 1970). (*From* Minnich, 1978).

Table 1. Comparison of body fluid volumes, plasma solutes, and solutes in bladder urine (liquid fraction) in hydrated and dehydrated desert tortoises (values are $\bar{x} \pm$ SE, sample size in parentheses)

Parameter	Units	Hydrated	Dehydrated	P[a]
Total body water	ml/100 g	67.8±1.47(9)	66.8±0.79(8)	NS[a]
Extracellular fluid volume (SCN space)	ml/100 g	24.5[b] (1)	32.2±0.55(7)	
Plasma [Na]	meq/l	122 ±22.4	150 ±4.61(15)	NS
Plasma [K]	meq/l	5.3±0.67(6)	3.8±0.16(15)	$P<.05$
Plasma [Cl]	meq/l	85.8±10.1(6)	120 ±2.78(15)	$P<.05$
Plasma [NH_3]	mmol/l		1.4±0.5 (14)	
Plasma [urea]	mmol/l	7.8[c]	8.0±1.4 (14)	
Plasma [urate]	mmol/l		0.33±0.08(11)	
Plasma contribution to osmolality[d]	mosm/l		288 ±9.9 (10)	
Plasma osmolality	mosm/l	291 ±3.3 (6)	334 ±3.7 (15)	$P<.001$
Bladder urine [Na]	meq/l	14.7±5.9 (11)	10.0±3.7 (17)	NS
Bladder urine [K]	meq/l	5.6±3.12(11)	89.8±6.9 (17)	$P<.001$
Bladder urine [Cl]	meq/l	14.7±5.7 (11)	3.3±1.8 (17)	NS
Bladder urine [NH_3]	mmol/l	(4.05)[e]	38.2±4.5 (17)	
Bladder urine [urea]	mmol/l	(0.93)[e]	23.0±5.8 (17)	
Bladder urine [urate]	mmol/l	(9.44)[e]	13.5±1.0 (13)	
Bladder urine contribution to osmolality[d]	mosm/l		168 ±10.9(13)	
Bladder uring osmolality	mosm/l	82.7±13.8 (11)	337 ±12.4(17)	$P<.001$

[a] Probability of significant difference between hydrated and dehydrated tortoises.

NS = not significantly different ($P>.05$).

[b] Data from 1 hydrated, laboratory-maintained tortoise.

[c] From Dantzler and Schmidt-Nielsen (1966).

[d] Calculated by adding millimolar concentrations of Na, K, Cl, NH_3, urea and urate. Calculation assumes complete dissociation of electrolytes.

[e] Data from hydrated, wild-caught Texas tortoises (*Gopherus berlandieri*) (Baze and Horne, 1970).

Table 2. Water and electrolyte content of feces and bladder urinary precipitates from normally hydrated and dehydrated, established desert tortoises at Stoddard Valley, California, during July-August 1970 (values are $\bar{x} \pm$ SE, significant differences indicated by asterisk[a])

Excretion product	Hydration state	N[b]	H_2O content (ml/g dry wt)	Electrolyte content					
				meq/kg dry wt			meq/l of H_2O		
				Na	K	Cl	Na	K	Cl
Feces	Hydrated	8	0.99±0.29	27± 8.0	57±12.8	43± 5.8	31± 7.6	82±23.5 *a	58±10.3
	Dehydrated	9	0.73±0.14	33±23.0	145±43.4	29±15.5	43±25.3	192±32.4	29±12.5
Urinary precipitates[c]	Dehydrated[c]	8[b]	2.6 ±0.35[d]	137±43.7	1176±181	4.2±2.77	38± 9.7	484±80.3	2.1± 1.46

[a] * $P < .05$, Wilcoxon 2-sample test. No asterisk indicates that groups are not significantly different.

[b] N = sample size. Sample size was 7 for Cl content of urinary precipitates.

[c] Only dehydrated tortoises had precipitates present in bladder urine.

[d] Water content of bladder urinary precipitates does not include H_2O of liquid fraction of bladder urine.

Water Turnover of Free-living Gopher Tortoises, *Gopherus polyphemus*, in Central Florida

John E. Minnich and Marc R. Ziegler

Water turnover rates utilizing tritiated water (HTO) were measured on a field population of the gopher tortoise, *Gopherus polyphemus*, at the Archbold Biological Station (Lake Placid, Florida) during June to early August 1974. The average H_2O intake for the population was 3.1 ± 0.13 ml $(100\ g)^{-1} day^{-1}$ and the average loss was 3.0 ± 0.13 ml $(100\ g)^{-1} day^{-1}$ ($N = 11$). The maintenance H_2O budget was 3.1 ± 0.18 ml $(100\ g)^{-1} day^{-1}$ ($N = 9$) for the population, which averaged 3,182 ± 378 g body weight ($N = 11$). The average rate of weight change was +0.234 ± 0.088 g $(100\ g)^{-1} day^{-1}$ ($N = 11$). Water turnover per unit body weight did not vary significantly with time, rainfall, variation in body size or rate of weight change. Bladder urine was always hyposmotic to plasma and lacked urate precipitates. Urinary electrolytes averaged 32.3 ± 4.78 meq/l Na^+, 42.9 ± 6.49 meq/l K^+ and 39.3 ± 3.20 meq/l Cl^- ($N = 11$). Fecal electrolytes averaged 38.1 ± 7.46 meq/l Na^+, 119 ± 40.2 meq/l K^+ and 98.2 ± 26.4 meq/l Cl^- ($N = 2$). Fecal values were higher than those observed in the dietary plants of the animals, which averaged 20.6 ± 5.23 meq/l Na^+, 59.4 ± 13.5 meq/l K^+ and 58.2 ± 18.0 meq/l Cl^- ($N = 5$). The plants fed upon by *G. polyphemus* contained abundant water (78.5 ± 3.33 ml H_2O/100 g fresh weight, $N = 5$), their burrows were humid (98.7 ± 0.23% relative humidity at 25.5 ± 0.54°C average temperature, $N = 4$) and rainfall was plentiful.

These observations indicate that the gopher tortoise, unlike the closely related desert tortoise *(G. agassizi)* (Minnich, 1976, 1977), had sufficient H_2O available in its environment to balance its H_2O and electrolyte budgets during the summer of 1974.

Closely related animals living in contrasting habitats provide an interesting study, especially when the contrast in their habitats significantly affects their physiology and bahavior.

Such is the case with tortoises of the genus *Gopherus*. Although most members of this genus are found in arid and semiarid habitats, *G. polyphemus* (the gopher tortoise) occurs in the humid subtropical woodlands in the southeastern United States (Conant, 1975). An obvious difference in the habitat of this species, compared to that of other members of this genus, is its greater water availability. Average annual precipitation and average July relative humidity at local noon in the range of *G. polyphemus* are 1,140-1,650 mm and 55-70%, respectively, compared to values of $<$130-1,020 mm and 20-65% in the ranges of the western species *Gopherus agassizi* and *Gopherus berlandieri* (Kincer, 1941).

Another contrasting difference in the habitats of these tortoises is in the potassium concentrations of their principal dietary plants. As will be shown below the K levels in hydrated desert plants in western North America are $>$ 5 X those in the major dietary plants of *G. polyphemus*. Because K concentrations in body fluids are precisely regulated in tortoises (Minnich, 1976) as in most other animals (Schmidt-Nielsen, 1975; Minnich, 1978), dietary K concentrations significantly affect the physiology and behavior of tortoises. This has already been studied in desert tortoises *(G. agassizi)* (Minnich, 1976) (also see paper by Minnich, 1977, in these proceedings).

The objective of this study is to examine the H_2O and electrolyte metabolism in free-living gopher tortoises studied at the Archbold Biological Station (Lake Placid, Florida) and to contrast their physiology and behavior with that already studied in desert tortoises *(G. agassizi)* (Minnich, 1976, 1977).

METHODS

Study Site. The field studies presented in this paper were carried out on a population of gopher tortoises at the Archbold Biological Station (Lake Placid, Florida) during summer 1974. A detailed description of the station habitats is presented by Douglass and Layne *(in press)*. The station is located on an elevated portion of the Central Highlands, known as the Lake Wales Ridge, in peninsular Florida. The ridge area in the vicinity of the station is characteristically xeric woodlands, dominated by turkey oak *(Quercus cerris)* and south Florida slash pine *(Pinus caribaea)* (Fig. 1). Transient ponds and ditches which are often dry are present on the property, but at several times during the year (especially during the present study) they are filled with water. Tortoises were active during the time that the temporary water was available; however, the predominantly sandy soil was often dry at its surface by midday.

Field Observations. During the study, animals were seen feeding on plants. Samples of the principal dietary items, as determined by personal observations and unpublished log books at the station, were collected and analyzed for H_2O content and electrolytes. Animals appeared to prefer new shoots or pads and avoid older growth on all plants. Animals were observed to determine if drinking took place in the field. Burrows were observed for activity and sampled for temperature and humidity over 24-h periods at 4-h intervals. This was done to assess the relative importance of burrow microclimate in reducing evaporative H_2O loss. Animals were captured to permit measurement of tritiated H_2O turnover and to monitor changes in osmotic and electrolyte concentrations of the bladder urine. Fecal samples were collected and analyzed to assess this route as an important avenue of H_2O and electrolyte excretion. Collection of samples and measurement of H_2O turnover, body H_2O content and of H_2O, osmotic, and electrolyte content of dietary plants, feces and bladder urine were done in the same manner as on the desert tortoise (Minnich, 1977). The only exception is that body water content in *G. polyphemus* was monitored throughout the study by periodic reinjection of tritiated water (HTO).

Capture of Animals. Study animals were captured by hand while they were foraging and moving about on the surface. Animals were captured at the burrow mouths either by blocking the mouth of the burrow with a fork-like screen after the tortoise exited or by using live animal traps activated to close as the animal crossed a treadle. The live animal traps were covered with a thick terry cloth to eliminate exposure of the animals to long periods of direct sunlight. Tortoises were in traps for a maximum of 5 h; however, most of the captured animals remained in the traps for no longer than 2 h. Animals in traps never exhibited signs of overheating, such as mouth frothing or bladder urine release. Captured animals were taken to the station laboratory building (Fig. 1) for processing, where the room temperature was 22°C. Animals injected or reinjected with tritiated H_2O were maintained in captivity for periods of 24 to 32 h. If animals were not reinjected, they were released no longer than 3 h after capture. In all cases the animals were released at the site of capture.

Burrow Microclimate. To determine relative humidity and temperature within the burrow, 4 separate burrows were analyzed, each on a different day. To do this a Hygrometer Indicator ™, model 15-3030E and a Yellow Springs ™ Telethermometer were attached to captured animals. These animals were released and allowed to take the probes into their burrows, where the probes were released from the shell of the tortoise by a clasp operated from the surface by a rope. Readings were taken every 4 h for 24 h.

Rainfall. Rainfall data were collected daily from the official U.S. weather station located on the Archbold station property (U.S. Weather Bureau, 1974).

Statistical Tests. Comparison of urinary osmotic and electrolyte concentrations in tortoises was done using Kramer's modification of the Duncan multiple range test. Other comparisons between means were done using the Student two sample *t*-test. Equations for straight lines were calculated by the method of least squares and the differences of the slopes from zero were tested using a Student *t*-test. A least squares equation relating H_2O turnover to rate of body weight change was used to estimate the "maintenance" water budget. (The maintenance budget is that amount of H_2O taken in that equals the animal's H_2O loss. It does not necessarily represent minimal H_2O requirements.) The maintenance budget was assumed to be the H_2O turnover at zero body weight change (Minnich and Shoemaker, 1970). This reasoning appears valid, because fractional body H_2O remains constant in *G. polyphemus*. Comparison of water turnover in tortoises of varying body sizes with that of lizards (Minnich, 1978) was done by analysis of covariance. In all cases the level of significance used was $P = .05$. Variation in this paper is expressed as the standard error (SE).

RESULTS

Water Turnover. Figure 2 shows the rate of tritium decline in *G. polyphemus* (corrected for reinjection of tritiated H_2O) as a function of time and rainfall. The constant rate of tritium decline throughout the study indicates that there were no changes in water turnover with rainfall or time. In contrast desert tortoises exhibited sharp increases in H_2O turnover after a rain because they drank rainwater (Minnich, 1976, 1977). Water turnover remained constant in gopher tortoises because they were never observed drinking and because they consumed preformed H_2O in their food regularly. Moreover, the slopes of the lines in Fig. 2 are all nearly the same, suggesting that H_2O turnover rates were uniform within the population.

The average H_2O intake for the population was 3.1 ± 0.13 ml $(100\ g)^{-1}day^{-1}$ while H_2O loss averaged 3.0 ± 0.13 ml $(100\ g)^{-1}day^{-1}$ ($N = 11$). Average total body H_2O (which remained constant throughout the study) for the population was 69.5 ± 5.29 g/100 body weight ($N = 11$). This compares favorably with the value of 69.9 ± 0.97 ml/100 g body weight obtained from drying carcasses of *G. polyphemus* by Thorson (1968). The average rate of weight change for the population was + 0.234 ± 0.088 g $(100\ g)^{-1}day^{-1}$ ($N = 11$). In only 1 animal of the 11 studied was there a net loss of weight during the study (Fig. 3). These data show that the animals were in positive H_2O balance, because their H_2O gain exceeded their loss and the population gained weight throughout the study.

The relationship of water turnover to rate of weight change is shown in Fig. 4. This figure allows estimation of the maintenance H_2O budget (3.1 ± 0.18 $[s_a]$ ml$(100\ g)^{-1}day^{-1}$, $N = 9$) at the y-intercept of the line at zero weight change (s_a = standard error of the y-intercept). Because the slope of the line is not significantly different from zero, H_2O turnover is not strongly correlated with the rate of body weight change, as it is in desert lizards (Minnich and Shoemaker, 1970; Nagy, 1972).

The effect of body size on the total H_2O turnover is seen in Fig. 5 and is compared to that of arid-adapted lizards (Minnich, 1978). Because the slope of the line representing *G. polyphemus* is not significantly different from 1.0, there appears to be no variation in H_2O intake per unit of body weight as body weight increases. This means that small tortoises turn over H_2O at about the same rate per unit of body weight as large tortoises. This is different from arid-adapted lizards, where small animals turn over H_2O at a faster rate per unit of body weight. This is seen in the slope of the line for lizards being significantly below 1.0 ($P < .05$) (Fig. 5) (Minnich, 1978). The line representing *G. polyphemus* lies significantly above the line for lizards ($P < .005$). This indicates that *G. polyphemus* is turning over H_2O much more rapidly than arid-adapted lizards of equivalent body size.

The calculated value of the maintenance water budget for *G. polyphemus* can be compared to those of other animals only after a correction for body size is made. Minnich (1978) found that maintenance water turnover in lizards was proportional to the 0.84 power of the body weight (Fig. 5). When maintenance H_2O turnover rates of *G. polyphemus* and lizards are calculated as a function of the 0.84 power of body weight, the water turnover rate of the gopher tortoise is higher than those of lizards (Table 1). This is also seen in Fig. 5 as the higher positioning of the line representing gopher tortoises as compared to lizards. The high H_2O turnover rate in *G. polyphemus* reflects the great availability of water in its environment.

Dietary Plants. The gopher tortoise is a strict vegetarian. The plants it was most often seen feeding upon, according to personal observations and unpublished log books of naturalists at the Archbold Biological Station, are listed in Table 2. These data show that the gopher tortoise feeds upon plants that contain much water. Average H_2O content was significantly higher than in representative desert plants eaten by the lizard *Dipsosaurus dorsalis* ($P < .001$) (Table 2). Because no animal was ever seen drinking during the study, plants appear to be the major source of preformed H_2O for gopher tortoises. In plants eaten by *G. polyphemus*, both the concentrations of sodium and chloride were not significantly different from those of representative desert plants (Table 2). However, K concentration and Na + K concentrations were significantly higher in desert plants ($P < .001$) (Table 2). The combined Na + K concentrations of plants eaten by *G. polyphemus* (Table 2) are $\approx$ 56% of those of their own body fluids ($\approx$ 144 meq/l--Ross, 1977). This indicates that gopher tortoises were feeding on plants that were fairly dilute in terms of their electrolyte concentrations.

Electrolyte and Osmotic Concentrations of Bladder Urine. Table 3 compares the concentrations of sodium, potassium, chloride and total solutes in bladder urine of *G. polyphemus* with those of *G. agassizi* (Minnich, 1976, 1977). Urinary sodium and chloride concentrations in wild-caught *G. polyphemus* were significantly greater than in either hydrated or dehydrated *G. agassizi*. Urinary potassium, sodium + potassium and osmotic concentration in *G. polyphemus* were significantly lower than in dehydrated *G. agassizi*, but were significantly higher compared to hydrated *G. agassizi* (Table 3).

Ross (1977) measured Na and K concentrations in bladder urine of captive, hydrated and dehydrated *G. polyphemus*. Although his urinary Na concentrations were in the same range as our values, his K levels, even in hydrated tortoises, were significantly higher (Table 3). This suggests that his "hydrated" animals may have been either dehydrated or hyperkalemic at the beginning of his experiments (see Minnich, 1977, and discussion below).

Urinary sodium + potassium concentrations in our *G. polyphemus* (74.3 ± 9.15 meq/l, Table 3) were not significantly different from those in dietary plants (80.0 ± 17.6 meq/l, Table 2).

Urinary osmotic concentrations (Fig. 6) were always below the hydrated plasma values of 275-300 mosm/l in tortoises (Ross, 1977; Dantzler and Schmidt-Nielsen, 1966; Minnich, 1976,1977). Similarly, urinary Na + K concentrations (Table 3) were below the hydrated plasma value of 144 meq/l (Ross, 1977). Urinary sodium + potassium concentrations parallel osmolalities (Fig. 7). The correlation between urinary osmolality and sodium + potassium concentrations (Fig. 7) has a level of significance of $P < .01$ ($N = 65$). Sodium + potassium concentrations constitute 55.0 ± 2.61% of urinary osmolalities.

Bladder urine of gopher tortoises in this study was never observed to contain urate precipitates. However, Ross (1977) observed bladder precipitates in gopher tortoises subject to dehydration.

Fecal Samples. The average H_2O content of 2 fecal samples collected from gopher tortoises was 70.9 ± 1.32 ml/100 g fresh weight and the electrolyte concentrations were 38.1 ± 7.46 meq/l Na^+, 119 ± 40.2 meq/l K^+ and 98.2 ± 26.4 meq/l Cl^-. Although not significantly different, the concentrations of all 3 electrolytes are generally higher than in the dietary plants (Table 2).

Burrow Microclimate. Burrow microclimatic data are presented in Table 4. In all burrows, after a period of equilibration (4-16 h, depending on the burrow) temperature did not change > 1.2°C and averaged 25.5 ± 0.54°C. None of the burrows had a change in relative humidity > 2% after equilibration and averaged 98.7 ± 0.23%. The long equilibration period for one burrow (No. 117) was due to the presence of the tortoise after the burrow had been empty for a long period. The moderate temperature (below the panting threshold of gopher tortoises, ≈ 32°C--Ross, 1977), coupled with the very high relative humidity, certainly limited evaporative H_2O loss when *G. polyphemus* occupied their burrows (see evaporative water loss values of *G. polyphenus* published by Ross, 1977).

DISCUSSION

The great availability of water in the habitat of *G. polyphemus* is readily apparent. Rain fell in copious amounts on most days during the study (Fig. 2), H_2O content of principal dietary items was high (Table 2) and burrow humidities were near saturation (Table 4). Thus it is not surprising that most tortoises gained weight (Fig. 3), and were in positive H_2O balance. Moreover their bladder urine was always hyposmotic to plasma (Fig. 6) and contained no urate precipitates and comparatively low K concentrations (Table 3). All of these observations indicate that gopher tortoises were well hydrated. Even the maintenance water budget was high for a reptile of its size (Table 1). Nevertheless the maintenance estimate must be interpreted with caution. It does not represent the minimal water requirement of this species, as it probably does in desert species (see Table 1 and Fig. 5), because environmental water availability was very high during this study. It is conceivable that gopher tortoises of equivalent body size can balance their H_2O budgets at a value lower than 3.1 ml $(100\ g)^{-1}$ day^{-1} during a drier summer.

Several striking contrasts were observed in the physiology and behavior of the gopher tortoise, as compared to its close relative, the desert tortoise *G. agassizi)* (Minnich, 1976, 1977). During the dry summers of 1970 and 1971 desert tortoises in the Mojave Desert were inactive, did not eat and exhibited negative H_2O budgets, weight loss and elevated osmolalities of both plasma and bladder urine. Furthermore, urinary K levels were considerably elevated (Table 3) and bladder urate precipitates were present (Minnich, 1976, 1977). Clearly these tortoises were dehydrated.

The behavior of these 2 species of tortoises in their respective environments was also very different. Unlike desert tortoises, gopher tortoises were active and feeding daily, including at midday (see Douglass and Layne, *in press*). Desert tortoises are rarely active at midday during the summer unless the weather is cool (McGinnis and Voigt, 1971). The behavior of gopher tortoises during summer rainstorms also differs drastically from that of desert tortoises. We never observed gopher tortoises to drink from the temporary rain pools at the study site. Moreover, the activity of gopher tortoises decreases noticeably during rain (Douglass and Layne, *in press*). In contrast, the activity of desert tortoises increases dramatically after rains and tortoises drink avidly from rain pools (Minnich, 1976, 1977).

The major differences in the physiology and behavior of these 2 species are due not only to the contrast in water availability of their environments, but also to differences in their dietary potassium concentrations. As mentioned above, the average K concentrations in the principal dietary plants of gopher tortoises are only about 1/5 those of hydrated desert plants (Table 2). By contrast, there are no significant differences in the plant sodium or chloride concentrations (Table 2). The reason for the importance of dietary K is that body K concentrations, both intracellular and extracellular, are regulated very precisely in almost all animals (Schmidt-Nielsen, 1975; Minnich, 1978). Body sodium and chloride are not regulated as precisely and reptiles frequently tolerate elevation in their concentrations in the extracellular fluid (reviewed by Minnich, 1978). Most animals, however, do not tolerate any elevation in extracellular or intracellular K because it disrupts many basic cellular processes (see discussion by Minnich, 1977, in these proceedings). Because tortoises lack functional salt glands (Schmidt-Nielsen, 1964; Minnich, 1978), the only routes through which they can extrete dietary potassium is in the feces and urine.

As already pointed out in these proceedings (Minnich, 1977), desert tortoises become inactive and do not eat during summer drought because their normal dietary plants are dry and contain very high K levels. They cease feeding as a means of protecting themselves from accumulating toxic levels of K at a time when insufficient H_2O is available to excrete it. They exhibit elevated urinary K because their cells leak K in response to cellular dehydration. Urate precipitates are present because they are an important vehicle for storing the excreted K in the urinary bladder. Urinary chloride is low (Table 3) apparently because in dehydrated tortoises urate is a major anion (see Minnich, 1972, 1976). Furthermore, desert tortoises drink rainwater because it (1) permits excretion of the stored urinary K and urates and (2) is stored in the urinary bladder as a dilute urine. This "water reserve" even allows tortoises to feed on dry dietary items, despite their high K levels (Minnich, 1976, 1977).

In contrast to desert tortoises, the low K concentrations in the diet of gopher tortoises can easily be excreted in their feces and urine without incurring significant H_2O losses. Although urinary K concentrations are about the same as in their dietary plants, those in their feces are much higher (see Tables 2 and 3 and p. 134 of the text). Furthermore, gopher tortoises are capable of excreting dietary K in more concentrated form than we observed in this study. Ross (1977) measured urinary K concentrations in both hydrated and dehydrated gopher tortoises that were about 2 X those in the urine of our animals (Table 3). Moreover, he also observed excretion of bladder precipitates by dehydrated gopher tortoises. These precipitates, as in desert tortoises, were probably potassium urate (see Minnich, 1972, 1976). Thus dehydrated gopher tortoises also appear to be capable of excreting K by storing precipitated potassium urate in the bladder.

Evaporative H_2O losses in free-living gopher tortoises appear to be low because of (1) the large body size of these tortoises (Table 1) and (2) the very high environmental relative humidities, especially in burrows (Table 4). Their positive water balance indicates that tortoises lose H_2O (through all routes) at a slower rate than they consume it.

The availability of water explains the long activity periods of gopher tortoises. Unlike desert tortoises, gopher tortoises do not remain in burrows for several days as a means of reducing H_2O losses. Because gopher tortoises consume adequate amounts of H_2O in their food, they can afford to lose evaporative H_2O at a moderate rate by remaining active at the surface. Such activity in desert tortoises would cause rapid, severe dehydration, because they did not consume preformed H_2O during drought. Gopher tortoises, unlike desert tortoises, can remain abroad at midday because of (1) the great availability of shade in their environment and (2) their slow heating rates that are due to their large body size.

The difference in behavior during rain in these 2 tortoises is also due to the contrast in environmental water availability. Desert tortoises increase activity during rain because they drink rainwater that is necessary for rehydration and resumption of daily activity and feeding (Minnich, 1976, 1977). Gopher tortoises, on the other hand, decrease activity during rain and do not drink because they obtain all needed preformed water in their food.

In summary, the gopher tortoise does not conserve H_2O as stringently as the desert tortoise because of the great availability of water in its environment. The plant material that *G. polyphemus* eats (Table 2) contains lower potassium concentrations than that eaten by *G. agassizi* (Minnich, 1976), the tortoise utilizes a moist burrow (Table 4) and rainfall is plentiful (Fig. 2). This is reflected in its relatively high H_2O turnover (Table 1).

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We thank Dr. James N. Layne of the Archbold Biological Station for making possible the use of the facilities and for general assistance. Mr. John F. Douglass kindly provided us with several references on the natural history of gopher tortoises. Most of the material in this paper constituted the M.S. thesis of M.R.Z. at the University of Wisconsin—Milwaukee.

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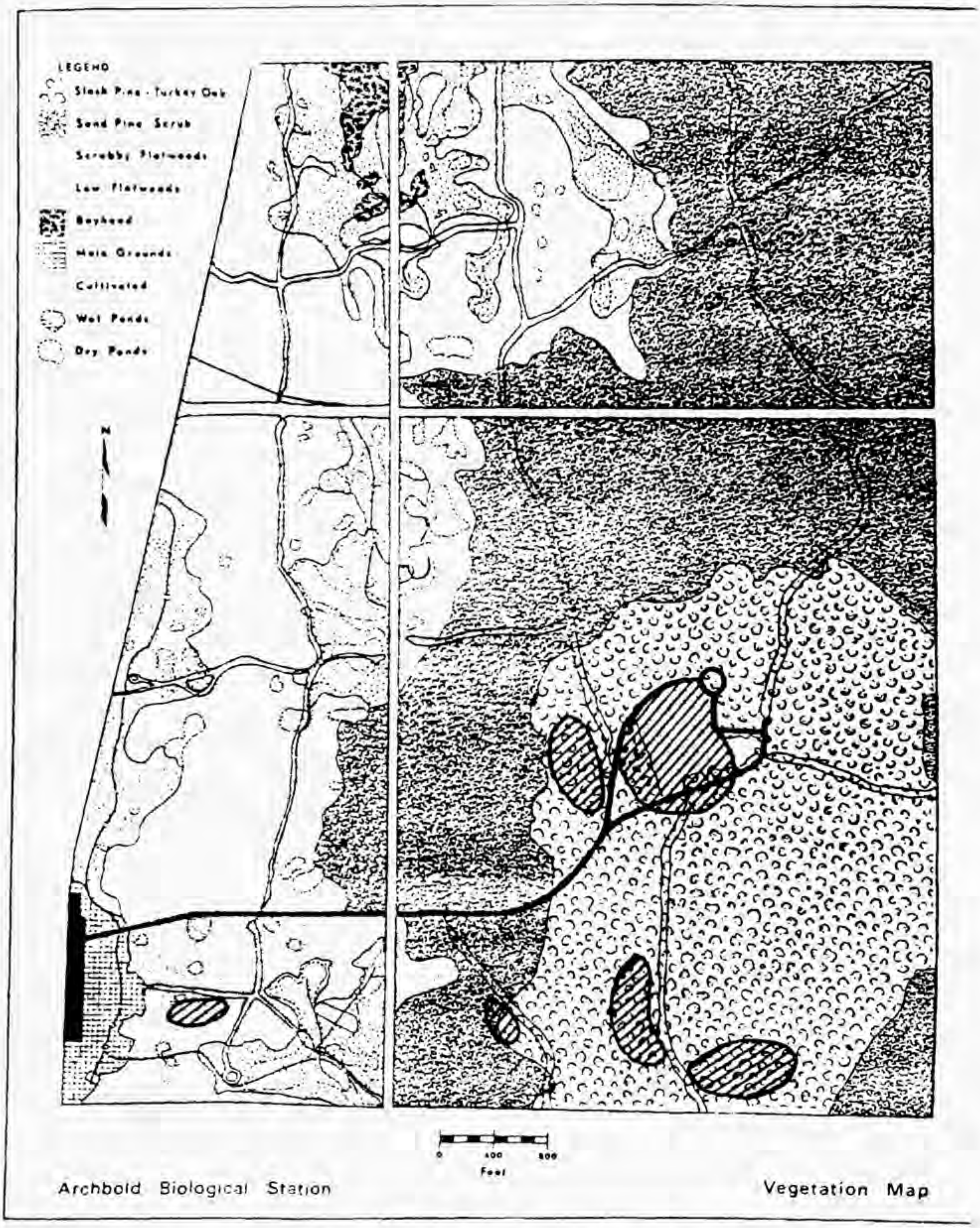

Fig. 1. Vegetation map of Archbold Biological Station (Lake Placid, Florida) where *G. polyphemus* was studied during the summer of 1974. Diagonally hatched areas represent areas where most captures and observations were made. Analysis of samples was done in laboratory building, shaded black. Black line is an asphalt road. Feet X 0.3048 = metres.

Fig. 2. Changes in tritium activity (corrected for reinjection of tritiated H_2O) in the bladder urine of individual *G. polyphemus* and rainfall during the summer of 1974 at the Archbold Biological Station (Lake Placid, Florida). T = trace (amount too small to be measured). DPM = disintegrations/minute.

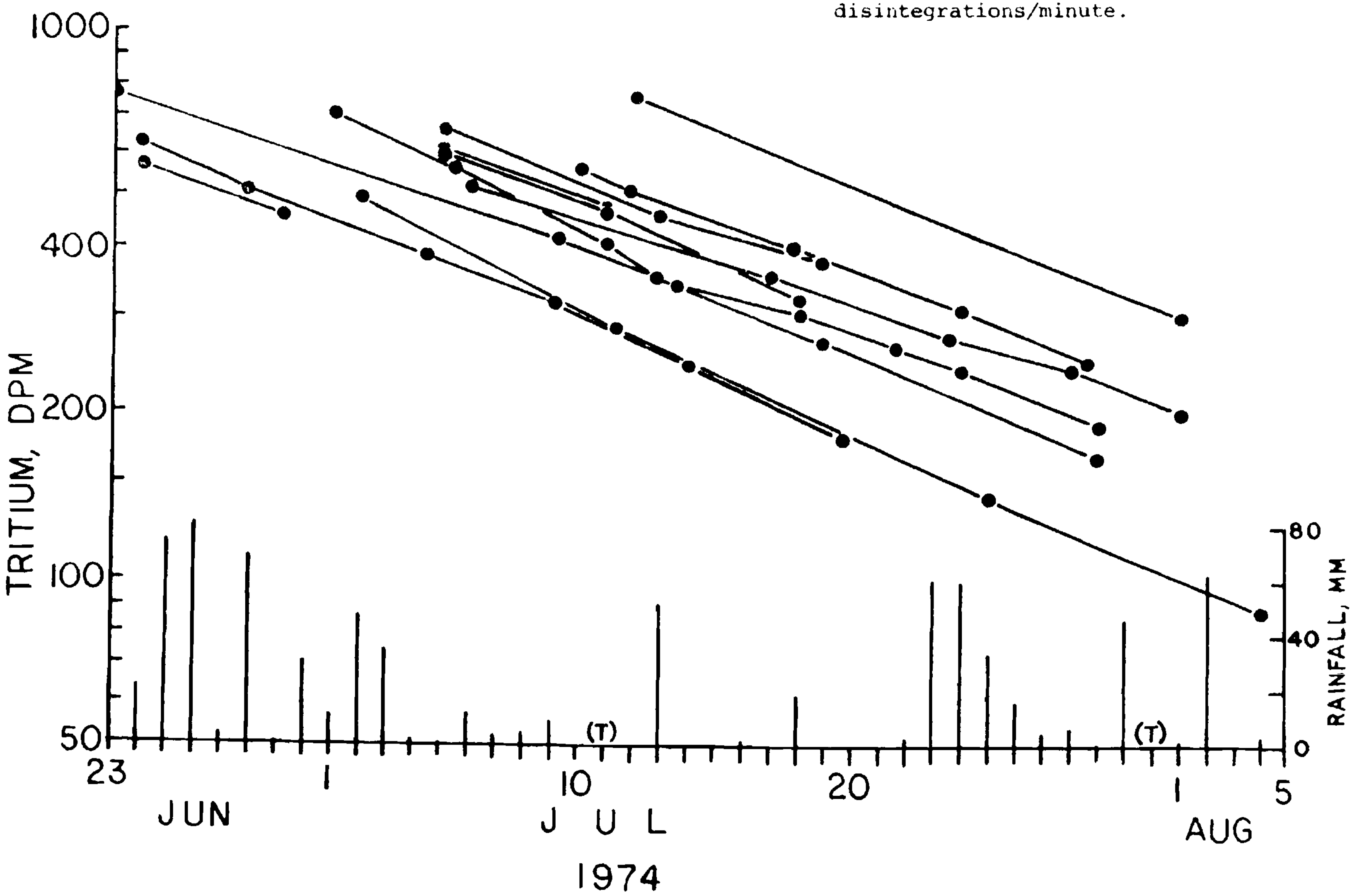

Fig. 3. Changes in the percent initial body weight of individual *G. polyphemus* at the Archbold Biological Station (Lake Placid, Florida) during the summer of 1974.

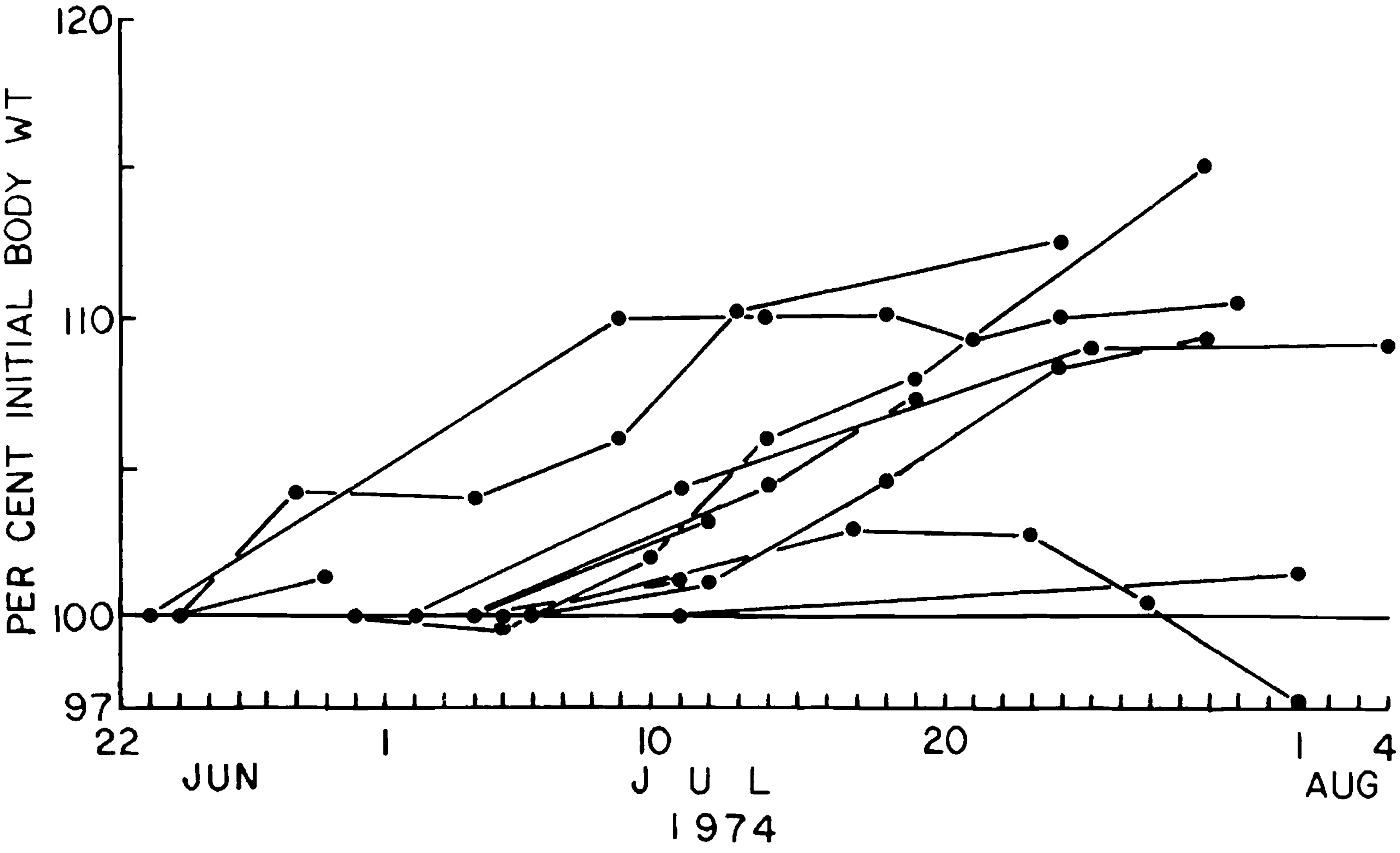

Fig. 4. Relation between H_2O intake and rate of body weight change in *G. polyphemus* during summer 1974 at the Archbold Biological Station (Lake Placid, Florida). The maintenance H_2O budget was calculated as the average H_2O intake at zero weight change for tortoises measured over a period of > 7 days.

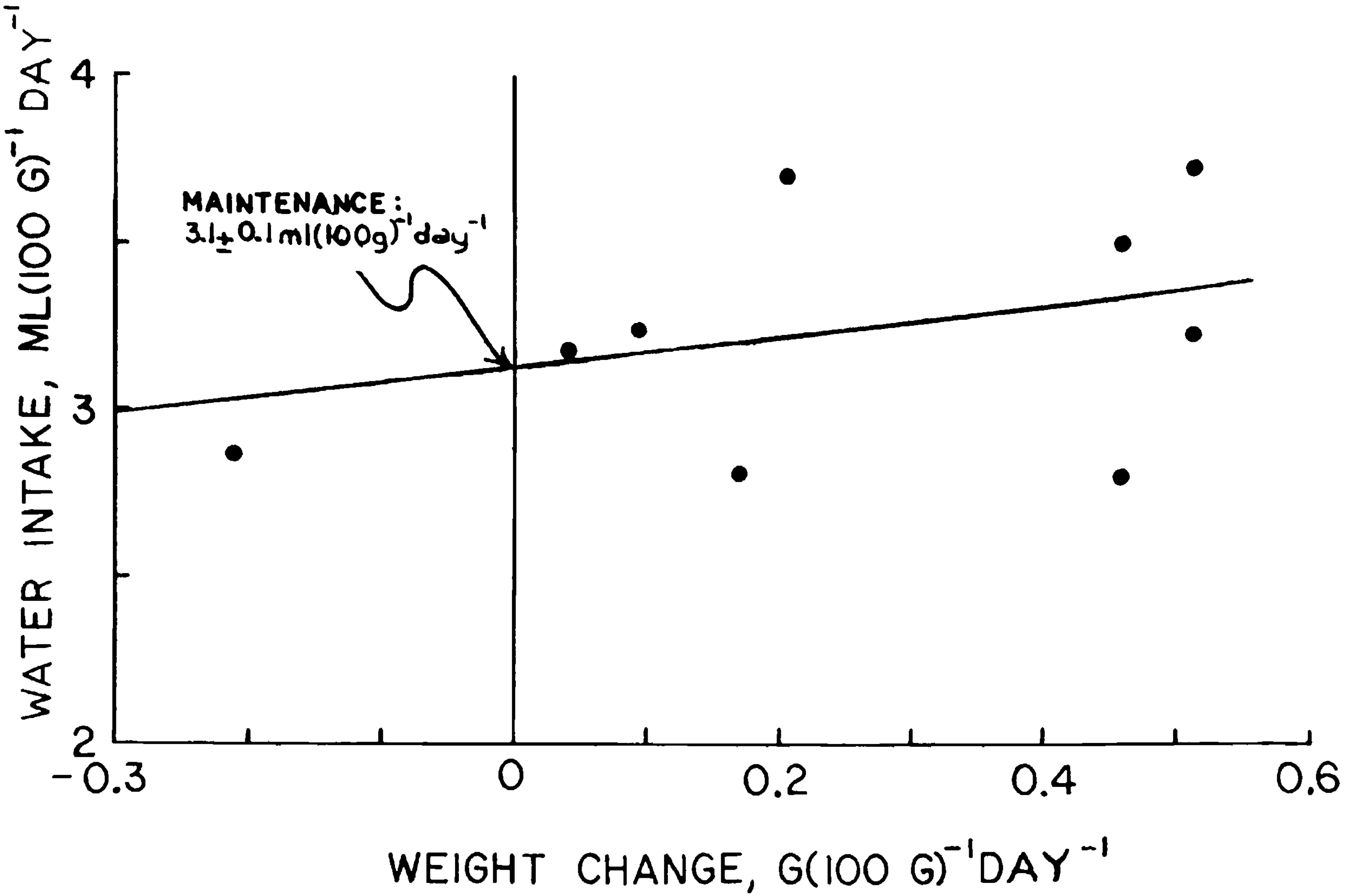

Fig. 5. Relation between total H_2O intake and body weight in *G. polyphemus* during summer 1974 at the Archbold Biological Station (Lake Placid, Florida). The line for lizards is from Minnich (1978).

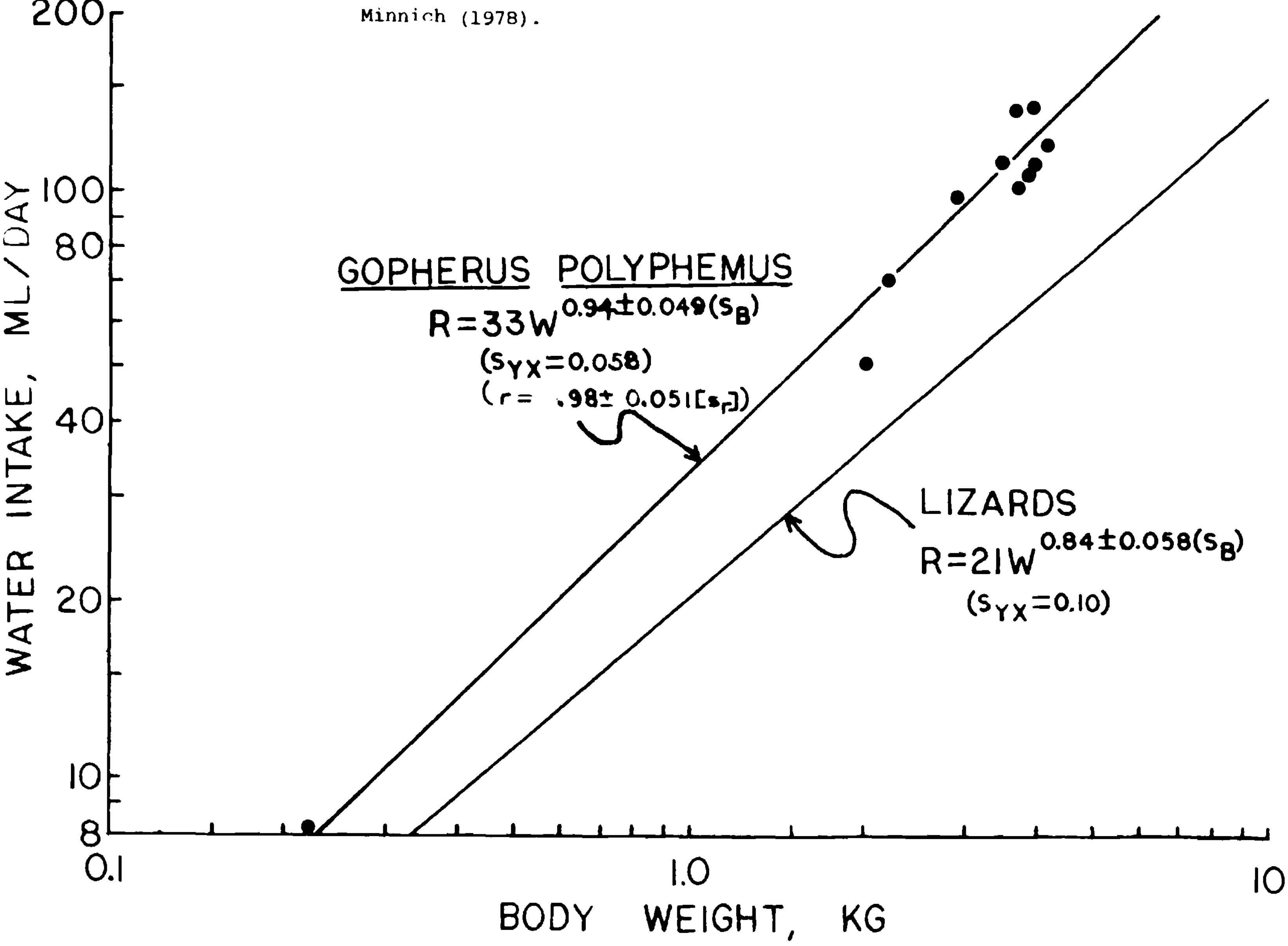

Fig. 6. Osmotic concentrations in bladder urine of *G. polyphemus* during summer 1974 at the Archbold Biological Station (Lake Placid, Florida). All values are below the normal hydrated plasma osmolality of 275 mosm/l (Ross, 1977).

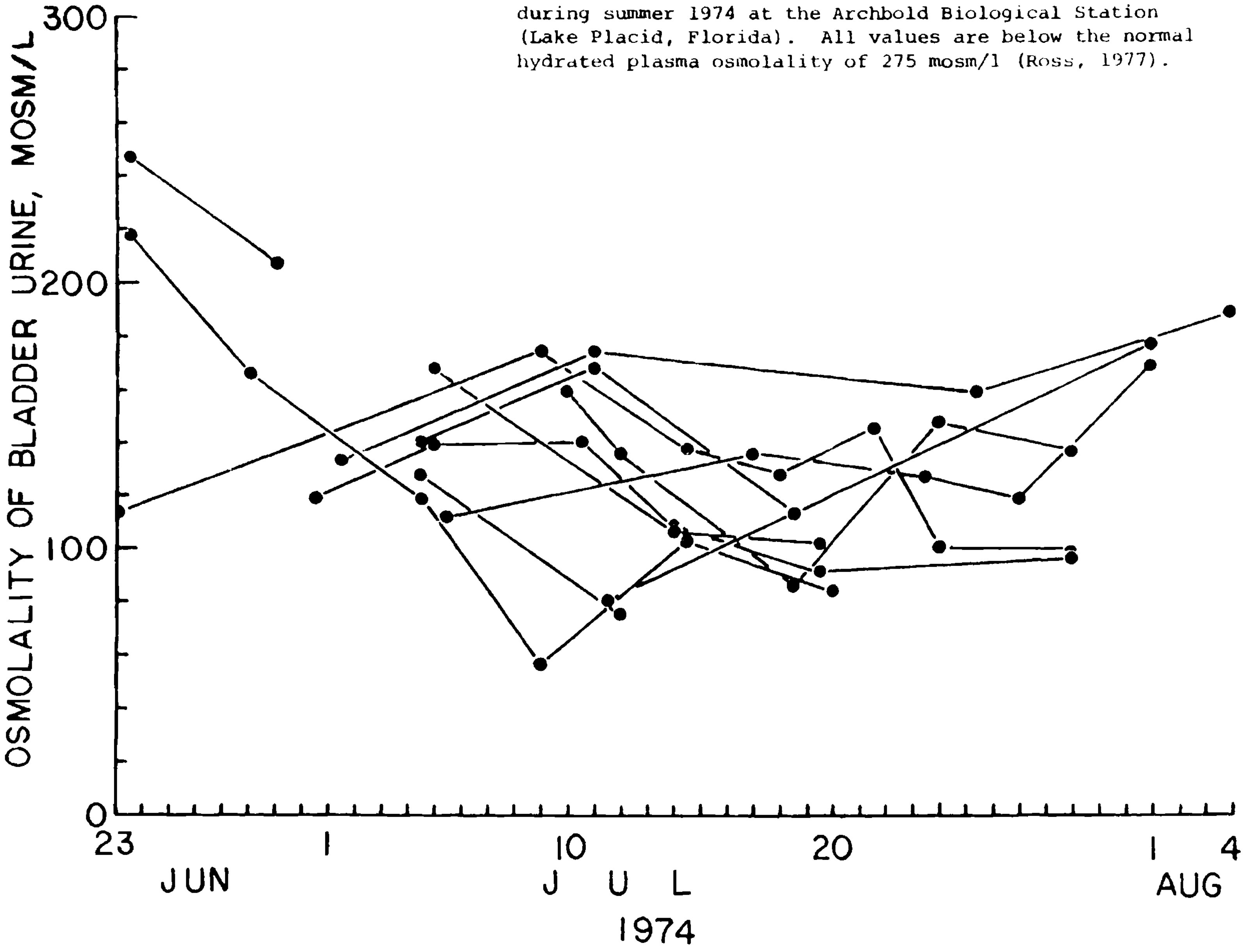

Fig. 7. Relation between osmotic concentrations and Na + K concentrations in the bladder urine of *G. polyphemus* during summer 1974 at the Archbold Biological Station (Lake Placid, Florida).

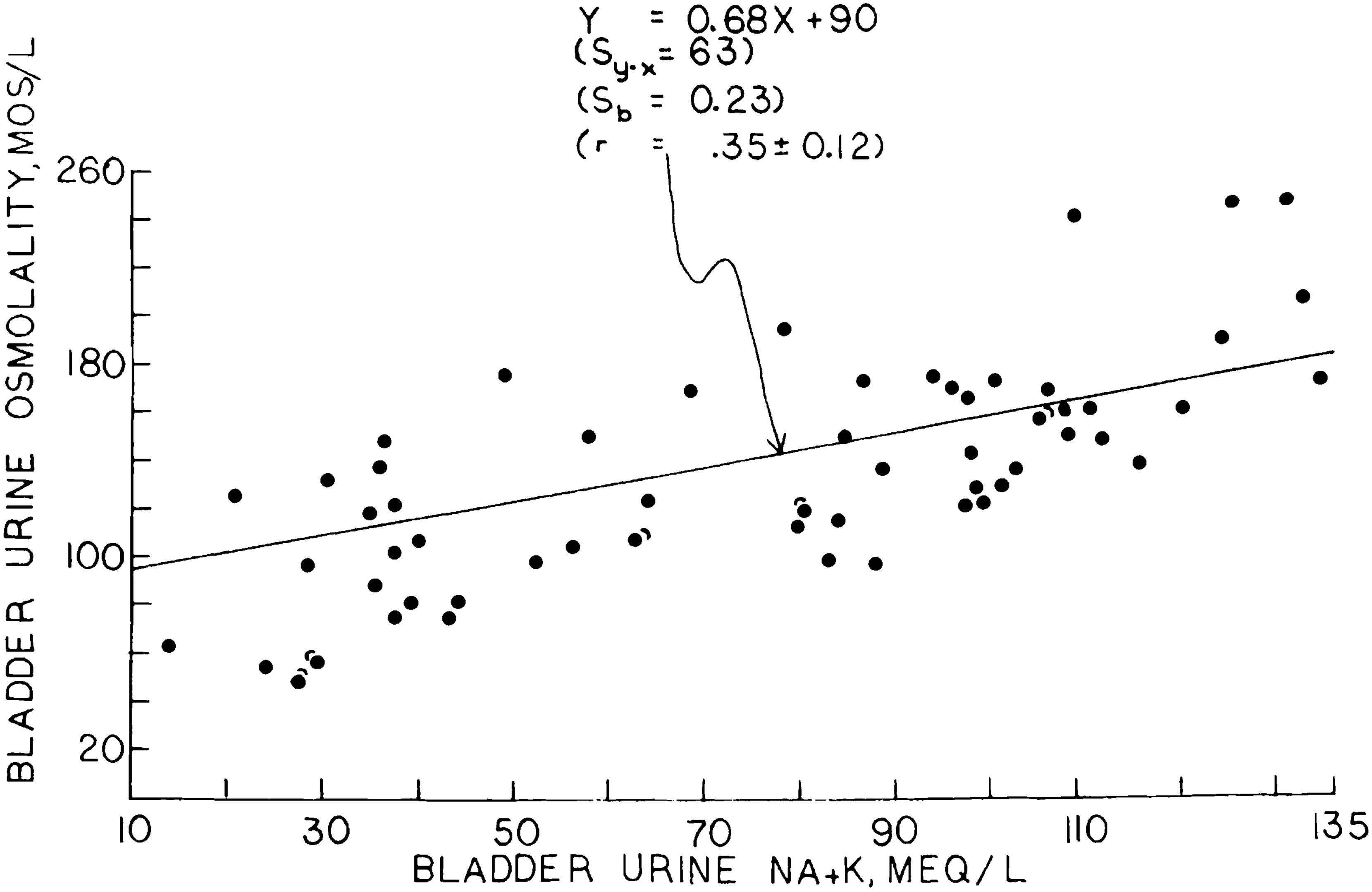

Table 1. Comparison of water turnover rates of *Gopherus polyphemus* with those of other reptiles (see also Fig. 5 of Minnich, 1977)

Species	Body wt (g)	Season	Average intake/day		Average loss/day	Reference
			ml/100 g	$ml/(100g)^{-0.84}$	ml/100 g	
Balanced H_2O budgets						
Testudines						
Gopherus polyphemus	3,182	Summer	3.09	5.38	. . .	This study
Sauria						
Amphibolurus ornatus[a]	6.9	Summer	5.60	3.65	. . .	Baverstock (1975)
	23.7	Summer	2.90	2.30	. . .	
Dipsosaurus dorsalis	50	Summer	3.05	2.73	. . .	Minnich and Shoemaker (1970)
Sauromalus obesus	200	Late spring	2.40	2.68	. . .	Nagy (1972)
Varanus gouldii	1,004	Summer	2.20	3.18	. . .	Green (1972)
Negative H_2O budgets						
Testudines						
Gopherus agassizi	613	Summer	0.27	0.36	0.45	Minnich (1976, 1977)
Sauria						
Agama mutabilis[b]	12.6	Summer	3.37	2.42	3.99	Bradshaw et al. (1976)
Uma scoparia	5.0	Summer	2.41	1.49	2.72	Minnich and Shoemaker (1972)
	20.0		1.18	0.93	1.58	

[a] Water turnover figures assume a body H_2O content of 73 ml/100 g (Bradshaw, 1970).

[b] ♂♂ only.

Table 2. Comparison of water content and electrolyte concentrations of dietary plants[a] of *Gopherus polyphemus* with those of representative desert plants[b]

Taxa (common name)	Plant part		H_2O content (ml/100 g fresh wt)	Electrolyte concentrations (meq/l)			
				Na	K	Cl	Na+K
Amaranthaceae							
Froelichia floridana (cottonwood)	Leaves only		73.2	31.3	104	129	135
Cactaceae							
Opuntia austrina (prickly pear cactus)	New pads		86.3	7.31	55.0	29.1	62.3
Commelinaceae							
Commelina erecta var. *augustifolia* (dayflower)	Flowers and stems		85.5	8.80	22.8	39.0	31.6
Gramineae							
Eremochloa ophiurodes (centipede grass)	Leaves and stems		69.4	30.4	69.9	47.1	100
Rubiaceae							
Diodella teres	Leaves only		78.0	25.1	45.3	46.5	70.4
		$\bar{x}$	78.5±3.33[c]	20.6±5.23	59.4±13.5	58.1±18.0	80.0±17.6
Representative desert plants[b]		$\bar{x}$	56.4±2.46[c]	21.0±3.45	300 ±32.1	77.0±16.8	321 ±32.8
			P[d] $< .001$	NS	$P < .001$	NS	$P < .001$

[a] Based on single determinations for each species.

[b] From Minnich and Shoemaker (1970) and based on the 10 most important native plants eaten by the lizard *Dipsosaurus dorsalis* in summer (*Ambrosia dumosa, Coldenia plicata, Dalea emoryi, Dalea schottii, Dicoria canescens, Eriogonum inflatum, Euphorbia polycarpa, Hoffmannseggia microphylla, Larrea tridentata, Palafoxia linearis*).

[c] Standard error.

[d] Probability of significant difference between plants fed upon by *G. polyphemus* and representative desert plants (Student's t-test). NS = not significant.

Table 3. Comparison of electrolyte and total osmotic concentrations in bladder urine of *Gopherus polyphemus* with those of *Gopherus agassizi*[a]

Species	Season	Hydration state	Sample (*n*)	Electrolyte concentration (meq/l) Na	K	Cl	Na+K	Total osmotic concentration (mosm/l)	Reference
Gopherus polyphemus	Summer	Hydrated	11	32.3±4.78	42.9±6.49	39.3±3.20	74.3±9.15	136 ±10.5	This study
	Captive[b]	Hydrated	7	17 ±3.5	94.9±5.0**	. .	. . .	. . .	Ross (1977)
		Dehydrated[c]	13	33 ±7.0	87.4±5.0**	. . .	. . .	. . .	
Gopherus agassizi	Summer	Hydrated	11	14.7±5.87*	5.6±3.12**	14.7±5.72**	20.3±6.33**	82.7±19.8*	Minnich (1976,1977)
		Dehydrated	17	10.0±3.68**	89.8±6.92**	3.3±1.78**	99.8±4.83**	337 ±12.4**	

[a] Values are $\bar{x}$ ± SE.

[b] *G. polyphemus* studied by Ross (1977) were animals maintained in a laboratory during the study.

[c] Dehydrated tortoises were held in cages at 32°C without food or H_2O for 14 days, losing an average of 173±31.4 g body weight for the 14-day period. Samples were collected daily over mineral oil and frozen for later analysis. (Ross, 1977).

* $P < .05$, compared to wild-caught *G. polyphemus* (Duncan test), **$P < .01$. Values lacking an asterisk are not significantly different, compared to wild-caught *G. polyphemus*.

Table 4. Average temperatures and relative humidities in 4 burrows of *Gopherus polyphemus* during equilibration with soil[a]

Burrow no.	Measurement dates (1974)	Daily "Surface"[b] temp (°C)		Daily "Surface"[b] relative humidity (%)		Depth (cm)	Equilibration time (h)	Measurements (*n*)	Mean temp (°C)	Mean relative humidity (%)
		Max	Min	Max	Min					
117	6 Jul	40.0	21.5	66.9	38.2	310	12	4	24.4±0.12	98.6±0.21
Q	8 Jul	30.6	22.2	77.2	59.0	360	8	5	25.1±0.14	98.9±0.08
E_1	29 Jul	33.9	23.3	79.8	61.2	350	4	6	26.9±0.12	99.2±0.50
J_1	4 Aug	36.7	22.8	83.1	42.8	280	0	7	25.5±0.11	98.1±0.35
$\bar{x}^c$						325	. . .	4	25.5±0.54^c	98.7±0.23^c

[a] Values are $\bar{x}$ ± SE.

[b] "Surface" denotes conditions in a standard U.S. Weather Bureau shelter aboveground at the Archbold Biological Station (U.S. Weather Bureau, 1974).

[c] $\bar{x}$ and SE based on average conditions of the individual burrows.

Seasonal Water and Energy Relations of Free-living Desert Tortoises in Nevada: a Preliminary Report

Kenneth A. Nagy and Philip A. Medica

A year-round study of H_2O and energy balance in desert tortoises is being done in Rock Valley, Nevada Test Site. Water fluxes and rates of CO_2 production are measured in field animals using the doubly-labeled water method. Some preliminary results are presented here. Tortoises became active about the beginning of April 1976, and gained weight during spring while eating ≈ 3-4% of their body mass in succulent annual plants each day. When annual plants began dying and drying out in late May, tortoises continued feeding on dry vegetation for a while, but surface activity declined into summer, as the animals spent progressively more time in burrows. From spring to summer, H_2O influx rates dropped from about 25 to 5 ml $(\text{kg}\cdot\text{day})^{-1}$ and metabolic rates declined from about 0.15 to 0.08 ml CO_2 $(\text{g}\cdot\text{h})^{-1}$. Tortoises were dehydrating slowly in summer, judging by their declining body masses and the increasing osmotic pressure of their plasma (from ≈ 290 to 360 mosM) and bladder urine (from ≈ 180 to 330 mosM). With the advent of several thundershowers in late July, many tortoises quickly emerged and drank rainwater before it soaked into the ground. Some animals apparently did not drink during this period. Subsequent showers in September induced germination and growth of winter annuals during the fall. Tortoises fed on these plants and gained weight through October. Nearly all animals had entered deep winter burrows by mid-November.

Of the many reptiles inhabiting the Mojave Desert, the desert tortoise is the most long-lived, and appears to be the least perturbed by seasonal or multi-year droughts. These observations suggest that tortoises are well-adapted physiologically and behaviorally to withstand the rigors of desert life. Little is known about the details of these adaptations, so this study is being done to assess the water balance, behavior and energetics of desert tortoises *(Gopherus agassizi)* in the field, by using the doubly-labeled water method (Lifson and McClintock, 1966; Nagy, 1975). As the study is still in progress, only a short report of initial results is presented here.

MATERIALS AND METHODS

The study area is a 9-ha fenced plot containing natural vegetation (*Larrea—Ambrosia* plant community) in Rock Valley, a part of the Nevada Test Site in Nye County, Nevada. Detailed descriptions of this area have previously been published (Vollmer et al., 1976;

Ackerman and Bamberg, 1974). Measurements began in March 1976, when tortoises became active that year. The following is a brief account of methods used; these are described in detail in Nagy (1972) and Nagy and Shoemaker (1975).

Animals are captured, dusted off and placed in plastic pans to catch any voided urine and feces. The point of capture is recorded and the tortoises are transported to a trailer laboratory a few kilometres away. Here, they are weighed, plastron length is recorded, blood samples are taken from an orbital sinus, urine samples are taken by bladder puncture, and labeled water is injected intraperitoneally. Tortoises are kept overnight to permit the isotopes to become thoroughly mixed in the body water. The following morning, blood samples are taken, and the animals are released where captured. This procedure is repeated every 2 weeks when tortoises are active, and every month when animals are in winter burrows (only 5 to 9 of the 11 labeled animals in the study area are recaptured at one time).

Each animal is marked with numbers painted on the carapace as well as with notches in marginal scutes, and most tortoises are fitted with small radio telemeters (range about 30 metres, battery life 3 to 5 months) to facilitate recapture. To capture animals during winter, they are first radiolocated, then a vertical hole is dug next to their burrow to remove the animal without harming the burrow. After processing, the tortoises are returned to their burrows and the access hole is blocked with a board and refilled. Most animals remained in the same burrow through the winter, despite our manipulations.

Daily behavior patterns and plant species eaten are recorded during 1 or 2 days of continuous observation (with binoculars) every other week during the activity season. Samples of all plants in the enclosure are collected biweekly for analysis of water, energy, nitrogen, salt and mineral contents. Meteorological data are continuously recorded at several weather stations in Rock Valley.

Blood samples are analyzed for doubly-labeled water ($H^3H^{18}O$) by first microdistilling them to obtain pure water, which is then measured for tritium specific activity by liquid scintillation, and for oxygen-18 by charged particle activation using cyclotron-generated protons (Wood et al., 1975). These data are used to calculate rates of water input, water output and CO_2 production (metabolic rate), which can then be used to calculate feeding and drinking rates (Nagy, 1975). The end result will be itemized energy and material budgets for free-living tortoises for each season of the year.

To assess critical aspects of water balance and osmoregulation, urine and plasma samples are analyzed for electrolyte and total osmotic concentration.

During 1977, several tortoises will be brought into the laboratory, where they will be fed measured amounts of natural diets. Urine and feces will be collected and analyzed along with the food in order to determine energy and material assimilation and excretion. These results will permit itemization of field budgets, and estimation of minimum dietary requirements for comparison with seasonal changes in food plant quality.

PRELIMINARY RESULTS

Spring. After emergence from winter burrows in late March and early April, tortoises fed on succulent annual plants and gained weight into mid-May. During this period, water influx rates increased from about 12 to 25 ml $(kg \cdot day)^{-1}$, and metabolic rates increased from about 0.07 to 0.15 ml CO_2 $(g \cdot h)^{-1}$. We estimate that tortoises in May were consuming 3-4% of their body weight in food each day. From May to June, annual plants died and dried out, but tortoises continued to feed, consuming primarily the dry grasses that remained from May. During this period, water influx rates declined to about 5 ml $(kg \cdot day)^{-1}$, and energy metabolism declined to about 0.08 ml CO_2 $(g \cdot h)^{-1}$ as animals spent progressively more time in burrows. During spring, osmotic concentrations increased in both plasma (from 290 to 360 mosM) and bladder urine (from 180 to 330 mosM), indicating that even the spring situation presents a water stress problem to tortoises.

Summer. From mid-June to mid-July, tortoises spent most of their time in burrows, and did not feed. As a result, they had low water fluxes $\left[5 \text{ ml } (kg \cdot day)^{-1}\right]$ and metabolic rates $\left[0.08 \text{ ml } CO_2 \ (g \cdot h)^{-1}\right]$, and plasma osmotic concentrations increased slightly. Between 15 July and 1 August, several thunderstorms dropped 13 mm of rain on the study area, and about half of the tortoises emerged and drank $\approx$ 10% of their body weight in rainwater. This was associated with a decline in osmolarity of both plasma (from 360 to 310 mosM) and bladder urine (from 330 to 60 mosM). On overcast days during this period, tortoises were seen scraping shallow depressions in the soil in open spaces between shrubs. These basins subsequently caught rainwater, and apparently served as drinking sites for tortoises. Then, tortoises again began feeding on dry grasses for a time, before becoming inactive again. Not all animals emerged to drink and feed during this period.

Fall. Rain in early September provided sufficient moisture to induce germination of annual plants. In addition to drinking again in September, tortoises began feeding on the fall crop of "winter" annuals, and gained weight into mid-October when declining temperatures limited surface activity. By mid-November, most animals had entered deep winter burrows.

DISCUSSION

Several tentative conclusions emerge from these results. Clearly, tortoises are not impervious to seasonal fluctuations in weather conditions and food quality. The changes in plasma and urine osmolarity in spring and summer indicate that tortoises are osmotically stressed even when green forage is available in spring. Osmotic concentrations returned to normal when tortoises drank rainwater in summer, and some of this water was retained, apparently in the urinary bladder (Dantzler and Schmidt-Nielsen, 1966) to offset future osmotic stresses. Similar results were obtained by Minnich (1976 and this volume) from tortoises living near Barstow, California, in the central Mojave Desert.

Tortoises are remarkably skilled at obtaining drinking water. Many of our animals (which had spent at least the 3 preceeding weeks in burrows) rapidly emerged during a mid-July rain and drank water before it soaked into the soil. Some of the tortoises appeared to have anticipated the precipitation, and constructed shallow basins in the soil several hours before rain actually began falling. The mechanism(s) by which tortoises detect or anticipate rain deserves further investigation.

Few "summer" annual plants occur in the northeastern Mojave Desert, and "winter" annuals usually grow between autumn and late spring, provided that autumn rainfall is adequate (Beatley, 1974). Thus, succulent annual vegetation is usually not available to tortoises during the middle portion of their annual activity season. Despite this, tortoises showed normal increases in length and mass during 1976, as compared with growth rates previously observed by Medica et al. (1975). There appear to be several reasons that account for this. First, tortoises continued to feed in late spring, even after food plants became very dry. This is in marked contrast to another herbivorous desert reptile, the chuckwalla *(Sauromalus obesus)*, which does not eat dry plants and dies quickly when it is forced to do so (Nagy, 1972), possibly because of osmotic stress. The ability of tortoises to eat dry plants may be related to their relatively high body water content and their tolerance of osmotic stress. This would permit tortoises to extend their feeding activities further into summer. Second, the ability to detect and consume rainwater, and to store some of it in the urinary bladder could allow tortoises to consume dry plants even later in the summer, by providing the necessary water that is not present in the diet. Third, the early crop of "winter" annuals evoked by the rains in September 1976 provided green forage in fall, and allowed animals to feed and gain weight before entering winter dens. Extrapolation of our results indicates that, had rain not fallen in summer and early fall, tortoises would probably have shown a net loss in body mass through their 1976 activity season. As tortoises also occur in areas where summer rainfall is rare or absent, such as in the western part of the Mojave Desert, comparative data from various areas within the geographic range of these animals could be very enlightening.

ACKNOWLEDGMENTS

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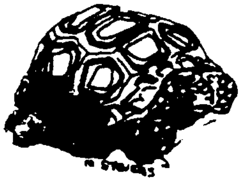

Growth and Shell Relationships in the Desert Tortoise

Robert Patterson

In the desert tortoise, *Gopherus agassizi*, shell thickness, percentage of body weight represented by the shell and shell density all increase with an increase in carapace length. It appears that other species of tortoise may behave differently.

Knowledge of how the animal, its shell and its characters change with increasing age is only partly known for the desert tortoise, *Gopherus agassizi*. Medica et al. (1975) have shown that in *G. agassizi* body weight is approximately equal to the cube of the plastron length. They have also determined that the plastron length and carapace length are highly correlated ($r = .99$). Others have shown that carapace length increases with age in a regular manner in *G. agassizi* (Patterson and Brattstrom, 1972) and in *Testudo gigantea* (Gaymer, 1973).

The present study examined several unanswered questions about tortoise shell growth. These included: Does shell thickness increase with age? Does the percentage of total body weight represented by the shell increase with age? Does shell density increase with age?

METHODS

A collection of 10 *G. agassizi* shells were drilled in the middle of the fourth costal element of the right side of the carapace. Shell thickness at the site of the drill hole was then determined using a depth vernier caliper.

Twelve *G. agassizi* that had been weighed prior to natural deaths were reweighed after thawing and specific body components were also weighed (Patterson, 1973).

Seventeen *G. agassizi*, 5 *Geochelone elegans* and 3 *Geochelone elephantopus* were weighed and measured prior to death or just after death. They were opened, cleaned and shell volume and mass (both wet and dry) was determined. Shell mass (grams) divided by shell volume (millimetres) provides a measure for shell density.

Data on *Testudo gigantea* (Hughes et al., 1971) were analyzed to determine the percentage of body weight represented by the shell.

RESULTS

A strong positive correlation ($r = .95$) was found between shell thickness in millimetres (Y) and carapace length in centimetres (X). As shown in Fig. 1, the associated equation is: mean shell thickness ($Y) = 0.165X - 0.44$.

The percentage of total body weight represented by the shell (Y) in *G. agassizi* was found to be positively correlated ($r = .72$) with carapace length in centimetres (X). As shown in Fig. 2, the associated equation is: mean percent body wt shell ($Y) = 0.599X + 5.64$.

The percentage of total body weight represented by the shell (Y) in *Testudo gigantea* was found to be weakly but positively correlated ($r = .625$) with carapace length in centimetres (X). As shown in Fig. 3, the associated equation is: mean percent body wt shell ($Y) = 0.034X + 8.16$.

A strong positive correlation ($r = .836$) was found between the density of the shell in grams/millilitre (Y) and carapace length in centimetres (X) for *G. agassizi*. As shown in Fig. 4, the associated equation is: mean shell density ($Y) = 0.23\ X^{0.566}$.

A tentative relationship ($r = .85$) was found between the density of the shell in grams/millilitre (Y) and carapace length in centimetres (X) for *Geochelone elegans*. As show in Fig. 5, the assoiated equation is: mean shell density ($Y) = 0.858\ X^{0.178}$. For comparative purposes, the only available data for *Geochelone elephantopus* are plotted in Fig. 6 with a visually drawn regression line.

The regression equations for all figures except Fig. 6 were determined using the method of least squares.

TABLE 1. Results of regression coefficient tests.
NS = not significant; CL = carapace length.

Species	Regression equation	t-value	P
Gopherus agassizi	Shell thickness vs. CL	1.51	$<.05$
Gopherus agassizi	Percent body wt shell vs. CL	2.62	$<.10$
Gopherus agassizi	Shell density vs. CL	3.86	$<.01$
Testudo gigantea	Percent body wt shell vs. CL	0.08	NS
Geochelone elegans	Shell density vs. CL	0.58	NS
Geochelone elephantopus	Shell density vs. CL	. . .	NS

A null hypothesis of no difference between the obtained regression coefficients and a value of zero was tested using Student's distribution. Because of the limited sample size and the tentative nature of the present work, a P-value of .10 was regarded as being significant. As shown in Table 1, the null hypothesis was rejected for all regression equations involving *G. agassizi* but was accepted for the other species studies.

SUMMARY

It thus appears that in *G. agassizi* there are positive relationships between: increasing shell thickness and carapace length, increasing percentage of total weight represented by the shell with increasing carapace length and, increasing shell density with increasing carapace length.

While not significant, on the basis of the limited data available, it appears that other species of tortoise behave differently from *G. agassizi* with regard to these variables.

ACKNOWLEDGMENTS

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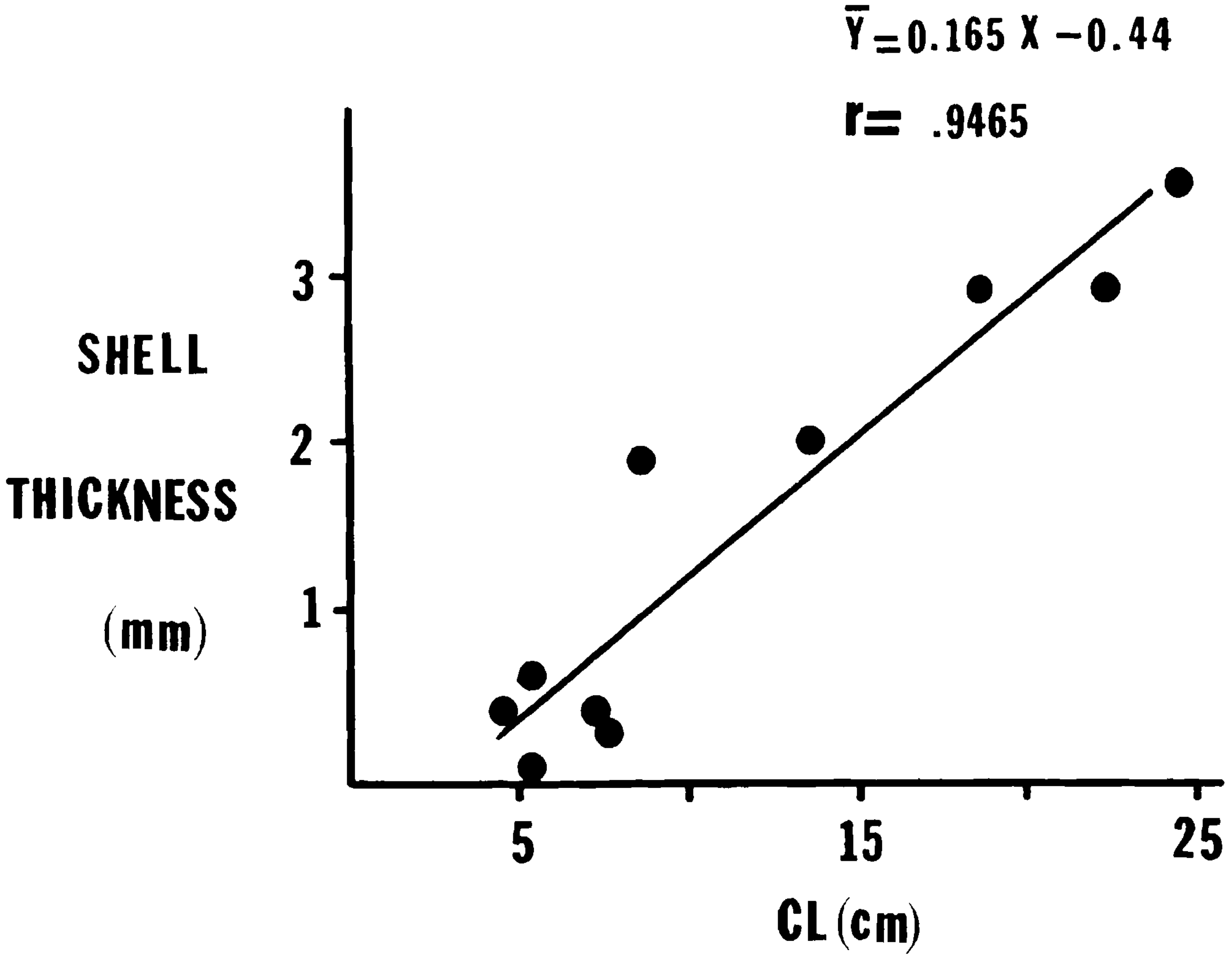

Fig. 1. The relationship between thickness of shell in millimetres, measured at the middle of the fourth costal element of the carapace (X) and carapace length in centimetres (Y) in *Gopherus agassizi*.

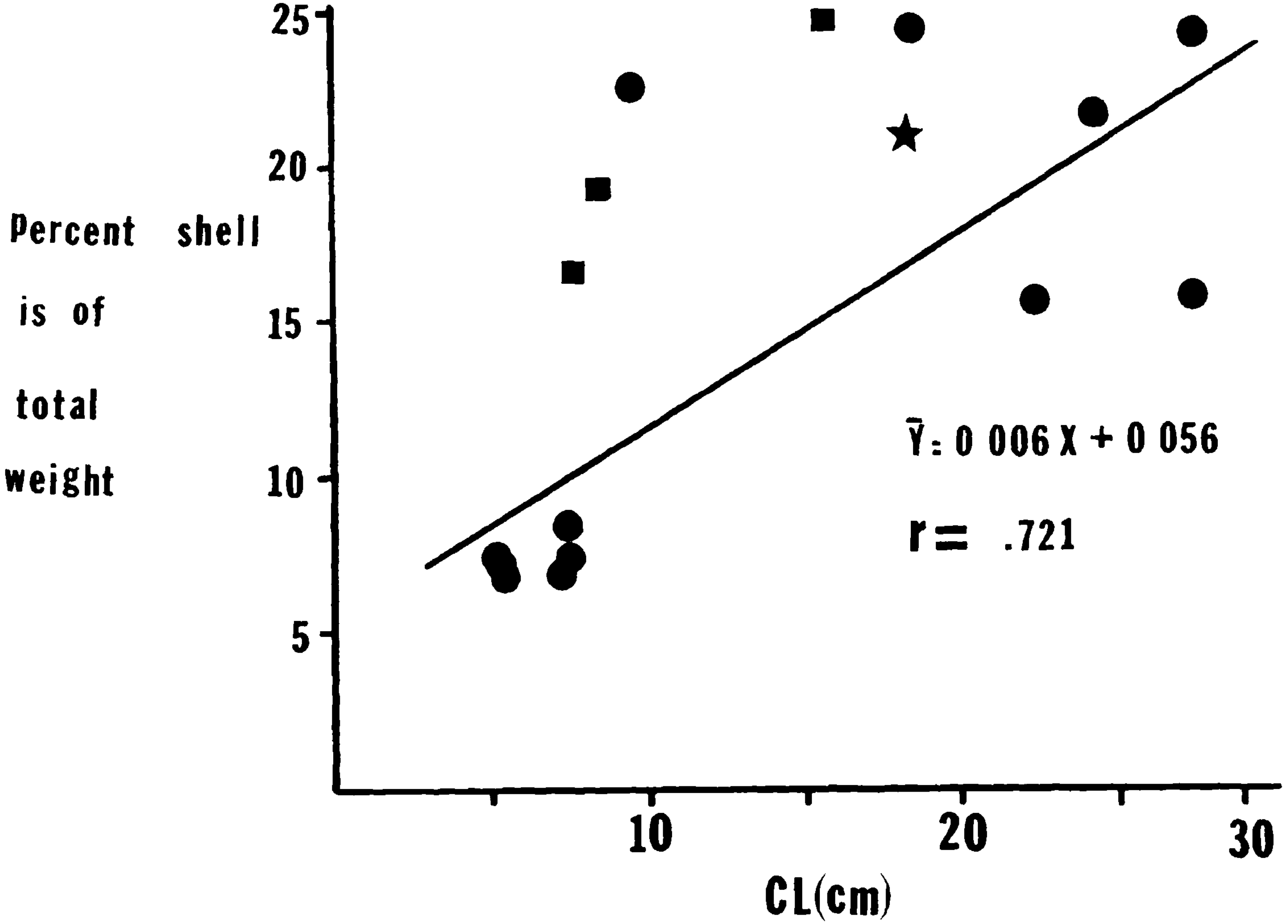

Fig. 2. The relationship between the percent of the total body weight represented by the shell (Y) and carapace length in centimetres (X) in *Gopherus agassizi*. Only the data for *G. agassizi* (circles) were used in calculating the regression equation; however, the data for *G. berlandieri* (squares) and *G. polyphemus* (stars) are included for comparative purposes.

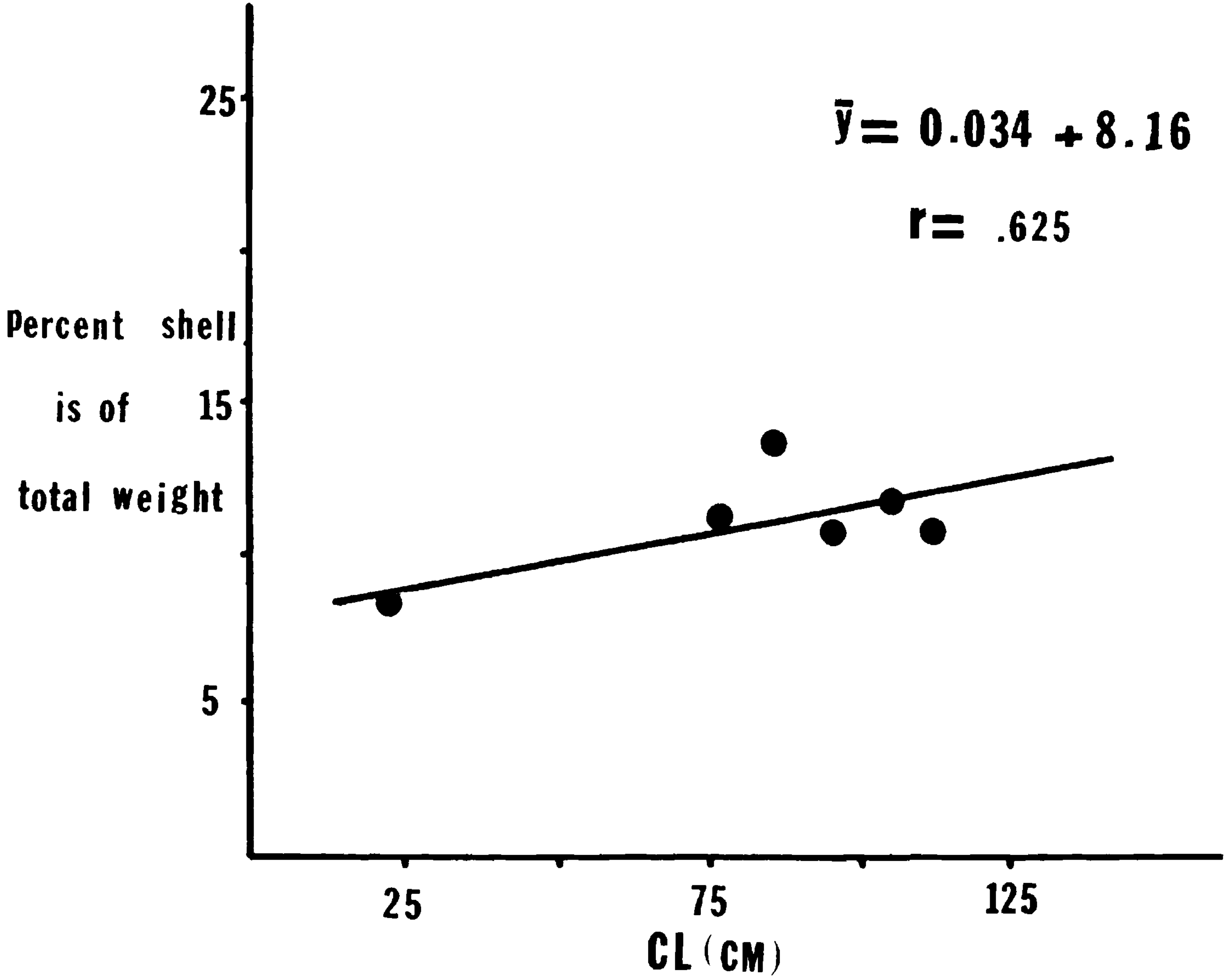

Fig. 3. The relationship between the percent of the total body weight represented by the shell (Y) and carapace length in centimetres (X) in *Testudo gigantea*.

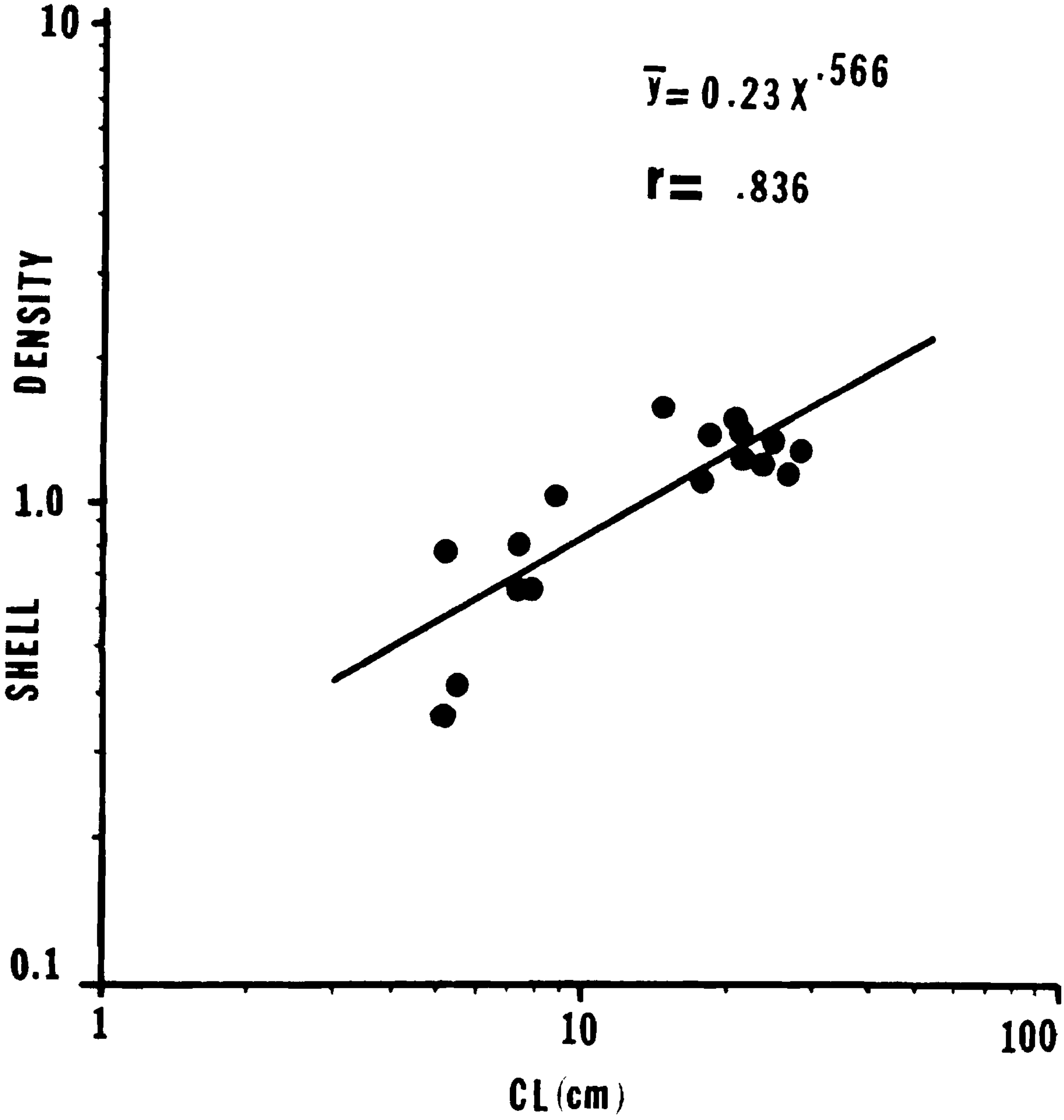

Fig. 4. The relationship between shell density (y) and carapace length in centimetres (x) in *Gopherus agassizi*.

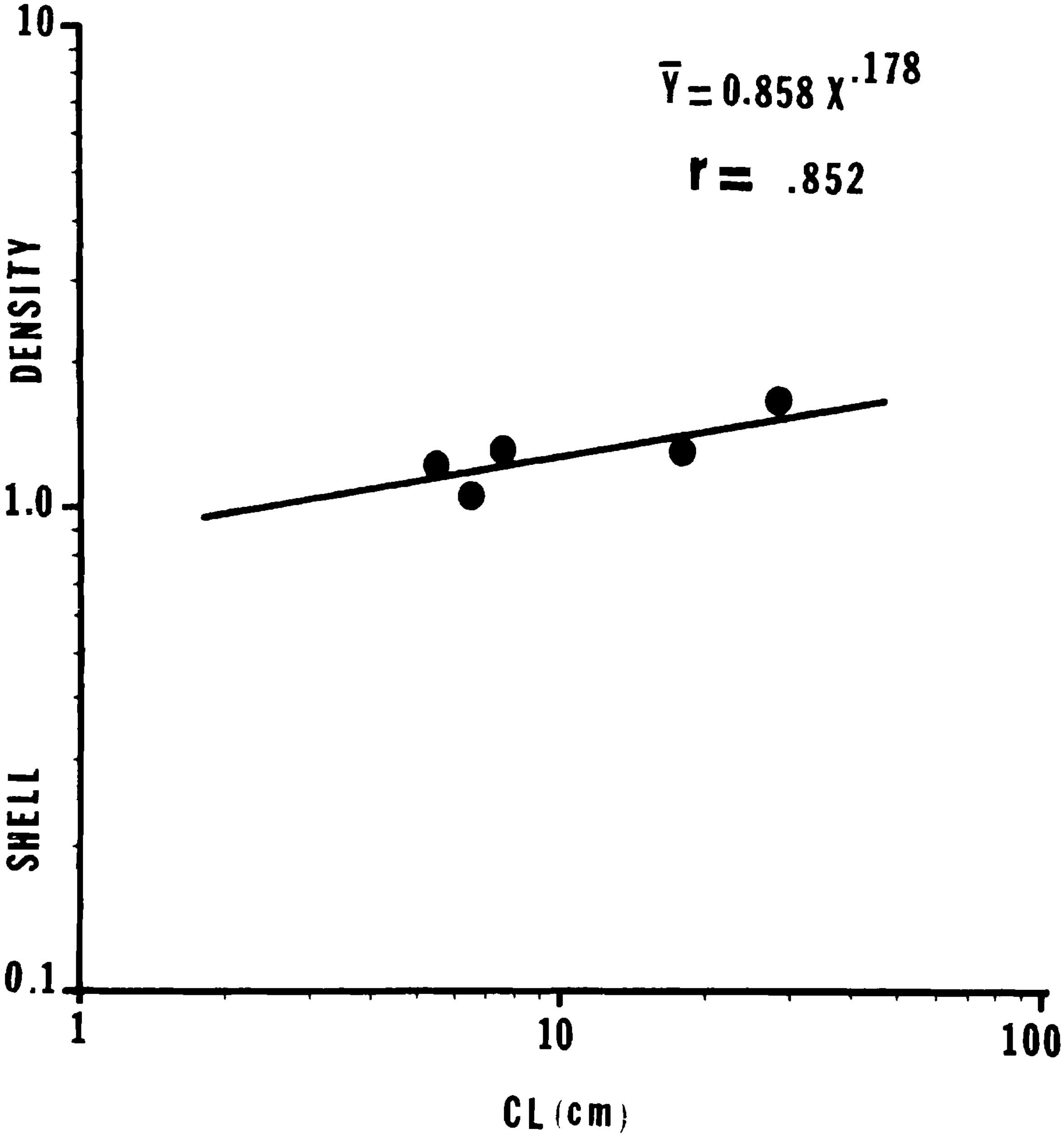

Fig. 5. The relationship between shell density (*Y*) and carapace length in centimetres (*X*) in *Geochelone elegans*.

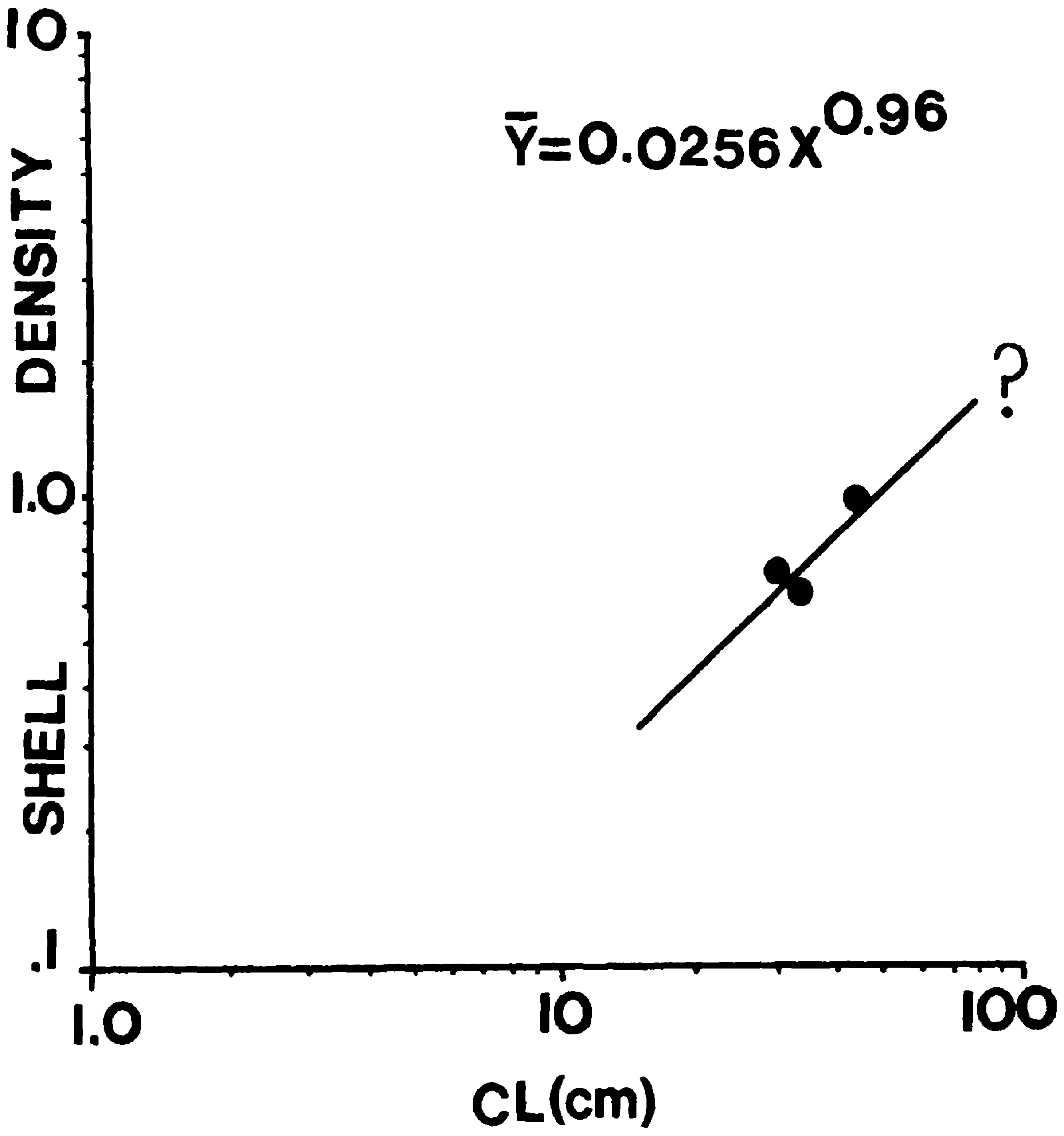

Fig. 6. The relationship between shell density (Y) and carapace length in centimetres (X) in *Geochelone elephantopus*.

The Status of the Mexican Bolson Tortoise, *Gopherus flavomarginatus*

David J. Morafka

The Mexican Bolson tortoise *Gopherus flavomarginatus* is the largest terrestrial reptile in temperate North America. Adults commonly reach carapace lengths in excess of 340 mm. It is closely related both by anatomy and behavior to the gopher tortoise *(Gopherus polyphemus)* of the southeastern United States.

The species is confined to < 40,000 km^2 of closed basin drainage (Bolson de Mapimi) of southeastern Chihuahua, southwestern Coahuila, and northeastern Durango, Mexico. Local distribution often reveals a pattern of clustering and discontinuity between populations. Significant extirpation by man has taken place.

The tortoises live in desert areas with extreme temperatures and low precipitation (250-375 mm) that mostly falls in the summer. Populations occur from 1000-1300 m elevation; mostly on sandy slopes with 1-2½% grade. Burrows are 1.5-2.5 m deep and 2.7 m long with a single opening usually followed by a steep down grade. Adults feed largely upon late summer growth of the bunchgrass called tobosa or wireweed *(Hilaria mutica)*. The diet is supplemented by cactus (*Opuntia* sp.) fruit and herbaceous annuals.

Known population density ranges from < 1 per 10,000 m^2 to a maximum of 7 per 10,000 m^2. Most of the population consists of adults, and the structure appears to favor individuals of > 262.5 mm shell width (20 years of age or older), as they constitute almost half (47%) of active burrow dwellers.

Human predation is severe and increasing. Other potential predators include carnivores such as coyote and badger, large falconiform birds, and large-bodied snakes. All, except man, could be significant only to eggs and hatchlings. Parasites are generally unknown.

Human impact is negative. Man both preys upon the tortoise directly and destroys its habitat through overgrazing and irrigation. The tortoise apparently was extirpated from suitable grassland habitat near villages, roads, and railroad lines. During the last half century, human and livestock densities have been rising rapidly in the remaining, previously remote, portions of the tortoise range. A continuation of present trends could lead to extinction of this species. Present legal statutes on the tortoise prohibit its trade or transport across international boundaries without special permits. But the existing regulations are vague, generalized, and do not specify the Bolson tortoise.

Protection within Mexico is difficult to enforce due to the remote region inhabited by the species. A recent organization of Durango land owners and residents by the Mexican government and its Ecology Institute may result in one locally managed and protected tortoise reserve.

Future measures should include: alerting key border stations on both sides of the U.S.—Mexican boundary as to the legal status of tortoise, organizing more extensive native refuges, extending ecological information about the tortoise, establishing a tagging program, initiation of a captive breeding program (followed by some re-introduction into former habitats), and proposing the tortoises as an endangered species.

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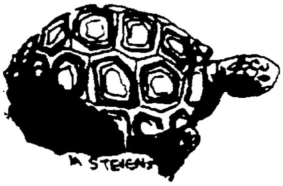

Censusing Desert Tortoise Populations Using a Quadrat and Grid Location System

R. Bruce Bury and Roger A. Luckenbach

We developed a census technique for the desert tortoise *Gopherus agassizii*, using a 25- to 100-ha quadrat subdivided into 1-ha sections in a grid. Systematic search of the sections accurately locates tortoises, burrows, pallets, and landscape features. An effective data-recording system is presented for fieldwork. Wider adoption of the quadrat system, which has several advantages over linear transect sampling techniques, would provide comparable data on tortoise populations for different areas and habitats.

Objectives, designs, and methods of data collection of several recent ecological field studies of the desert tortoise, *Gopherus agassizii*, varied considerably (Engberg et al., 1976). We believe that it is important to census tortoise populations in different regions by the same techniques so that the effect of different environmental regimes on population characteristics may be examined. Toward this goal, we propose a standardized system for censusing tortoise populations.

We earlier found that a removal method in defined quadrats (1- to 2-ha squares) was effective in sampling lizards and tortoises (Bury et al., 1977). The present census technique evolved from this removal method and was first developed for comparing tortoise populations in large (25 ha) areas undisturbed and disturbed by off-road vehicles near Barstow, California. On each quadrat we counted all tortoises, tortoise burrows, and pallets to obtain an estimate of the abundance of the resident tortoise population. Such established quadrats can be revisited in the future to estimate population sizes and to relate changes in population to habitat conditions. This census system is presented for consideration by other research biologists and managers concerned about the status of the desert tortoise.

STUDY SITE LOCATION

Most past and present desert tortoise study sites are in the northern or western Mojave Desert (Fig. 1). We suggest that studies in the southern portion of the tortoise's range would provide a more complete picture of the ecology of this species.

USE OF QUADRATS

Anderson et al. (1976) and Luckenbach (1976) used surveys along line transects to census tortoise populations. We recognize that surveys using line transects sample areas rapidly and are useful for indicating the presence and relative abundance of tortoises. However, we believe that the use of quadrats is a better method of censusing tortoise populations. Tortoises can be permanently marked and repeatedly recaptured within a quadrat, whereas the probability of encountering a marked tortoise along a straight-line transect route is small. Further, we contend that it is difficult to sample effectively the transect area (an area extending 10-30 m to each side of the path).

Tortoises are usually active on the surface for only brief periods each day and for limited intervals from about March to October. Tortoises often rest at the mouths of their burrows or in pallets, where they may not be visible beyond 5 m. Young tortoises are easily overlooked unless shrubs and low vegetation are carefully examined at close range. Tortoises in burrows will be missed unless the interior of the burrow is illuminated. We observed that many pallets, burrows, and tortoises cannot be detected unless an area is viewed from more than 1 vantage point. Thus the actual size of a tortoise population is likely to be underestimated by linear transect methods.

We recommend line transects as a useful tool for general surveys only, and quadrat techniques as the standard for quantitative studies of tortoise populations.

ESTABLISHING THE QUADRAT

Although some tortoises remain in small areas, relatively large study areas (25-100 ha) should be established because adult tortoises are mobile and may be wide-ranging; some adults may travel > 500 m in 2 days (R. Marlow, *personal communication*). Larger quadrat size increases the chances of relocating marked animals. Also, only large quadrats provide sufficient numbers of individuals from which to determine population attributes. Densities of tortoise populations over most of the range appear to be low and vary from 5 to 50/km^2 (Burge and Bradley, 1976; Luckenbach, 1976).

Accurate quadrat delineation is important. We first establish a set point corner (0-0) using a permanent marker (township corner, landscape feature) and determine the outside boundaries with a surveyor's compass and 50-m steel tape. The quadrat is then clearly marked into 1-ha sections, forming a large grid (Fig. 2). Wooden poles (2-3 m long, with several pieces of flagging are useful markers for outside boundaries and alternating rows of the grid because flagging on shrubs or low poles is seldom visible beyond 200 m. We also found it helpful to alternate flagging color (even rows white; odd, red) and to label each 100-m marker (e.g., 200N-300E). Small flags of different colors were placed on 50-m intervals to help maintain bearings inside each 1-ha section.

Use of such a grid gives a coordinate location for every tortoise or other feature (burrows, pallets, washes) in the quadrat. We estimate actual locations to the nearest 5 m.

DATA COLLECTION

We search for tortoises during times that are favorable for surface activity. In the Mojave Desert, warm mornings and evenings in the spring are the times of greatest tortoise activity.

We record pertinent field data in notebooks and on a detailed field map (Fig. 2). Upon reexamination of these notes and maps, we can determine how far individual tortoises have moved; how many burrows and pallets they use; the appearance, number, and location of new burrows; and changes in population size, composition, and spatial distribution.

Search Method. Each hectare of the quadrat is systematically searched. Observers walk along 1 edge and then crisscross the area along parallel lines spaced about 5 m apart, being careful to examine areas beneath shrubs and large perennials. Thus every part of the grid is viewed from a minimum of 2 vantage points and at distances of 5 m or less.

Because it may be possible to correlate numbers and characteristics of pallets and burrows with sizes of tortoise populations, these features are recorded. We measure several factors: depth in cavity, height and width of opening, compass direction that the opening faces; distance to nearest shrub or perennial (e.g., 0.5 m from base of creosote); climatic conditions; and duration of search.

Marking and Coding. Chelonians have been marked according to several different coding schemes (Cagle, 1939; Schwartz and Schwartz, 1974). Most workers mark the marginal scutes of the carapace and avoid using the bridge area, but we find no disadvantage in using this area of the shell. A distinctive, long-wearing mark can be made on any marginal scute; a hacksaw blade or fine saw can be used to cut a groove.

A simple coding system is employed (Fig. 3). We also paint the number of the tortoise on the posterior carapace with white enamel paint. Painted numbers are useful both for recognizing tortoises at a distance without disturbing them and for identification of marked animals in their burrows.

Taking and Recording Measurements. Our data recording system (Fig. 4) uses a printed, firm card (13 X 21 cm) containing spaces and outline drawings for data.

Information categories may be modified for individual needs but we strongly urge all workers to record certain measurements (CL, CW, D, PL, pl, and Wt) in a standard manner. Table 1 explains our abbreviations. All parameters are straight-line measurements; small tortoises and short lengths may be measured with dial calipers but lengths > 150 mm require the use of sliding field calipers designed to measure tree diameters (available from forestry supply dealers).

Spring scales are best for weighing animals; the larger tortoises are gently lifted in a bandanna sling. Disturbed animals frequently discharge stored water, but gentle handling and pressing the tail firmly against the cloaca will often prevent urination while the tortoise is being measured.

Recaptured animals are noted on location field cards (Fig. 5). Only a few measurements are taken, minimizing disturbance to the animal.

SUMMARY

The use of a quadrat plot to census tortoises enables accurate estimates of many population attributes. With our system, a field worker can record data from individuals (measurements, weights, morphology), their habitats (vegetation, topography, burrows, and pallets), and their populations (spatial distribution, age—sex composition, density, biomass) in quantitative, descriptive terms. Quadrats may also serve as sampling stations for long-term monitoring of population characteristics.

We offer this system as a means by which to characterize and follow population trends in *G. agassizii*. The system is flexible and suggestions for improvement are welcome.

We urge that a series of permanent quadrats be established over the entire range of *G. agassizii*. This would allow assessment of the status of tortoise populations and the formulation of sound conservation plans.

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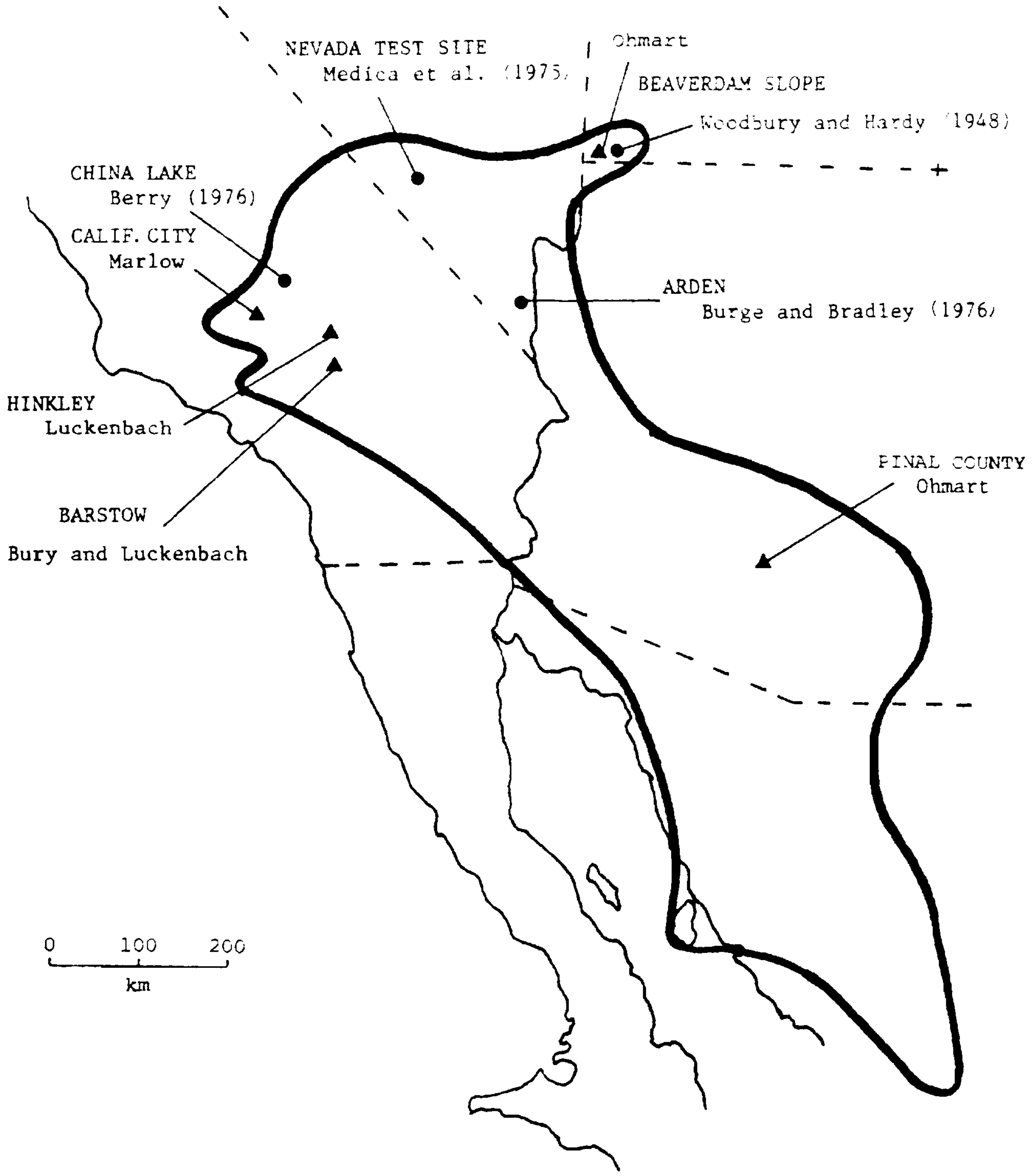


Fig. 1. Location of study areas on the ecology of the desert tortoise. The general range is outlined by the solid line. Triangles = ongoing studies; circles = published results.

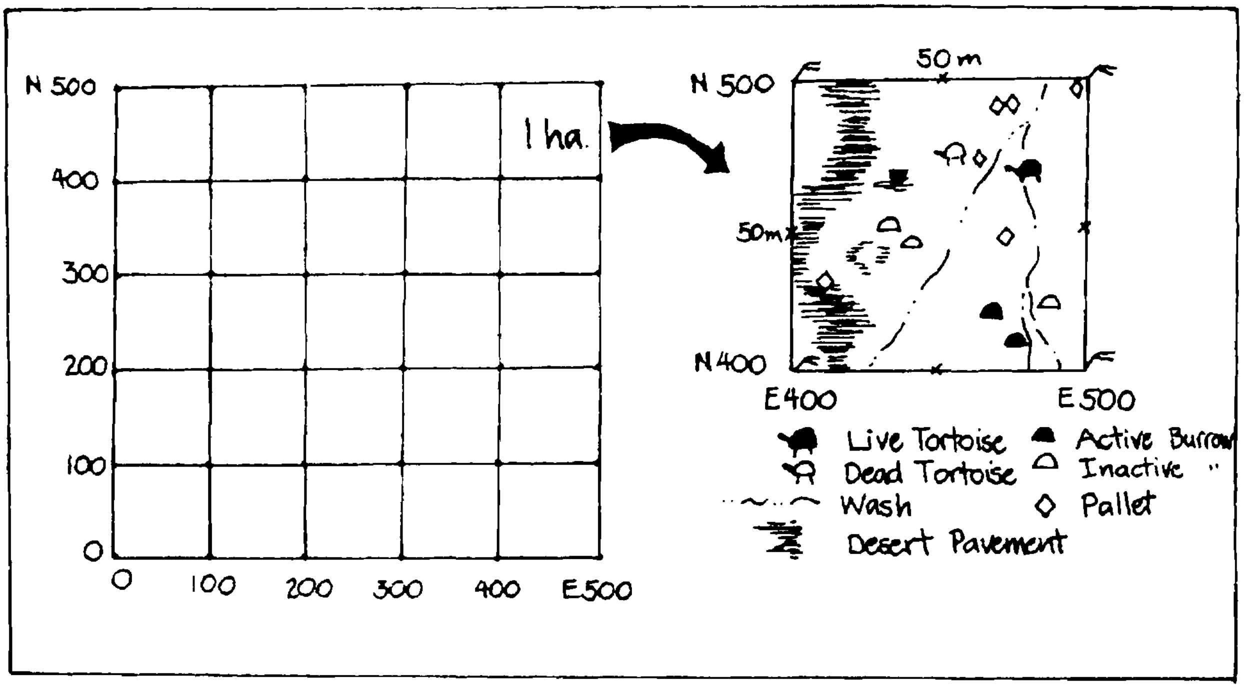


Fig. 2. Representative quadrat (25 ha) showing grid system. Insert shows details of features drawn on field map (1-ha section).

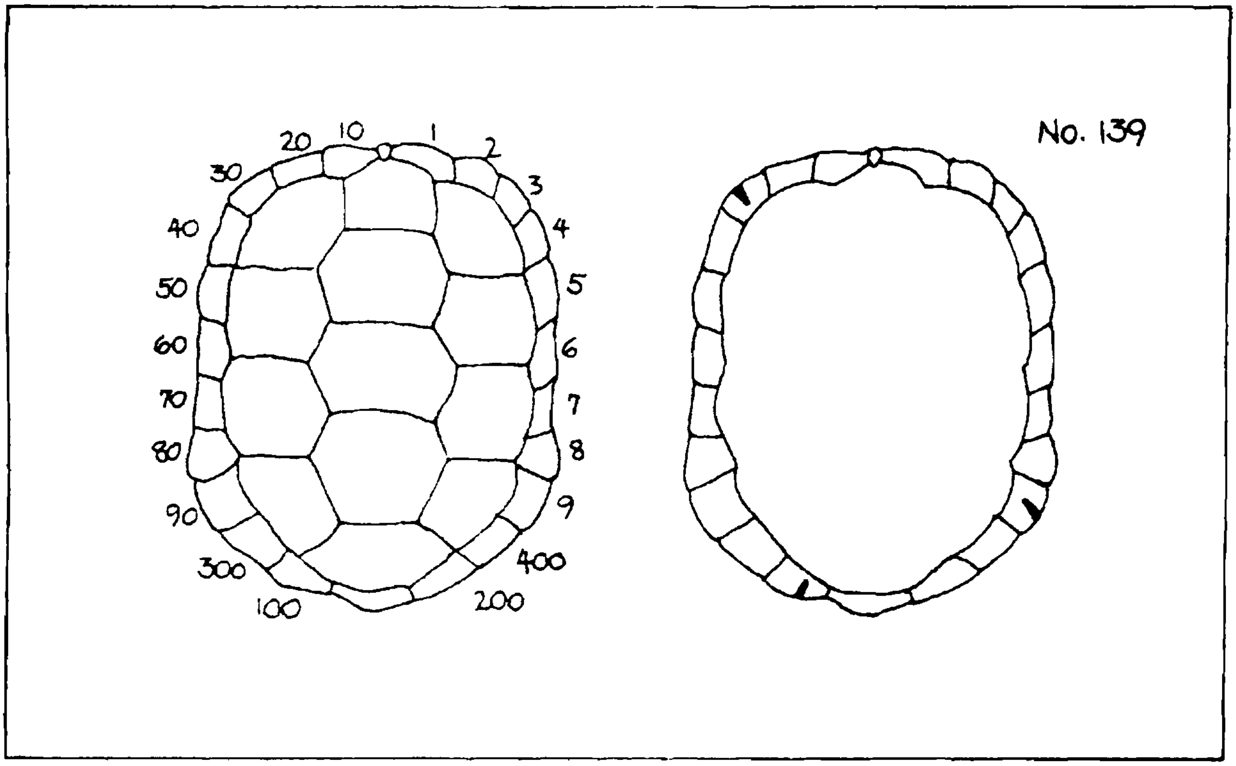
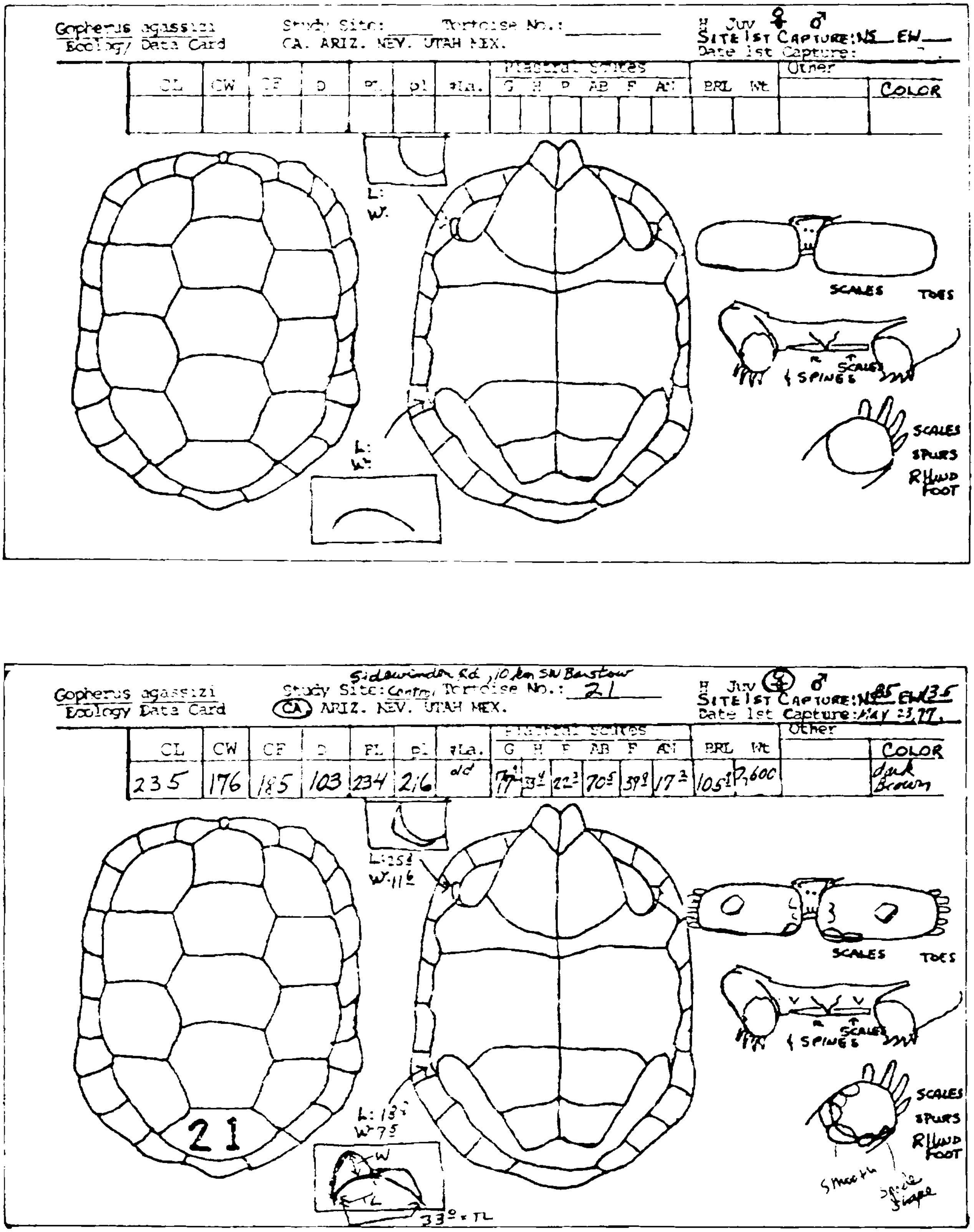


Fig. 3. Coding system used on *Gopherus agassizii*.



Gopherus agassizi
Ecology Data Card

Study Site: ____ Tortoise No.: ________
CA. ARIZ. NEV. UTAH MEX.

H Juv ♀ ♂
SITE 1ST CAPTURE: NS__ EW__
Date 1st Capture:

							Plastral Scutes								Other	
CL	CW	CF	D	PL	pl	#La.	G	H	P	AB	F	AN	BRL	Wt		COLOR

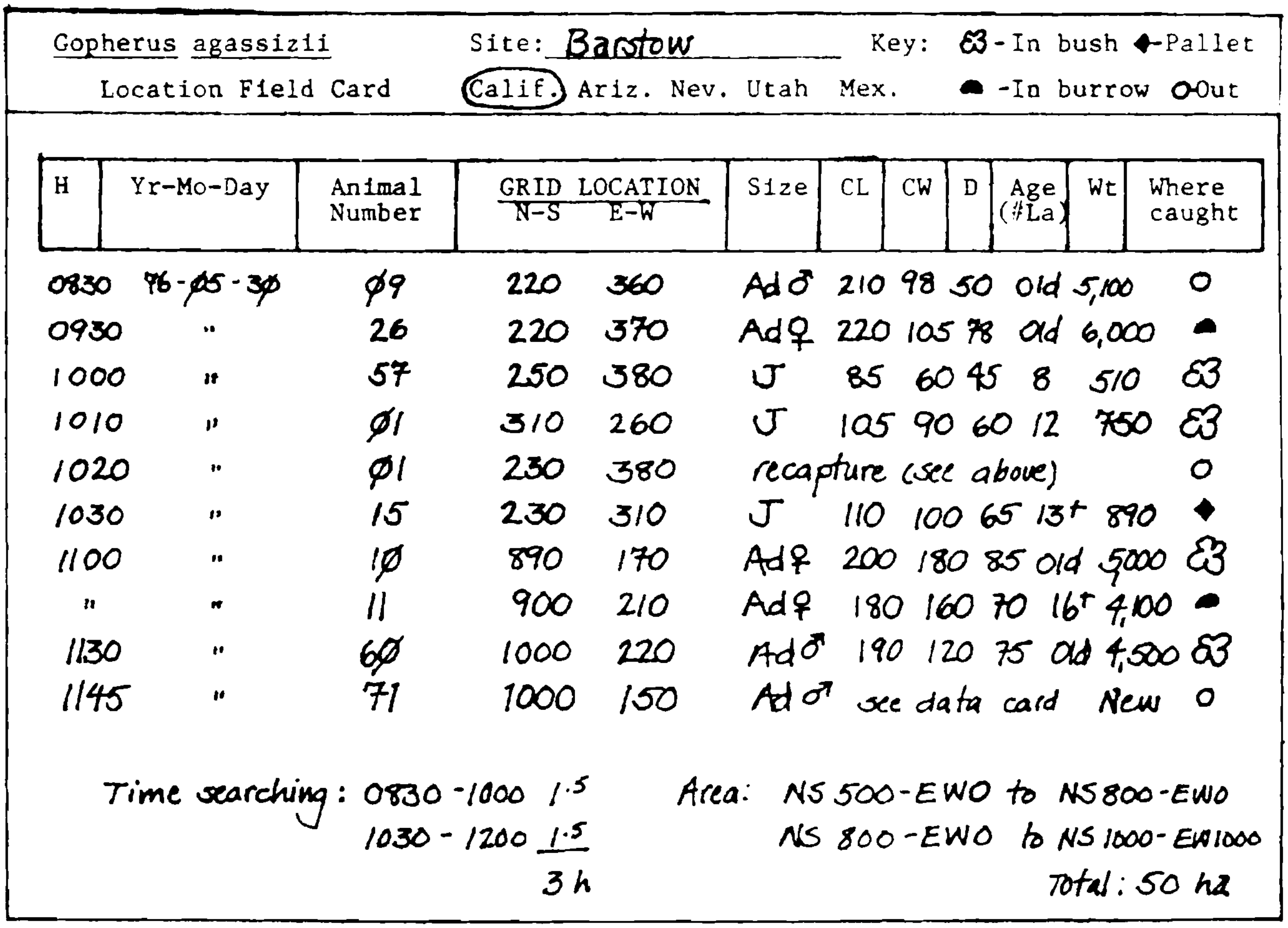
Sidewinder Rd, 10 km SW Barstow
Gopherus agassizi
Ecology Data Card

Study Site: Control Tortoise No.: 21
[✓ CA] ARIZ. NEV. UTAH MEX.

H Juv [✓ ♀] ♂
SITE 1ST CAPTURE: NS 85 EW 135
Date 1st Capture: May 23, 77.

							Plastral Scutes								Other	
CL	CW	CF	D	PL	pl	#La.	G	H	P	AB	F	AN	BRL	Wt		COLOR
235	176	185	103	234	216	d/d	17^{1}	33^{4}	22^{3}	70^{5}	39^{9}	17^{3}	105^{1}	2,600		dark Brown

Fig. 4. Blank and completed data cards.



Gopherus agassizii Site: Barstow Key: ✿ - In bush ◆-Pallet

Location Field Card [✓ Calif.] Ariz. Nev. Utah Mex. ● -In burrow ○-Out

H	Yr-Mo-Day	Animal Number	GRID LOCATION N-S	GRID LOCATION E-W	Size	CL	CW	D	Age (#La)	Wt	Where caught
0830	76-05-30	09	220	360	Ad♂	210	98	50	old	5,100	○
0930	"	26	220	370	Ad♀	220	105	78	old	6,000	●
1000	"	57	250	380	J	85	60	45	8	510	✿
1010	"	01	310	260	J	105	90	60	12	750	✿
1020	"	01	230	380	recapture (see above)						○
1030	"	15	230	310	J	110	100	65	13^+	890	◆
1100	"	10	890	170	Ad♀	200	180	85	old	5000	✿
"	"	11	900	210	Ad♀	180	160	70	16^+	4,100	●
1130	"	60	1000	220	Ad♂	190	120	75	old	4,500	✿
1145	"	71	1000	150	Ad♂	see data card				New	○

Time searching: 0830-1000 1·5
1030 - 1200 1·5
3 h

Area: NS 500-EW0 to NS 800-EW0
NS 800-EW0 to NS 1000-EW1000
Total: 50 ha

Fig. 5. Card for recording data on recaptured tortoises.

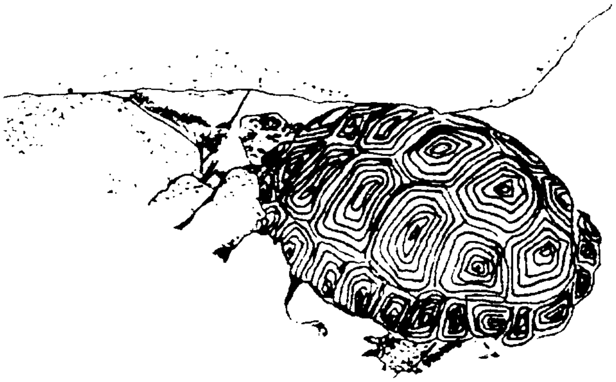
Table 1. Categories of data recorded on tortoises. All are straight-line measurements. The abbreviations are used on the data cards (Fig. 4).

Abbreviation	Term	Definition
		Shell and whole body
CL	Carapace length	Tip of nuchal to posterior edge of carapace.
CW	Carapace width	Greatest width across middle of carapace at approximately marginal 6.
CF	Carapacial flare	Greatest width of carapace in area of flare on marginals 8 or 9.
D	Depth	Greatest depth of shell.
PL	Plastron length	Greatest length from tip of gular to tip of anal scutes.
pl	Inside plastron length	Length from center of gular notch to center of anal notch.
#La	Number rings on lamina	Number of distinctive growth annuli (only useful on young).
BRL	Bridge length	Least distance between axillary and inguinal notches.
Wt	Weight	
		Plastral scutes (length along midline)
G	Gular	From inside of gular notch to contact with humeral.
H	Humeral	Total length of scute.
P	Pectoral	Total length of scute.
AB	Abdominal	Total length of scute.
F	Femoral	Total length of scute.
AN	Anal	From contact with femoral to inside of notch.
		Axillary and inguinal scutes
L	Length	Greatest length of scute.
W	Width	Greatest width of scute.
TL	Total length	Length of all scutes comprising inguinal (may be 2-3).

Erratum

Burge, B.L., and W.G. Bradley. 1976. Population density, structure, and feeding habits of the desert tortoise, *Gopherus agassizi*, in a low desert study area in southern Nevada. *In* Desert Tortoise Council Symposium Proceedings, 1976:51-74.

Page	Paragraph	Line	With correction should read:
52	3	6	303.5 ha
53	1	22 to end of paragraph	...totaled 46.8 mm and for 1974-1975, 37.2 mm.
53	2	5 and 6	...plots; and for the understory, by sampling m^2 plots at 6-m intervals. Relative...
55	Table 2		IV of *Chorizanthe rigida* should be 5.9
60	Table 3		*N*/ km^2 Study area totals >100 mm <100 mm >100 mm <100 mm
61	4	1	36-44/km^2
65	Table 5		Sex ratios and *N*: males : females



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Meetings will take place quarterly. You will be notified of the time and place. Place of meetings will be changed to allow members from all areas to participate. Minutes of each meeting will be sent to all members.

All checks or money orders should be made payable to the DESERT TORTOISE COUNCIL *and sent with the application to:*

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