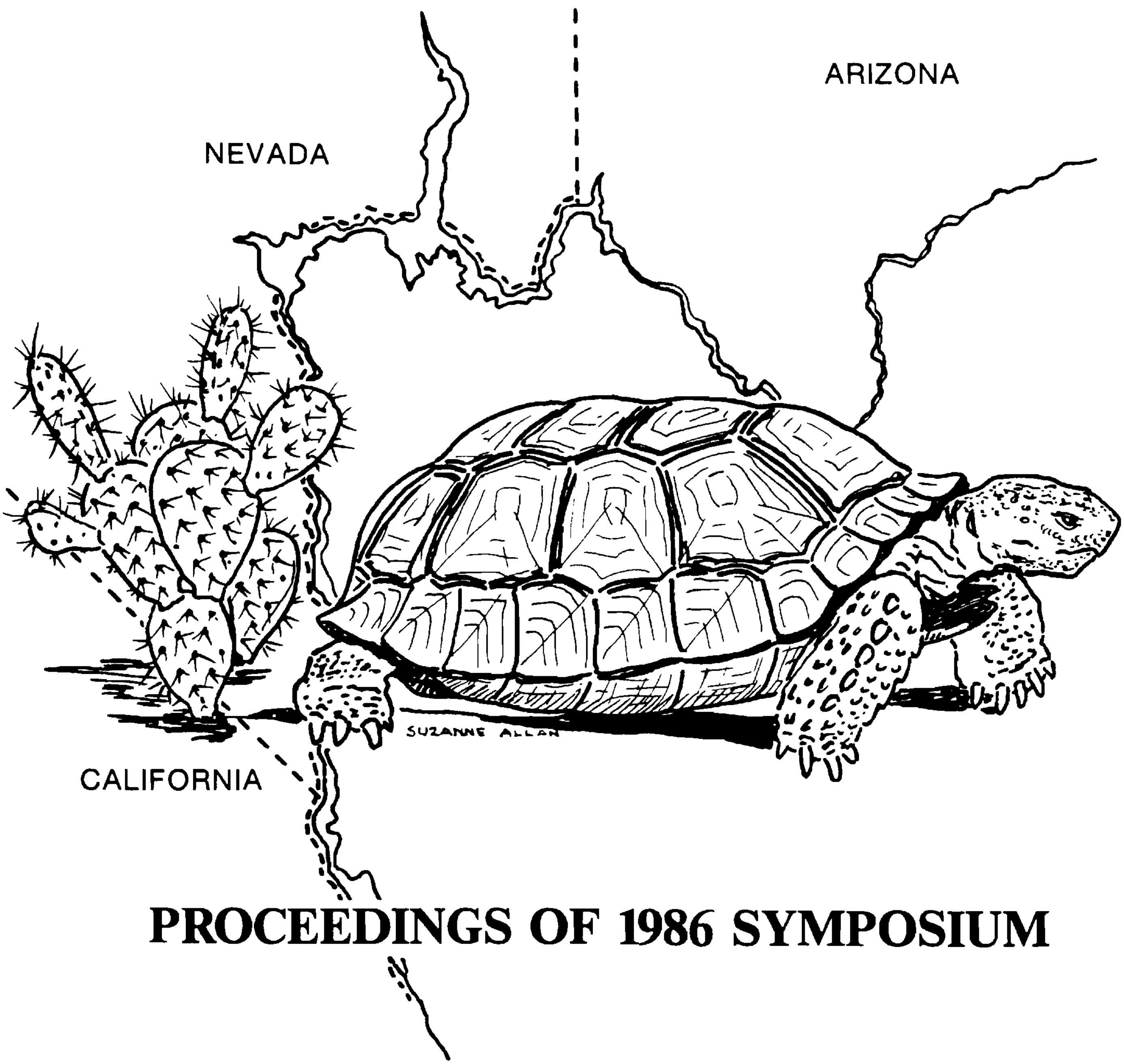
THE

THE DESERT TORTOISE COUNCIL



PROCEEDINGS OF 1986 SYMPOSIUM

DESERT TORTOISE COUNCIL
PROCEEDINGS OF THE 1986 SYMPOSIUM

A compilation of reports and papers presented at
the eleventh annual symposium of the Desert Tortoise Council,
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in Palmdale, California

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CALIFORNIA (Continued)

GENERAL PAPERS

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DESERT TORTOISE COUNCIL SYMPOSIUM FIELD TRIP

Trip Coordinator: Jeff Aardahl
Trip Leaders: Jeff Aardahl, Kristin Berry, David Consoli

The symposium field trip began at 8:00 a.m. on March 24 and was well attended by interested individuals and biologists from various government agencies. The field trip included the Desert Tortoise Natural Area and the West Rand Mountains Area of Critical Environmental Concern (ACEC). The weather was ideal and many tortoises were observed at each site. A more detailed account of each area follows:

DESERT TORTOISE NATURAL AREA

Participants took a 1 1/2 hour hike into Section 30, located on the west side of the natural area. This area of public land was the location of research conducted by Ronald Marlow in the early 1970s on energy relations of the desert tortoise. The group hiked approximately 1/2 - 3/4 mile and approximately 10 adult tortoises were observed (no juveniles were seen). Several shells were found, including one that had been marked (notched) during the Marlow study. One shell contained a hole with characteristic conchoidal fracturing, indicating the tortoise had been shot, probably with a .22 caliber bullet. Because of the intense sunlight and warm temperatures, most tortoises seen were located in shaded areas on the north side of shrubs, however, one large female was found aggressively feeding on a carpet of yellow flowers (alkali goldfield or *Coreopsis*). She continued to feed and even showed an affinity for some of the photographers who approached within several feet.

After lunch, management of the natural area was discussed. Detailed maps of the area were provided showing the boundary and land ownership as well as major land purchases within the natural area by the Nature Conservancy using money raised by the Desert Tortoise Preserve Committee, Inc. Discussion included the history of the area, the protective withdrawal from mining, and the canceling of permits for sheep grazing. Also discussed were boundary fence construction and maintenance, unfenced areas and incursion by off-road vehicles, etc. A regional map of the area with land ownership revealed that the natural area is an "island" of public land surrounded by land privately owned which is used for agriculture, proposed for urban expansion or held for real estate speculation in an undeveloped state. The group proceeded to the West Rand Mountain ACEC at approximately 1:30 p.m.

WEST RAND MOUNTAINS ACEC

This ACEC is located in the western portion of Fremont Valley and the Rand Mountains. It is immediately northeast of the Desert Tortoise Natural Area, and was designated by the Bureau of Land Management in 1980 in the California Desert Conservation Area Plan. A management prescription for this area is the study of the effects of off-road vehicles on the desert tortoise. However, the BLM recognized the need to control and manage off-road vehicle and recreation uses in the area to provide protection of a significant wildlife values area, namely the desert tortoise, Mojave Ground squirrel and upland game.

There are many wildlife water catchments or "guzzlers" in the Rand Mountains, and the entire area is designated as "Highly Crucial Habitat" for the desert tortoise. Historically, the Fremont Valley and Rand Mountains were an off-road vehicle "open area" and remained as such until 1980 when the area was classified as a "Moderate Use Area" by the Bureau of Land

Management. The area contains numerous vehicle routes, many of which are used by motorcycle and four-wheel drive enthusiasts. Vehicle route proliferation occurred during the late 1960s and throughout the 1970s as a result of organized and casual vehicle racing and exploring. Thus, a great abundance of vehicle routes exist in both upland game and desert tortoise habitat. Four motorcycle races were authorized by the Bureau of Land Management in this area in 1986. The average number of participants per race is 300. No formal races are allowed from March 15 to May 30 so that direct conflicts with the desert tortoise are minimized. Public demand for racing in this area is much lower than in the 1970s, when up to 20 races were authorized per year. Almost all races begin in Fremont Valley in an existing "staging" and camping area. Much of the vegetation in this area, except for large creosote bushes, has been removed over the years by vehicle use and camping activity. In addition to the seasonal racing closure, the Bureau of Land Management plans to close several major routes in tortoise habitat as well as most routes within 1/2 mile of guzzlers. No date has been identified for field implementation.

David Consoli, unit manager for the Department of Fish and Game, led the group to land within the ACEC recently acquired by the Department of Fish and Game for protection of habitat for the desert tortoise. The land, totaling 640 acres, was donated by an individual. The Department plans to fence the land to exclude off-road vehicles and livestock. Hunting will be allowed unless studies demonstrate that it is conflicting with protection of the desert tortoise. Guzzlers may be placed in the southern portion of the area adjacent to the Rand Mountains. A census of the tortoise population is planned, and qualified volunteers are encouraged to contact Dave if interested in doing this work. Ten tortoises were observed in the area on a brief hike. The population density is likely high. One tortoise shell was found which appeared to have been shot. Two juvenile tortoises were encountered.

The field trip ended at about 4:30 p.m. Everyone appeared to be very interested in the two areas, enjoyed observing many tortoises in the wild, and were interested in the overall management of the habitat.

PARTICIPANTS

Jeff Aardahl
Walter Allen
Sherry Barrett
Jeanne Belliman
Peter Bennet
Kristin Berry
John Brode
Ray Butler
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Karla Kramer
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June Latting
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THE DESERT TORTOISE WORKSHOP

Frederick B. Turner
Laboratory of Biomedical and Environmental Sciences
University of California, Los Angeles

The Southern California Edison Company (SCE) is a large public-owned utility serving much of southern California, and almost all desert areas of the state. SCE is responsible for ensuring adequate electrical power for consumers in this service area, and at the same time must abide by all relevant laws and regulations bearing on preservation of the environment and natural resources. The desert tortoise has been, and will continue to be, an important ecological consideration in the development of new energy sources in arid parts of southern California.

In 1984 SCE asked that a Desert Tortoise Workshop be arranged for the early spring of 1985. The purpose of this meeting was to provide SCE with recommendations enabling the utility to formulate an effective plan for tortoise-related research. The workshop was sponsored by SCE and the U.S. Department of Energy and held at the UCLA Conference Center in Malibu, 3-5 March, 1985.

The plan of the workshop included initial presentations defining problems faced by SCE and clarifying responsibilities of four federal and state agencies charged with the protection of wildlife resources (Table 1). Against this background, the workshop continued with a review of past work with the tortoise in California and nine position papers dealing with research topics of potential importance to SCE (Table 2). Proceedings of the workshop were published in the first issue of Volume 42 of *Herpetologica* (1986). References are listed in the bibliography.

Table 1. Tortoise Workshop presentations dealing with SCE's position and the regulatory responsibilities of four Federal and State agencies.

Daniel Pearson, Southern California Edison Company
Robert Haussler, California Energy Commission
Larry Foreman, U.S. Bureau of Land Management
Karla Kramer, U.S. Fish and Wildlife Service
John Brode, California Department of Fish and Game

At the conclusion of the workshop, participants were given a list of six research topics (Table 3) and asked to rank them in order of importance to SCE. Participants were allowed to assign ties, to provide written criticisms of the roster of topics, and to discuss reasons for their rankings. Ballots were not solicited from SCE staff members. Ballots were received from 12 participants: John Brode, Joan Diemer, Larry Foreman, Whit Gibbons, Robert Haussler, Brian Henen (graduate student with the UCLA Department of Biology), Karla Kramer, Kenneth Nagy, Melvin Schamberger, James Spotila, Frederick Turner and Laurie Vitt (UCLA Department of Biology). Table 4 gives mean ranks, ranges in ranking, and numbers of first place votes for each of 6 research categories. The lower the mean rank, the higher the perceived importance of the topic.

Table 2. Discussions of past research on the desert tortoise and of nine research topics of potential interest to SCE.

Kristin Berry, U.S. Bureau of Land Management; Riverside, CA
Review of desert tortoise research, 1979-1985.
James Spotila, State University College; Buffalo, NY
Temperature-dependent sex determination in turtles.
Kenneth Nagy, Laboratory of Biomedical and Environmental Sciences; UCLA
Water and energy fluxes in tortoises: implications for reproduction.
Frederick Turner, Laboratory of Biomedical and Environmental Sciences; UCLA
Measuring egg production by desert tortoises.
J. Whitfield Gibbons, Savannah River Ecology Laboratory; Aiken, SC
Movements and potential for genetic exchange between populations of freshwater turtles in southeastern U.S.
Kristin Berry, U.S. Bureau of Land Management; Riverside, CA
Movements and homing potential of desert tortoises; implications for relocation.
Charles Taylor, Department of Biology; UCLA
Genetic differentiation in vertebrates and potential effects of tortoise relocation.
Joan Diemer, Florida Game and Freshwater Fish Commission; Gainesville, FL
Management of the gopher tortoise in southeastern U.S.
Melvin Schamberger, U.S. Fish and Wildlife Service; Fort Collins, CO
Habitat evaluation models and possible applicability to the desert tortoise.
Hartmut Walter, Department of Geography; UCLA
Conservation of the desert tortoise; natural areas and reserves.

Table 3. List of six research topics to be prioritized by workshop participants.

DOES temperature-dependent sex determination occur in the desert Tortoise?
PHYSIOLOGICAL and ecological investigations of the process of egg production by desert tortoises.
MEASUREMENTS of genetic differentiation in desert tortoises.
ANALYSES of habitat relationships of tortoises; how do various factors influence carrying capacity?
EXPERIMENTS to determine homing ability in desert tortoises
RELOCATION experiments

Research supported by SCE is congruent with the relative importance of general research areas as perceived by workshop participants (Table 4). Work supported during 1985 and 1986 included a major effort devoted to the process of egg production (at Goffs), research on the habitat relations of tortoises, and analyses of genetic differentiation in California tortoises. The latter topic, originally based on allozyme analyses of two populations in California (Kramer and Chemehuevi Valley) by Donald Buth at UCLA, was expanded to include analyses of mitochondrial

DNA among tortoises at these two locales and five others (Fremont Valley, north of Barstow, Fenner Valley, Ivanpah Valley and Chuckwalla Bench). Trip Lamb of the University of Georgia's Savannah River Ecology Laboratory carried out this work.

Table 4. Voting of 12 workshop participants on six research topics.

Research Topic	Mean rank	Range in ranks	Number first place votes
Temperature-dependent sex determination	5.0	1-6	1
Egg production, energy budgets and rainfall	2.5	1-6	4
Genetic differentiation	3.4	1-6	2
Habitat relationships	2.0	1-4	4
Homing	4.6	3-6	0
Relocation	3.5	1-6	1

ACKNOWLEDGMENTS

The desert tortoise workshop and the preparation of this report was supported by contract (C0603915) between the Southern California Edison Company and the University of California and by contract DE-AC03-76-SF00012 between the U.S. Department of Energy and the University of California.

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1986 ANNUAL AWARD: PROFILE OF RECIPIENT, MARTHA L. STOUT

During 1984, 1985 and 1986 Dr. Martha L. Stout made major contributions to the conservation of the desert tortoise throughout its geographic range in the United States. As an employee of Defenders of Wildlife, she led an effort among Defenders of Wildlife, Natural Resources Defense Council, and Environmental Defense Fund to federally list the desert tortoise as an endangered species. The task was complex and difficult from several standpoints, e.g., the extensive geographic range once occupied by the tortoise, the immense amount of data and the difficulty of understanding and interpreting the data during a short time period, differing academic views on the need for federal listing, widespread differences in interpretation of data, and varying opinions within government agencies on the need for listing.

Dr. Stout handled the task in a highly professional and efficient manner. She contacted 23 world-recognized senior scientists with expertise on turtles and tortoises, endangered species, and population biology. She convinced them to review lengthy summaries of data, including a 838-page report, "The Status of the Desert Tortoise (*Gopherus agassizii*) in the United States." She requested that the scientists write letters to the Fish and Wildlife Service about the tortoise and whether it qualified for federal listing. Most of the scientists responded with comments supporting a listing. Many of the letters were thoughtful and lengthy.

When Dr. Stout sensed that biologists within the Fish and Wildlife Service were wavering on listing the tortoise because of a complex statistical critique of the "status report," she again approached the issue professionally and assertively. She had the report in question evaluated by several biologists with expertise in statistical analysis of data. Again, the findings were transmitted to the Fish and Wildlife Service. Strong scientific endorsement was crucial in persuading the Service to accept the petition to list the tortoise. The Service's acceptance of the petition resulted from their recognition that the tortoise would eventually be listed.

The result of her efforts--and those of Defenders of Wildlife--was that the Fish and Wildlife Service found that listing of the desert tortoise was warranted but precluded by other pending proposals of higher priority. Hopefully, with the continued vigilance and support of biologists like Dr. Stout, the Fish and Wildlife Service will soon prepare a listing package for the tortoise.

Dr. Stout's work with the tortoise is part of a five-year career involving conservation of endangered species and environmental education. Dr. Stout graduated with a Bachelor of Sciences degree (with distinction) from the University of Michigan and a Ph.D. in Zoology from the University of California at Berkeley. She worked for the Office of Endangered Species in 1980 and 1981 and as a Consultant at the Center for Environmental Education, focusing on policies and administration of the Endangered Species Act, between 1981 and 1983. Since 1983, she has been an Endangered Species Scientist for Defenders of Wildlife and a Consultant.

Thank you, Martha Stout, for a job superbly and professionally done.

-Kristin H. Berry-

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STATE REPORT - NEVADA
TORTOISE MANAGEMENT IN NEVADA (1985)

Ross Haley
Nongame Biologist, Nevada Department of Wildlife
Las Vegas, Nevada

During 1985 the Desert Tortoise continued to receive priority management consideration through the Nevada Department of Wildlife's nongame program. The Department supported a sixty man-day survey on a newly created Permanent Study Plot (PSP) in Piute Valley and an additional 150 transects in Clark and Lincoln Counties.

The new study plot is located on the Christmas Tree Pass Allotment east of Highway 95 from the Piute Valley PSP. Although this area is in close proximity to the area which experienced the catastrophic die-off between 1979 and 1983, it has a different grazing history, and no apparent die-off was detected on this allotment during subsequent surveys which were conducted to determine the extent of the die-off (Mortimore and Schneider 1983). We felt that the apparent contrasting population dynamics in two adjacent grazing allotments were worthy of some additional attention, which is why the study plot was located so close to an existing plot. Although it is hoped that this arrangement may provide us with some insight as to the effects of various grazing systems on tortoise populations, many confounding variables do exist (e.g. soil composition and depth, slope, aspect, distance to nearest road and settlement, etc.) which still make comparisons very difficult. The results of this study will be presented at this symposium (Duncan and Esque in press A).

The transects were conducted as part of our continuing effort to delineate important habitat areas which deserve special management consideration. It is also believed that by conducting a few transects in areas which have been previously surveyed, general trend information can be acquired, and problem areas, which may require more intensive trend studies (i.e. PSPs), can be identified.

The area identified in the status report (Berry 1984) as the "Gold Butte Crucial Habitat" was particularly lacking in data. A relatively large crucial area was delineated in that report based on a very small number of transects. For this reason, top priority was given to conducting at least 20 additional transects in that area. It is hoped that with this data we will be able to better delineate tortoise distribution on the east side of the Overton Arm of Lake Mead. This is an area where crucial habitat should be relatively easy to protect due to geography. The Overton Arm tends to isolate this area from Las Vegas, thereby reducing collection pressure, ORV impacts, dumping, and other problems associated with proximity to an urban area. It is also in an area which isn't likely to be heavily impacted by transportation or utility corridors. However, overgrazing may be a problem, and mining could potentially cause some detrimental impacts in the future.

This year's transect research produced some very interesting results which will be presented in much greater detail in another paper to be presented at this conference. In particular, it seems that Nevada may have more areas which support high density tortoise populations than has been previously believed (Duncan and Esque in press B).

In addition to the field work outlined above, several meetings were held within the Department of Wildlife (NDOW) as well as with both the U.S. Fish and Wildlife Service (USFWS) and the Bureau of Land Management (BLM). These meetings resulted in the development of an official position statement regarding the petition to list the Desert Tortoise as an endangered species. This position statement included a rough estimate of the total number of wild tortoises living in Nevada and five management recommendations.

To summarize the position, it was felt that the implementation of, and adherence to, existing management options should meet the objective of maintaining the Desert tortoise as a viable component of Nevada's Mojave Desert ecosystem. In other words, we opposed federal listing because we believe that existing regulatory mechanisms are adequate. The position statement was presented at two public meetings of the Nevada State Board of Wildlife Commissioners, and was subsequently voted on and adopted by the Commission. There were very few public comments presented at these meetings, and the number of written comments received concerning this issue was also quite small.

The rough estimate of total population size within Nevada which accompanied the position statement provided a range of values based on some measurements conducted by Craig Mortimore of NDOW and Dave Pulliam of the BLM. Using a computerized planimeter, Mortimore and Pulliam measured total available tortoise habitat as well as areas which had been identified as supporting high (90-175/mi^2), medium (40-90/mi^2), and moderate (20-40/mi^2) densities. Measurements were made from 1:250,000 scale maps which had densities delineated on them according to the best available transect data. Utilizing the area measurements and density categories, we calculated the best estimate of the total number of tortoises residing in the state of Nevada (Table 1).

Table 1. Habitat Area and Population Estimates for the Desert Tortoise in Nevada.

Population Estimate	Sq. Miles	Minimum	Maximum
High Density (90-175 tortoises per square mile)	31	2,790	5,425
Medium Density (40-90 tortoises per square mile)	113	4,520	10,170
Moderate Density (20-40 tortoises per square mile)	637	12,740	25,480
Low Density (1-20 tortoises per square mile)	6,015	6,015	120,300
TOTALS	6,796	26,065	161,375

The Department is confident that Nevada's tortoise population lies somewhere within the size limits described in Table 1 (i.e. between 26,065 and 161,375), but obviously doesn't have a precise answer as to exactly how many tortoises reside in Nevada. We plan to continue monitoring Nevada's populations and, through additional habitat delineation work, hope to be able to somewhat narrow the confidence limits on this estimate. However, it seems apparent that the tortoise population in Nevada is quite sizable at the present time and therefore is not in immediate danger of extinction.

RECOMMENDATIONS

Management recommendations which were included in the Department's official position statement included:

(1) Retain the "sensitive" designation given the tortoise in the Memorandum of Understanding which already exists between the BLM and the NDOW. This designation insures priority management consideration by the BLM. The NDOW will continue to insure priority management through cooperative management agreements, habitat management plans, coordinated management and planning practices, direct consultation with the BLM and cooperative habitat management programs.

(2) Portions of the Arrow Canyon, Gold Butte and Piute Valley crucial habitats should be designated as Areas of Critical Environmental Concern (ACECs). If this is not possible, a conservation agreement between the BLM and the NDOW, which includes an interagency consultation process whenever any significant changes in management direction are proposed, might suffice.

(3) Fully implement the Clark County Grazing Environmental Impact Statement (EIS) to reduce competition between the tortoise and livestock. This document clearly states that all forage on public lands within Clark County is classified as ephemeral and therefore grazing should be allowed based on annual forage production. Decision number 10 of the Management Framework Plan (MFP) states that adequate forage will be provided to maintain population goals as mutually agreed to between the BLM and the NDOW.

(4) Additional surveys and research are needed to determine the effects of various land use practices on tortoise habitat. In particular, research is needed to determine the extent to which livestock compete with tortoises, what stocking levels are acceptable and what grazing systems should be utilized to minimize the impacts to tortoises.

(5) Continue monitoring Off-Road-Vehicle (ORV) use in areas identified as critical to tortoise populations.

In addition to these five recommendations, the Desert Tortoise remains a high priority species within the NDOW's nongame program. By opposing listing, we have not de-emphasized management of this species in any way. On the contrary, we have accepted the responsibility of managing Nevada's tortoise populations rather than trying to delegate that responsibility to the federal government. The federal government, as the primary landowner of tortoise habitat in Nevada, will continue to be involved in tortoise management in Nevada. But we feel capable of directing the management effort at the present time without the administrative burdens and legal restrictions which would ensue should the species become listed.

The Department recognizes the need for additional research; thus, we are in agreement with the present classification of the Desert Tortoise as a category 2 species. This field season, the establishment of a new PSP in the Coyote Springs area is planned. Although this is probably the most intensively surveyed area in the entire state as a result of studies conducted during the EIS research for the MX missile base of operations, new development pressures indicate a need to monitor population trends in the future. Negotiations are also under way at the present time for additional funding through the BLM and/or the USFWS to conduct additional transects and/or another PSP. The next PSP would probably be located somewhere within the Gold Butte crucial habitat or just south of the Mormon Mountains. Hopefully, this additional research will help us in our continuing effort to identify and preserve enough suitable habitat to maintain relatively large, viable populations of tortoises in Nevada for perpetuity.

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RECENT THREATS TO THE DESERT TORTOISE IN NEVADA

Betty L. Burge
Desert Tortoise Council
Las Vegas, Nevada

The Desert Tortoise Council has identified six crucial habitats for the desert tortoise in Nevada (Berry and Burge 1984). The Council has become increasingly concerned with new threats and impacts to two of the six -- Goodsprings and Arrow Canyon. In Goodsprings and Arrow Canyon the issues are: (1) habitat loss, (2) lack of mitigation and compensation for new land-use actions, (3) inadequate protection of populations and habitat from off-road vehicle (ORV) events, and (4) a proposed land acquisition which would remove a large portion of crucial habitat from public domain. A third habitat, Gold Butte, is also in trouble. A 1986 survey indicates that the population is in poor condition. A fourth crucial habitat, Piute Valley, has unresolved problems with overgrazing.

The problems experienced at Goodsprings and Arrow Canyon are due primarily to negligence or irresponsibility on the part of the Nevada Department of Wildlife (NDOW) and the Bureau of Land Management (BLM). Habitat is being lost at an alarming rate. The issues are discussed below by crucial habitat.

GENERAL ISSUES

Problems with Delineation of Crucial Habitats

The Las Vegas District of the BLM has not honored the crucial habitats delineated by the Desert Tortoise Council (Berry and Burge 1984). These habitats were delineated in 1982-3 by Berry, Burge, and representatives from the BLM and NDOW. Since that time, the BLM has outlined smaller, more fragmented crucial habitats which generally coincide with densities of > 50 tortoises/mi^2. The local BLM designations of crucial habitat exclude major areas of private land, and public land earmarked for sale. The Council believes that areas crucial to a species should be identified, regardless of land jurisdiction. The Council does not believe that the units selected by the BLM are viable because of their small size and fragmented nature. The BLM's crucial habitats do not represent natural boundaries or the minimum viable populations necessary to maintain the species in perpetuity, especially considering the ongoing impacts.

On March 27, 1987, members of the Council met with the Las Vegas District of the BLM, the NDOW, and the U.S. Fish and Wildlife Service to discuss definitions and delineation of crucial habitat boundaries. The subject remains unresolved. Representatives from BLM and the NDOW were not familiar with the tenets of conservation of biology and the literature on minimum viable population size, preserve size and shape, fragmentation, etc.

One important note: the six crucial habitats taken together are smaller than the Fremont-Stoddard or western Mojave Desert crucial habitat in California. They also are more fragmented and have lower densities.

Impacts to Crucial Habitat from Adjacent Land-use Activities

Development adjacent to Crucial Habitat can be as threatening to tortoise populations as development within Crucial Habitats because:

(1) delineations of crucial habitat are likely to represent the least area necessary to sustain viable populations into perpetuity;

(2) impacts beyond the crucial habitat boundaries reduce the resilience of populations within crucial habitat; and

(3) habitat degradation and loss of tortoises from collecting, shooting, and dogs increases with increasing proximity to developed land.

GOODSPRINGS DESERT TORTOISE CRUCIAL HABITAT

The Goodsprings crucial habitat occupies an area of 296 mi^2, most of which is public land with estimated densities of 50-124 tortoises/mi^2 (Berry and Burge 1984).

Habitat and Population Losses

(1) Urbanization -- recent development of private and public land -- approximately 11 mi^2 in and adjacent to crucial habitat, with an estimated loss of 550 to 1350 tortoises.

(2) Imminent sale of public land within the Las Vegas Sub-unit, an area designated by the BLM. The Sub-unit boundary is an area approximately 23 by 26 mi with Las Vegas at the center. Most of the undeveloped lands are public and are scheduled to be sold. About 34 mi^2 of the sub-unit are in crucial habitat. Approximately 1700-4250 tortoises will be lost when the public lands are sold and developed.

Approximately 40 mi^2 of private land, or area designated as Husite is owned by Summa Corporation and administered by Howard Hughes Properties. The land has remained undeveloped until about two years ago. In addition to lands already developed or sold, 7.5 mi^2 were recently annexed to Las Vegas, indicating imminent sale and development.

(3) A BLM exchange of approximately 6 mi^2 of public land beyond the Sub-unit in crucial habitat for approximately 8 mi^2 of private land (Howard Hughes Properties). The 8 mi^2 is adjacent to a natural mountain park and will be added to it. Both areas support tortoises, but the land adjacent to the park has considerably lower densities of tortoises (< 50/mi^2) and is far less desirable than the public land scheduled to be lost and developed (estimated densities of 50-124 tortoises/mi^2). Howard Hughes Properties will also receive about $2.8 million of the 8 mi^2. The fate of 300-740 tortoises on the 6 mi^2 is yet to be determined. However, mitigation and compensation packages for tortoises were not included in the exchange/purchase transactions.

(4) Flood Control Projects. Approximately 50 flood control structures will be located throughout the Las Vegas Valley. Six of the 50 are inside crucial habitat. One is under construction and another will be started within the next year or two. A third will be built within the next 3 to 4 years. The remaining

structures have no construction dates. The BLM has provided parcels ranging from about 0.25 to 1.0 mi^2. Structures may consume from 0.25 to 0.5 mi^2 of habitat.

Tortoises may be killed during construction. Once construction is completed, the dikes, floodways, and concrete-lined channels may be hazardous or obstructive to tortoises. Impacts are expected to be greatest during summer rains, when tortoises are particularly active and water is impounded or flowing. In addition, the altered drainage patterns may permanently affect localized forage production.

Lack of Mitigation.

(1) The BLM has not proposed mitigation or compensation for tortoises or habitat on public lands receiving impacts outside the BLM crucial habitat designations. This omission includes parcels sold and the seven sites for which permits to develop flood control structures have already been processed (two sites within the Desert Tortoise Council's Goodsprings crucial habitat and five outside of it).

(2) The BLM has not addressed the issue of impacts to tortoises on public land adjacent to private land under development and construction. Developers of private lands are usurping habitat, and, in the process, creating hazards. As tortoises attempt to use their home ranges, they move from public to private land and into the path of construction.

(3) The BLM and the NDOW have not addressed the issue of tortoises on public land that has been or is scheduled to be sold or otherwise disposed of. The NDOW and the BLM have not considered sites where tortoise refutes might be established.

The NDOW has not taken an active part in protecting wild tortoises on private land under development, either by approaching regional planners about the need to mitigate/compensate for tortoises or by providing regional planners with recommendations for mitigation measures.

Interpretation of existing wildlife regulations has produced a conflict. When the Nevada Wildlife Commission passed a state regulation (NAC 503.080) which allowed domesticated tortoises to be possessed legally without permit, the NDOW assumed that domesticated tortoises were inside urban areas. The regulation stated that only tortoises outside the urban areas are protected. At the present time, the NDOW considers wild tortoises outside and adjacent to the perimeter of developed Las Vegas to be within the urban area and therefore unprotected. By trying to define domesticated tortoises by geographic location, the NDOW has created an additional "classification," which they now term "the unprotected wild segment."[1]

[1] In 1982, immediately prior to adoption of the regulation, The Organization for Protection of Nevada's Resident Tortoises, Inc. (TORT-Group), wrote to the NDOW with two suggestions: (1) clearly define or change the ambiguous term "urban areas," and (2) develop a mitigation plan to deal with urbanization. The wording of the regulation was not changed and the ambiguity persists. The NDOW and the Wildlife Commission members suggested that TORT Group implement a mitigation plan.

Example: prior to the clearing of a square mile of relatively undisturbed tortoise habitat (private land) at the west edge of Las Vegas, concerned citizens contacted the NDOW about the threat to tortoises. The NDOW took no action to protect the tortoises from construction hazards.

Citizens took the initiative and removed more than 30 hibernating tortoises to safety. The rescuers considered the wild tortoises to be protected and the responsibility of the NDOW. The NDOW claimed that the tortoises were unprotected, according to NAC 503.080, by being within an urban area. Therefore the status of the tortoise was comparable to domesticated tortoise living as captives in yards throughout the Las Vegas Valley.

After holding the tortoises over the winter, the citizens offered the tortoises to the NDOW for handling as a wildlife resource. Citizens did not want to incorporate the wild tortoises into the captive or domesticated population. Under pressure, the NDOW accepted the tortoises and plans to mark and relocate them.

Tortoises in southern Nevada live almost exclusively in the valleys. The anticipated urbanization of southern Nevada will spread throughout the valleys. If the NDOW continues to consider wild tortoises outside the perimeter of development but by proximity to be inside "urban areas," a geometrically increasing number of wild tortoises will be condemned as urbanization extends into tortoise habitat.

Developers contacted by Burge as of early 1987 have not been willing to mitigate for tortoises voluntarily, if costs are involved. City and county planners indicated that incorporating tortoise mitigations into permit stipulations for developers may be difficult, in the NDOW continues to consider the tortoises involved to be unprotected.

Lack of protection from ORV events

The area in and around the Goodsprings crucial habitat receives heavy use from ORV races.

(1) In spite of recommendations of tortoise experts, the BLM continues to permit ORV races in crucial habitat (both BLM's and the Council's) and has adopted vehicle use limitations that are inadequate to protect tortoises or their habitat. Examples of mitigations include: seasonal closures; reductions in number of events, laps, and entrants; and routing races through washes.

(2) The NDOW has accepted the BLM's inadequate ORV use limitations.

(3) The BLM has not administered ORV events in a responsible manner. They have: (a) allowed ORV routes to be placed over and/or next to winter denning sites, (b) failed to require adequate signs (poor placement, poor materials, poor messages), and (c) failed to enforce race permit stipulations. Examples of non-compliance include: illegal passing and shortcutting by racers; unauthorized parking, ORV travel, and use of all-terrain vehicles on and adjacent to the course by spectators. Permittees are not always (infrequently) held accountable for violations of race permit stipulations. Lack of on-site monitoring of both spectators and racers has resulted in preventable habitat degradation.

(4) The BLM has failed to respond to recommendations from the Council for reducing impacts. One example was the recommendation to establish no-passing zones where predictable and progressive widening of the race course would exceed the allowable course width (100 ft). In such cases, course widening has been followed by encroachment of noxious weeds and the creation of barren and degraded areas. These deteriorated areas probably function as barriers to juvenile tortoises.

(5) The BLM has failed to deal responsibly with the public review process. The BLM has not prepared adequate environmental assessments, impact statements or maps and has not provided these and related data as requested by the Council. The BLM has not allowed comment and appeal periods of sufficient length. Races have been held on the dates proposed, regardless of the stage of the comment or appeal period.

Example: In January of 1987, part of a motorcycle race permitted by the BLM in Nevada was routed into the Ivanpah Crucial Habitat in California. The extension into California had been the practice for several years prior to 1987, but was revealed to the Council only when the Council was notified of the race for the first time in October of 1986. This routing was in violation of the BLM's California Desert Conservation Area Plan, 1980. In addition to the course violation, the BLM allowed insufficient time to handle the review and negotiations that should have followed the exposure of such problems. The BLM (California and Nevada) has still not provided the Council with a map of the 1987 course in California.

(6) In 1986 the BLM moved the annual Mint 400 race to the Goodsprings area. This race had been held elsewhere in the county for years. It is a major ORV event with 400 entrants driving 2-, 3- and 4-wheeled vehicles for about 400 miles (four laps over a 105-125 mile course). Approximately 60,000 spectators attend.

ARROW CANYON CRUCIAL HABITAT

Arrow Canyon crucial habitat occupies 469 mi^2 and is predominantly public land. The major threat is a proposed land exchange between the Department of Interior and Aerojet. A minor threat, but typical of the problems encountered with cumulative impacts, was the recent development of 30 acres by Georgia-Pacific for a gypsum wallboard plant.

The Aerojet Proposal

This proposal has very high potential impacts. A private corporation, Aerojet Nevada, wants to acquire approximately 67 mi^2 of public land on which to build a facility for the manufacture and testing of rocket motors. If the exchange takes place without adequate mitigation measures for tortoises, the core of the Arrow Canyon habitat will be lost and the crucial habitat remaining will be insufficient to perpetuate a viable population.

Under the Aerojet proposal, about 4.25 mi^2 within the 67 mi^2 would be developed and fenced, resulting in permanent loss of that habitat. An estimated 165-320 tortoises would require relocation, a procedure which is unproven as a mitigation and may not be successful. Aerojet plans to remove tortoises from the developed area, but refuses to study and monitor the relocated animals to determine if the relocation is successful or not. Essentially the animals will be placed in an area that is very probably already at carrying capacity.

Aerojet (statement of Ralph Clark at the Desert Tortoise Council Symposium, 1987) proposes to fence the heavily-used roads to protect tortoises. However, Aerojet proposes fencing only in "high" density areas. Such a proposal is inadequate. All tortoise habitat within the crucial habitat zone should be fenced and culverts (standard tortoise underpasses) should be placed at appropriate intervals.

Once Aerojet acquires the land, they retain rights to sell a substantial block after 20 years (Ralph Clark, Desert Tortoise Council Symposium, 1987). Several thousand tortoises would be placed at risk. Aerojet proposes to retain a small acreage as a wildlife preserve for 20 years. This acreage is too small for a tortoise preserve, has large peripheral boundaries, and is fragmented. The proposed wildlife preserve does not meet current standards established by recognized experts in conservation biology.

An additional problem is the way the proposal has been processed. The proposal is being handled directly through Congress by Aerojet and the U.S. Fish and wildlife Service. In this way, procedural safeguards, such as those in the National Environmental Policy Act, can be by-passed. These safeguards mandate public disclosure of potential impacts and provide for public review and commenting. The Council has learned that the regional office of the U.S. Fish and Wildlife Service altered a jeopardy opinion developed at the local level to a finding of no jeopardy.

In summary, the tortoise and its habitat have not been adequately protected against losses by the mitigations proposed by Aerojet and the Department of Interior. The tortoise is being placed at jeopardy in the Arrow Canyon crucial habitat.

The NDOW has not been sufficiently protective on the issue, in spite of concerns expressed by wildlife biologists at the Las Vegas Office. The issue is a political one--the Nevada governor and legislators want the project; the NDOW Director is appointed. The NDOW Director apparently has ignored:

(1) the potential for sale and development of tortoise habitat,

(2) The negative effects of loss, fragmentation, or deterioration of 67 mi^2 of habitat on the Arrow Canyon crucial habitat,

(3) the requirements necessary to maintain a minimum viable tortoise population, and

(4) the importance of the Arrow Canyon habitat--it is currently the least disturbed of the crucial habitats.

Georgia-Pacific Co. Gypsum Wallboard Plant

In November of 1986, Georgia-Pacific Co. requested use of 30 acres in the Arrow Canyon crucial habitat for a gypsum wallboard plant. The BLM did not prepare adequate mitigation measures and did not permit the Council time to comment on potential mitigation measures.

PIUTE VALLEY CRUCIAL HABITAT

In 1981 - 1982, the tortoise population on he Crescent Peak allotment experienced a significant decline, which the NDOW identified as a die-off. The population dropped precipitously. The NDOW stated that long-term overgrazing was the problem. They noted that tortoise populations to the immediate east, across a major highway and in a different grazing allotment, did not experience a die-off.

As of January 1987, the BLM has not instituted appropriate measures to allow the tortoise habitat and populations to recover. The NDOW contested decisions made by the BLM on the recent Crescent Peak Allotment Management Plan. The BLM apparently is reworking the Plan. The Council has not been provided copies of the Plan or been asked to comment on the Plan.

Tortoises must be allowed sufficient forage during spring, summer, and fall. Forage should be composed of annual herbs and grasses, cacti, and perennial grasses. Tortoises can eat dried plants when sufficient moisture is available, i.e. after summer rains, so dried plant material must be left on the ground in the form of litter. Trampling is also an issue. Grazing pressures must be reduced to the point where trampling of juveniles, adults, and tortoise burrows would be minimal to non-existent. Tortoises must have intact burrows or cover sites to prevent heat stress. If tortoises return to burrows which have been damaged or destroyed by livestock, they may die of overheating.

GOLD BUTTE CRUCIAL HABITAT

The Gold Butte population is not thriving. In fact it may be in serious condition. In 1986, Russell Duncan conducted a 60-day spring survey of a one-square mile study plot in the Gold Butte Crucial Habitat. Duncan summarized his findings at the 12th Annual Meeting and Symposium of the Council, held in Las Vegas in March of 1987.

According to Duncan, the density is estimated at 96 ($\pm$ 26) tortoises/mi^2 for adults and subadults and at 131 ($\pm$ 28) for the entire population. The population is top heavy and composed primarily of older individuals. Duncan found only seven individuals $<$ 15 yrs old and concluded that recruitment has been low or nonexistent for the last several years. Grazing, either the past or currently, may be the issue here. However, Duncan found little evidence of recent cattle grazing.

Of further interest is the genetic relationship of the Gold Butte population to other populations throughout the geographic range. According to Dr. Trip Lamb of the Savannah River Laboratory, this population is part of a small, discrete genetic unit which is limited to tortoises in eastern Nevada and the Beaver Dam Slope of Arizona and Utah. All populations in this particular genetic unit are in serious trouble.

[Dr. Trip Lamb has been conducting mitochondrial DNA studies of tortoise populations throughout the geographic range. He presented a poster paper at the 12th Annual Meeting and Symposium of the Desert Tortoise Council.]

DESERT TORTOISE COUNCIL RECOMMENDATIONS

(1) The BLM and the NDOW should honor crucial habitats delineated by the Desert Tortoise Council. Minor adjustments can be made for new data.

(2) The Aerojet-Nevada project in Coyote Spring Valley. Several options exist:

(a) Locate the Aerojet project in another area.

(b) Allow Aerojet to acquire about 4 mi^2 of land in Coyote Spring Valley. Retain the remaining 63 mi^2 in public domain, but at the same time provide severe restrictions on use and access. Develop appropriate relocation program with monitoring for tortoises removed from the 4 mi^2 area.

(c) See recommendations for tortoise mitigation submitted by the Council (January 7, 1987 letter to Nevada representatives).

(3) The BLM and the NDOW should limit vehicular use in crucial habitat. Ample evidence exists on impacts of ORVs, increased access, and presence of people to desert tortoises and their habitat.

(4) The BLM and the NDOW should provide for humane treatment of tortoises on public and private lands scheduled for development. The treatment of wild tortoises should be based on sound biological principles.

(5) The NDOW should consider free living treatises to be protected by law. Standard mitigation measures should be developed to protect the tortoises in the event development occurs in their habitats.

(6) The BLM should adhere to the 1976 Federal Land Planning and Management Act in spirit and letter (also for NEPA). Adequate environmental statements should be prepared; adequate commenting periods should be provided; adequate time for protests should be allowed.

(7) The BLM and the NDOW, working with tortoise experts, should set aside public lands as Natural Areas or Areas of Critical Environmental Concern for the tortoise. These should be representative areas and be sufficiently large to maintain tortoise populations into perpetuity.

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STATE REPORT - UTAH - 1985

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GENERAL DESCRIPTION

In Utah, the desert tortoise (*Gopherus agassizii*) is found in scattered populations in western Washington County and the Beaver Dam Slope. The most contiguous population is found on the Beaver Dam Slope and encompasses 91 mi^2 (235 km^2) of lower Sonoran vegetation that extends into the adjoining states of Arizona and Nevada.

The desert tortoise in Utah was listed as a federally protected, threatened species on August 20, 1980 with a 35 mi^2 (90.6 km^2) area of designated critical habitat. The current interpretation of the listing language by the USFWS states that all of the desert tortoises found on the Beaver Dam Slopes in Utah are protected by the federal register notice. All other desert tortoises found in Utah are protected under state code section 23-20-3, which requires a permit to possess or take any desert tortoise.

Present Management of the Desert Tortoise in Utah

In 1985, desert tortoise management in Utah has included the following:

(1) Monitoring of the population dynamics of the desert tortoise.

(2) Monitoring of livestock grazing seasons of use and vegetative conditions and possible trespass on the Beaver Dam Slope.

(3) Maintaining and updating a computer file for all numbered tortoises released on the Slope from 1973 to the present.

(4) Transplanting of displaced and captive desert tortoises into Washington County and monitoring these animals.

(5) Conducting a federally funded tortoise research project on the Beaver Dam Slope.

(6) Continuing to write and submit proposals for further research on desert tortoises in southern Utah.

DISCUSSION

(1) During all trips to the Beaver Dam Slope, observations were made and data collected on all tortoises and shells encountered. In 1985, three new native tortoises were found around the new plot, one native was recaptured in Welcome Wash and twenty-three captives were released or encountered. Of

the captive tortoises, two were released in Welcome Wash--one with a radio transmitter, fifteen tortoises were released in April at the Old Tin Can Dens area, and five were released at the new Red Cliffs release site off the Slope. The last captive was a recapture in Welcome Wash that had originally been released in 1982.

Two shells outside of the new plot were recorded. One was a captive release from Tin Can Dens that was shot and the other was an old male #28 found .4 mile south of the Slope plot. This tortoise had been originally released in 1973 at the Zella Tank area, 3 miles north.

Also in 1985, field investigations on desert tortoises in Washington County by an amateur herpetologist were coordinated and a brief summary prepared. In the last two years, Russell Bezette of Hurricane, Utah, has documented 88 tortoises in three separate areas: Red Cliffs, Red Hills, and Hurricane Cinder Cones. His preliminary work will be used as the basis for a more extensive survey of tortoise populations in Washington County planned for 1986.

(2) Livestock grazing operations continue to be monitored on the Slope and around the Woodbury/Hardy exclosure. Livestock trespass was documented in the exclosure at the NW corner from fence wire being lifted and was corrected. Also, a single cow entered the exclosure on the east side by the road and was removed after several weeks by the BLM.

Continued livestock grazing near the new Slope plot in late April of 1985 was reported to the BLM and all animals were removed by the first week of May. No grazing extension had been granted the permittee in 1985.

(3) During the winter of 1985, the Apple computer file was updated to include all new tortoise data including Bezette's work. Transfer of files to the DWR Wang system was delayed until a Wang-PC can be purchased in 1986. Printouts of this file are available to anyone wishing to do research in Utah.

(4) As of June 1985, the Utah DWR has accepted a policy of not releasing any more captive tortoises on the Beaver Dam Slope. Additionally, very tame captive tortoises are being placed with qualified individuals under certificates of registration. Whenever possible, tortoises are being paired up and any offspring will be turned over to the DWR for release at two release sites in Washington County. Healthy, normal captive or displaced native tortoises will be released at the two BLM approved release sites. In November of 1985, the BLM agreed to set aside two sites for tortoise releases: the Red Cliffs site near the Cottonwood Canyon WSA and the City Creek site north of St. George. BLM surveys of these areas have shown tortoises and gila monsters already exist at these two sites and that limited livestock grazing pressure should allow for larger populations.

As funding permits, studies will be conducted to monitor these two release sits in future years.

(5) In 1985, a federally funded tortoise project was conducted on the Beaver Dam Slope west of the highway. This project surveyed one square mile of habitat (2 mi x .5 mi) for all live tortoises and remains that could be located in the two-month period of May and June. A total of 26 live tortoises nd 19 shells or

shell remains were found during the study period. The two seasonal tortoise plot workers concentrated on finding tortoises and some limited tortoise sign. A separate radio telemetry study was conducted in the plot by the regional nongame manager. Seven of the eight adult females located during the project were radioed an will be followed for two years if funding allows. Further details on this will be presented later in this meeting.

(6) Funding requests were submitted to the USFWS for tortoise work on the Beaver Dam Slope to resurvey the 1981 plot in the Woodbury/Hardy exclosure and to continue monitoring work on the radioed adult females. Funding was obtained for only the redo of the 1981 plot but limited monitoring will continue on the 1985 radioed females. Currently nongame check-off funds are approved for a preliminary survey of other tortoise populations in Washington County.

Table 1. Red Hills Tortoises

BD#	Collector	Origin	Size Class	Sex	Date	MCL	Location
301	Bezette	N	AI	F	05/08/85	228	Red Hills PP
302	Bezette	N	AII	M	05/03/85	310	Red Hills PP
303	Bezette	N	AII	F	05/08/85	255	Red Hills PP
304	Bezette	N	AI	F	05/18/85	216	Red Hills PP
305	Bezette	N	IMI	F	05/18/85	150	Red Hills PP
306	Bezette	N	SA	M	05/18/85	183	Red Hills PP
307	Bezette	N	AI	M	05/18/85	220	Red Hills PP
308	Bezette	N	AI	F	05/18/85	223	Red Hills PP
309	Bezette	N	AII	M	05/18/85	286	Red Hills PP
310	Bezette	N	AII	M	05/18/85	272	Red Hills PP
311	Bezette	N	AI	F	05/18/85	221	Red Hills PP
312	Bezette	N	IMII	F	05/18/85	171	Red Hills PP
313	Bezette	N	AII	M	05/08/85	286	Red Hills PP
314	Bezette	N	IMI	F	05/18/85	127	Red Hills PP
315	Bezette	N	AI	M	05/18/85	216	Red Hills PP
316	Bezette	N	AI	F	05/18/85	214	Red Hills PP
317	Bezette	N	IMI	M	05/18/85	117	Red Hills PP
318	Bezette	N	AI	M	05/18/85	238	Red Hills PP
319	Bezette	N	JII	J	05/18/85	88	Red Hills PP
320	Bezette	N	AII	F	05/18/85	246	Red Hills PP
321	Bezette	N	AII	F	05/14/85	248	Red Hills PP
322	Bezette	N	AII	F	05/24/85	226	Red Hills PP
323	Bezette	N	AI	M	05/24/85	208	Red Hills PP
324	Bezette	N	AII	M	05/23/84	275	Red Hills PP
325	Bezette	N	IMII	F	05/24/85	179	Red Hills PP
326	Bezette	N	IMI	J	05/27/85	162	Red Hills PP
327	Bezette	N	IMI	J	05/27/85	125	Red Hills PP
328	Bezette	N	AI	M	05/27/85	208	Red Hills PP
329	Bezette	N	AII	F	05/27/85	243	Red Hills PP
330	Bezette	N	IMII	J	05/27/85	159	Red Hills PP
331	Bezette	N	AII	F	05/27/85	231	Red Hills PP
332	Bezette	N	IMI	J	05/27/85	129	Red Hills PP
333	Bezette	N	AII	M	06/04/85	250	Red Hills PP
334	Bezette	N	IMI	J	06/04/85	128	Red Hills PP
335	Bezette	N	IMII	F	06/04/85	175	Red Hills PP
336	Bezette	N	AII	M	06/04/85	275	Red Hills PP
337	Bezette	N	AII	F	06/04/85	267	Red Hills PP
338	Bezette	N	AII	F	06/04/85	246	Red Hills PP
339	Bezette	N	SA	M	06/10/85	180	Red Hills PP
340	Bezette	N	SA	M	06/10/85	182	Red Hills PP
341	Bezette	N	SA	F	06/10/85	181	Red Hills PP
342	Bezette	N	AII	F	06/10/85	249	Red Hills PP
343	Bezette	N	AII	M	06/10/85	275	Red Hills PP
344	Bezette	N	AII	F	06/10/85	142	Red Hills PP
345	Bezette	N	IMI	J	06/17/85	114	Red Hills PP

Figure I. Washington Co., Utah Tortoises - Red Hills Plot, 1985 (Bezette, pers. corresp.)

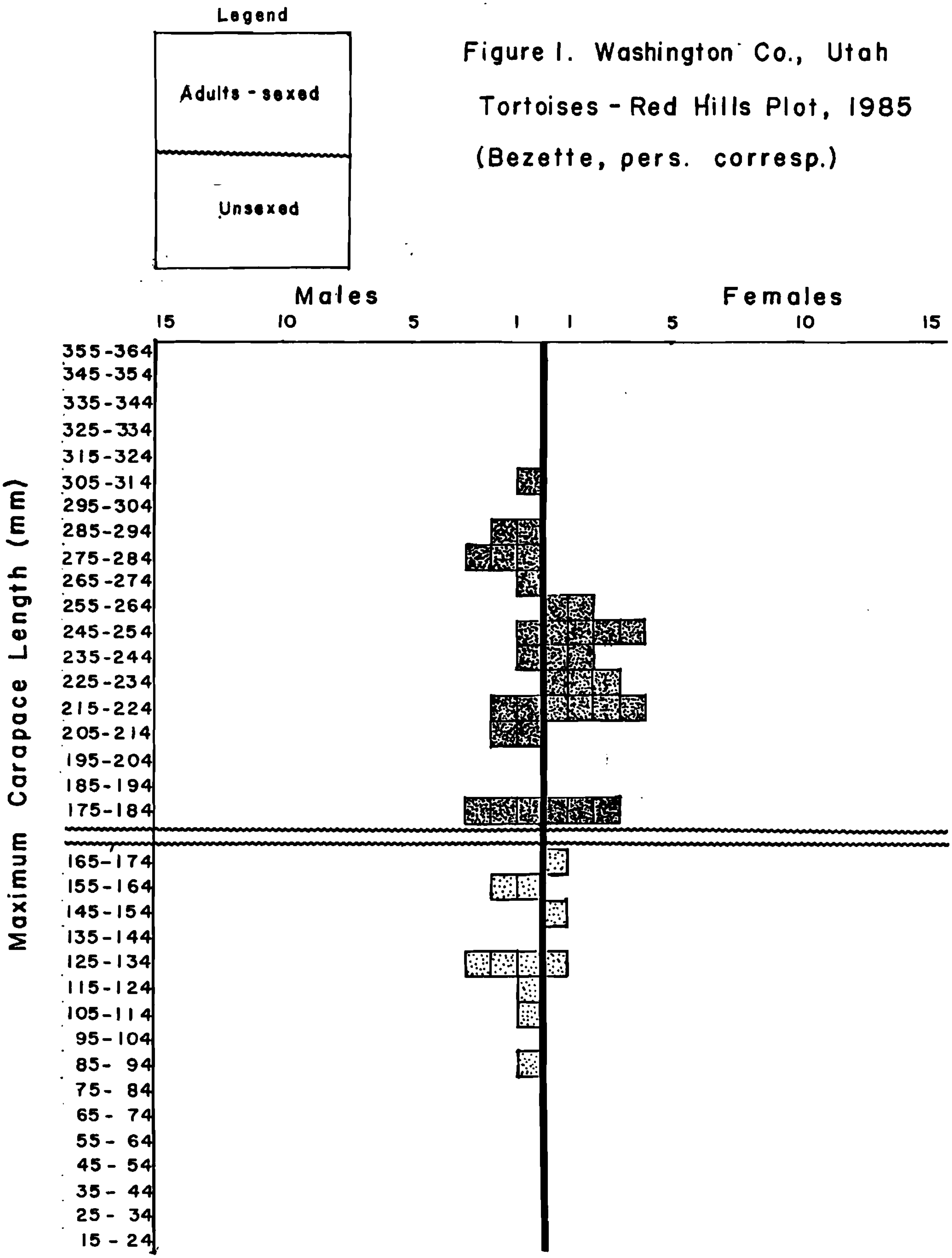


Table 2. Hurricane Tortoises

BD#	Collector	Origin	Size Class	Sex	Date	MCL	Location
201	Bezette	N	AII	M	05/23/84	247	Hurr.Cinder
202	Bezette	N	SA	F	05/22/84	190	Hurr.Cinder
203	Bezette	N	AII	F	05/23/84	246	Hurr.Cinder
204	Bezette	N	AII	F	05/23/84	248	Hurr.Cinder
205	Bezette	N	JI	J	05/23/84	49	Hurr.Cinder
206	Bezette	N	JII	J	05/25/84	75	Hurr
207	Bezette	N	JII	J	07/16/84	92	Hurr.Cinder
208	Bezette	N	IMII	J	08/27/84	163	Hurr.Cinder
209	Bezette	N	IMII	J	08/27/84	166	Hurr.Cinder
210	Bezette	N	AI	M	08/20/84	218	Hurr.Cinder
211	Bezette	N	SA	M	08/27/84	199	Hurr.Cinder
212	Bezette	C	AI	F	08/29/84	227	Hurr.Cinder
213	Bezette	N	AI	F	09/01/84	238	Hurr.Cinder
214	Bezette	C	AI	M	09/01/84	217	Hurr.Cinder
215	Bezette	C	IMI	J	09/16/84	110	Hurr.Cinder
216	Bezette	N	JI	J	09/29/84	43	Hurr
217	Bezette	N	JI	J	09/29/84	42	Hurr
218	Bezette	N	JI	J	09/30/84	45	Hurr
219	Bezette	N	AI	F	04/24/85	236	Hurr.Cinder
220	Bezette	N	JII	J	04/27/85	81	Hurr.Cinder
221	Bezette	C	AI	M	05/01/85	236	Hurr.Cinder
222	Bezette	N	SA	F	05/12/85	189	Hurr.Cinder
223	Bezette	C	AII	M	05/21/85	261	Hurr.Cinder
224	Bezette	C	JII	J	05/28/85	62	Hurr.Cinder
225	Bezette	C	JI	J	05/20/85	56	Hurr.Cinder
226	Bezette	C	JII	J	06/15/85	65	Hurr.Cinder
227	Bezette	N	JII	J	06/27/85	56	Hurr.Cinder
228	Bezette	N	AI	F	07/02/85	218	Hurr.Cinder
229	Bezette	N	SA	F	07/10/85	195	Hurr.Cinder

Figure 2. Washington Co., Utah

Tortoises - Hurricane Cinder Knolls,

1984-85

(Bezette, pers. corresp.)

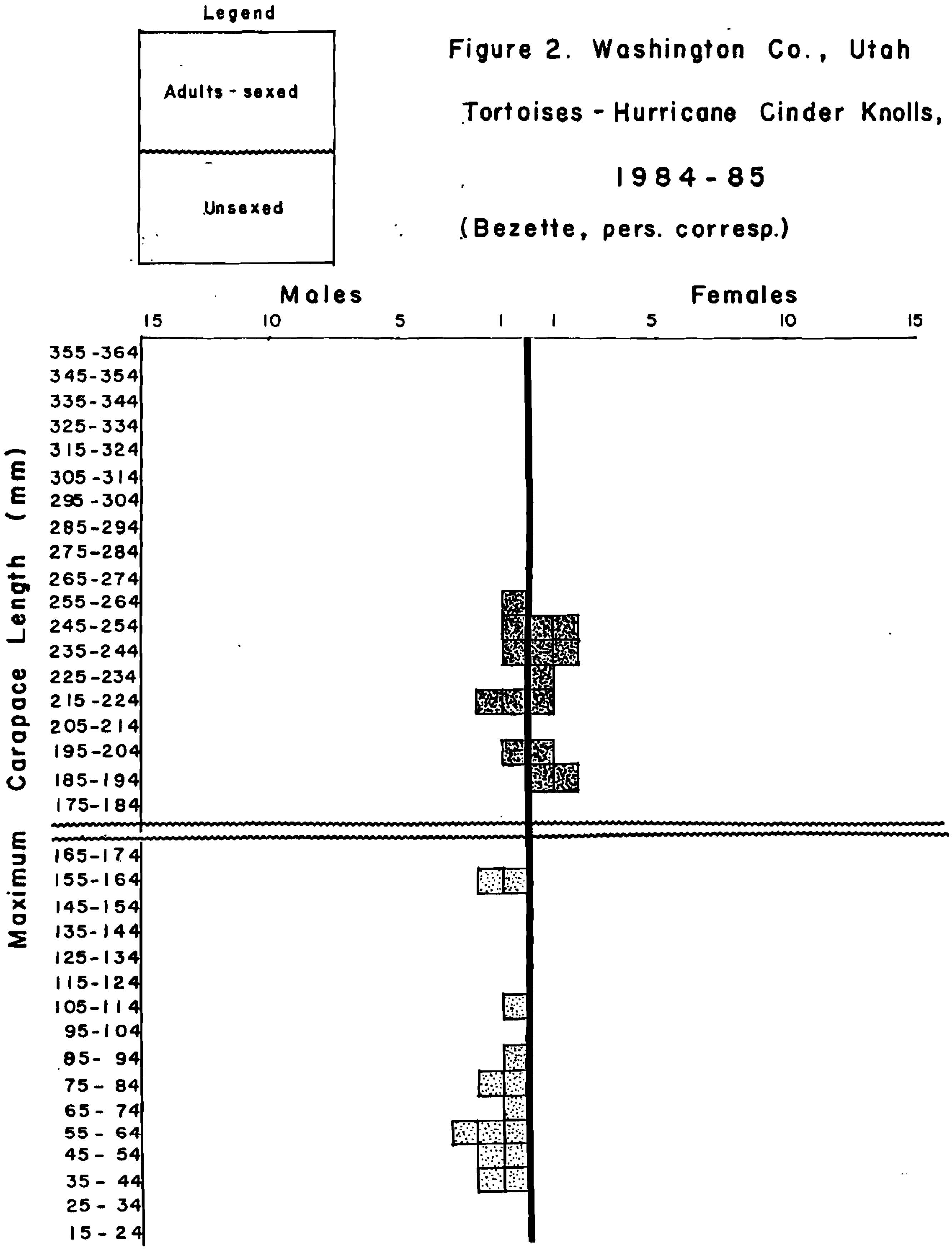
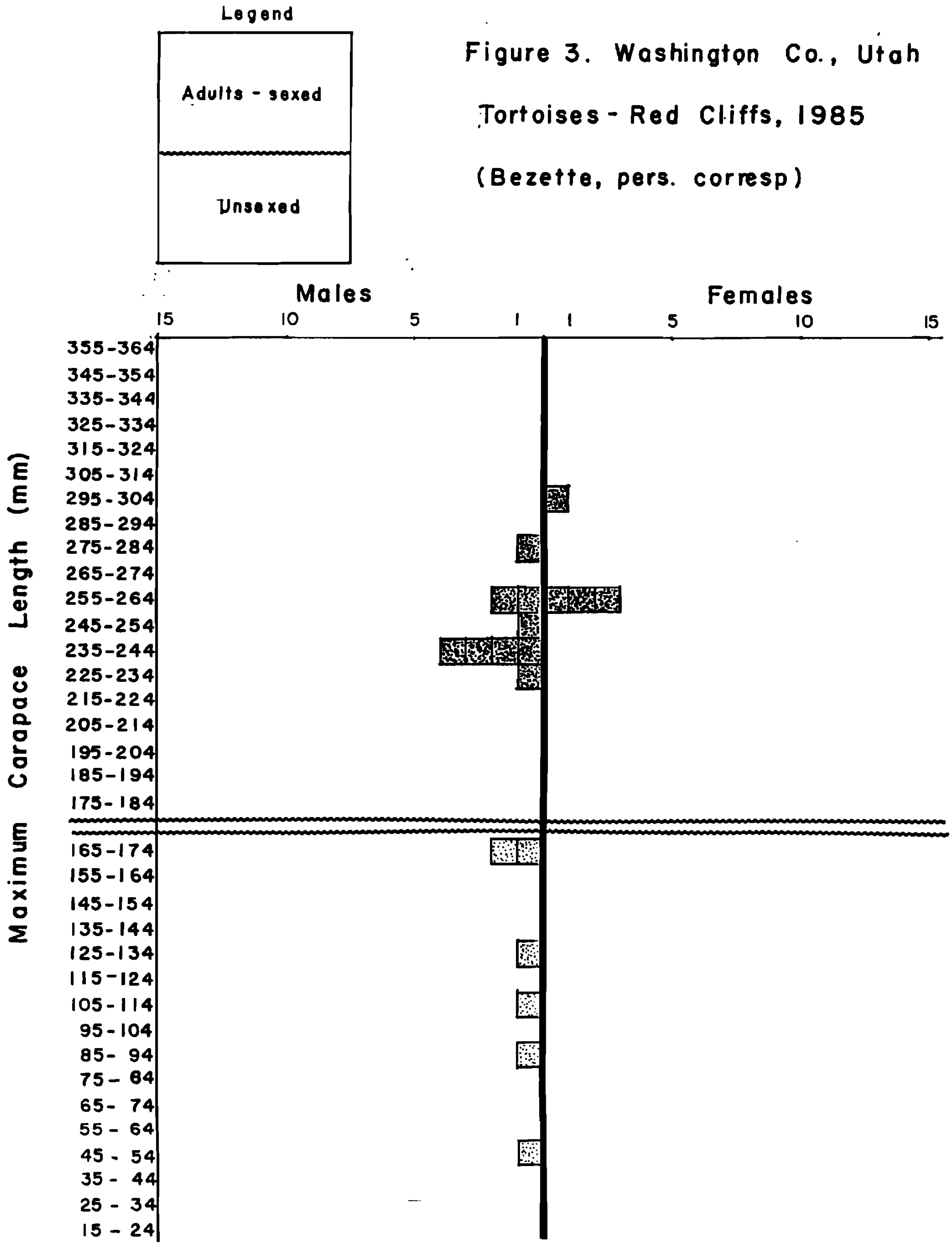


Table 3. Red Cliffs Tortoises

BD#	Collector	Origin	Size Class	Sex	Date	MCL	Location
401	Bezette	N	JII	J	05/17/85	85	Red Cliffs
402	Bezette	N	IMI	J	05/23/85	172	Red Cliffs
403	Bezette	N	IMI	J	05/23/85	126	Red Cliffs
404	Bezette	N	IMI	J	05/23/85	111	Red Cliffs
405	Bezette	N	AII	M	05/26/85	259	Red Cliffs
406	Bezette	N	AII	M	05/26/85	256	Red Cliffs
407	Bezette	N	AII	F	05/26/85	260	Red Cliffs
408	Bezette	N	AII	F	05/31/85	259	Red Cliffs
409	Bezette	N	JI	J	05/31/85	49	Red Cliffs
410	Bezette	C	AII	F	06/01/85	298	Red Cliffs
411	Bezette	C	AII	M	06/11/85	245	Red Cliffs
412	Bezette & Mckell	N	AII	F	06/14/85	264	Red Cliffs
413	Bezette & Mckell	N	IMII	J	06/14/85	168	Red Cliffs
414	Bezette	N	AII	M	07/27/85	281	Red Cliffs
533	Coffeen	C	AI	M	10/30/85	228	Red Cliffs
534	Coffeen	C	AII	M	10/30/85	241	Red Cliffs
535	Coffeen	C	AI	M	10/30/85	238	Red Cliffs
536	Coffeen	C	AI	M	10/30/85	236	Red Cliffs
537	Coffeen	C	AI	M	10/30/85	235	Red Cliffs


Legend
Adults - sexed
Unsexed
Figure 3. Washington Co., Utah
Tortoises - Red Cliffs, 1985
(Bezette, pers. corresp)
Males
Females
15
10
5
1
1
5
10
15
Maximum Carapace Length (mm)
355-364
345-354
335-344
325-334
315-324
305-314
295-304
285-294
275-284
265-274
255-264
245-254
235-244
225-234
215-224
205-214
195-204
185-194
175-184
165-174
155-164
145-154
135-144
125-134
115-124
105-114
95-104
85- 94
75- 84
65- 74
55 - 64
45 - 54
35 - 44
25 - 34
15 - 24

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STATE REPORT - ARIZONA
THE ARIZONA GAME AND FISH DEPARTMENT

Cecil R. Schwalbe
Herpetologist, Arizona Game and Fish Department
Phoenix, Arizona

POSITION STATEMENT

On April 5, 1986, the Arizona Game and Fish Commission voted unanimously to adopt a position statement on the desert tortoise in Arizona. The position statement says in part that:

> "currently available data do not support Federal listing of the desert tortoise in Arizona as either endangered or threatened. The Endangered Species Act defines an 'endangered species' as any species which is in danger of extinction throughout all or a significant portion of its range. A 'threatened species' is one that is likely to become endangered within the foreseeable future. The term 'species' includes any subspecies or any distinct population segment of a species. The criteria used to determine whether a species is threatened or endangered include habitat modification or destruction, over-utilization (collecting), disease or predation, inadequate regulatory mechanisms or other factors. The desert tortoise does not meet any of these criteria over a significant part of its range in Arizona. However, it is the position of the Department that, as one of Arizona's sensitive species, the desert tortoise should continue to receive priority management considerations on public lands in accord with the multiple use management concept. Mitigation for projects destroying desert tortoises or desert tortoise habitat on public lands should be encouraged. Research needs to be conducted on the population status of the tortoise in Arizona and on the effects of various management and land use practices on tortoise populations. The Department is developing an interagency research-management program to address the issue."

Desert tortoises occur in most areas supporting good paloverde/saguaro (Arizona Upland Desert) habitats in Arizona. More information is needed on differences between Mojave and Sonoran desert populations of tortoises in Arizona and elsewhere.

ARIZONA INTERAGENCY DESERT TORTOISE TEAM

The Department continued its participation on the Desert Tortoise Team. The team was formed to coordinate management of the desert tortoise and its habitat throughout Arizona.

DOG STUDY

At the recommendation of the Arizona Interagency Desert tortoise Team, the Department is undertaking a study to see if dogs might be used effectively to locate desert tortoises in the wild, as in a study of box turtles in the Midwest in the 1970s. Funding will be provided by the Nongame Checkoff.

NONGAME DATA MANAGEMENT SYSTEM

Using funds from the Nongame Checkoff, Howard Berna has been hired as a seasonal employee to enter desert tortoise and other reptile locality information into the data management system. More than 400 individual tortoise records are expected to be entered or updated by June.

DESERT TORTOISE COUNCIL RESEARCH ADVISORY COMMITTEE

Cecil Schwalbe has been appointed to the committee to assist in evaluating desert tortoise research proposals.

PICACHO PEAK STATE PARK - A DESERT TORTOISE PRESERVE?

Personnel from the Department, Arizona State Parks Department, U.S. Bureau of Land Management and U.S. Bureau of Reclamation evaluated desert tortoise habitat on Picacho Peak State Park. It was the consensus of those present that the quality of tortoise habitat in the park does not warrant designation as a desert tortoise preserve, but that efforts should be continued to find a suitable preserve site elsewhere in Arizona.

EDUCATION PROGRAMS, BALLOTS

The Department's Nongame and Audio-Visual branches collaborated with Mesa Public Schools in producing a 20 minute educational videotape entitled "Desert Neighbors," which discusses the ecology of the desert tortoise and other desert reptiles. The desert tortoise came in third (behind the Arizona ridge-nosed rattlesnake and the Gila monster) in a Department sponsored vote by elementary school children for their preference for Arizona's "official" state reptile. Ballots were cast from over 368 schools across Arizona. The results of the balloting will be passed to the State Legislature during the next session.

ADOPTION PROGRAMS

Desert tortoise adoption programs were continued in Tucson by the Arizona-Sonora Desert Museum and in Phoenix by the Department's Adobe Mountain Wildlife Center. Betty Vance adopted out 117 desert tortoises for the Museum during 1985. Cindy Dorothy adopted 44 tortoises from the Center.

NATIONAL TURTLE AND TORTOISE SOCIETY

The National Turtle and Tortoise Society was formed in Phoenix in the fall of 1985, focusing on captive husbandry of various chelonians.

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STATE REPORT - ARIZONA

Ted Cordery
Wildlife Management Biologist, Bureau of Land Management
Phoenix District

In Arizona, the BLM continues to consider the needs of the desert tortoise and its habitat as we manage the public lands throughout the state. The following is a summary of important events affecting the desert tortoise.

SAFFORD DISTRICT

The BLM is consolidating its ownership of lands in areas of high natural resource values, including habitat used by the desert tortoise. Two exchanges that will block up habitat used by the desert tortoise are near Aravaipa Canyon (51,077 acres) and the Muleshoe Ranch (23,472 acres) which is managed by The Nature Conservancy.

YUMA DISTRICT

In conjunction with the drafting of the Yuma RMP, eight Special Management Areas totaling 187,000 acres will be designated, allowing land use compatible with local resources such as desert bighorn sheep, the desert tortoise, scenic values, and sensitive cultural resources. A broad, extensive tortoise inventory was conducted with 106 1-1/2 mile transects on 53 sites during 1985. All transects were established in areas thought to be most likely to have sign, (e.g., incised washes, canyons, bajadas, foothills and ridges). The inventory showed that 30% of the transects had tortoise sign.

Results of this inventory may guide management prescriptions for special management areas, and be used in developing or revising HMP's.

ARIZONA STRIP

The BLM is implementing the Virgin River-Pakoon Habitat Management Plan which covers all the desert tortoise habitat in the district. In addition, the district has implemented guidelines and stipulations on livestock management and other activities in desert tortoise habitat. For example, livestock concentrations in desert tortoise habitat would be avoided by locations new water sources and other developments outside tortoise habitat. Additionally, utilization of key forage species is being held at less than 45%. For example, the average utilization for 6 allotments in 1985 was only 25%.

Existing tortoise data is being synthesized for district use to further improve our knowledge of tortoise distribution and densities. We intend to perform one or two follow-up studies in monitoring plots this year., and we are in the process of creating density distribution map using the Geographic Information System (GIS) to help in planning and monitoring activities in tortoise habitat, and, perhaps eventually assist in modeling their habitat relationships.

Also, within three designated wilderness areas there are a few canyons which harbor up to 18,700 acres of desert tortoise habitat. This habitat is now fully protected under the Wilderness Act.

PHOENIX DISTRICT

The draft Lover Gila South RMP was completed in 1985. The RMP provides some general guidelines for protection of desert tortoise habitat, and addresses the consequences of wilderness management on 47,000 acres of crucial desert tortoise habitat. In the RMP, the BLM proposes to designate 10,500 acres of desert tortoise habitat under wilderness. The draft Phoenix Wilderness EIS, completed in 1985, considered 6,400 acres of desert tortoise habitat in the Picacho Mountains WSA for wilderness designation. The proposed action did not recommend this designation, however, the area will be analyzed for special management in the Phoenix Resource Area Management Plan.

The BLM is beginning work on a Resource Management Plan for the Phoenix Resource Area that will cover approximately one million acres of scattered lands in the central corridor of the State. We are in the process of accumulating existing data and scoping for management issues. So far, the primary issue that has surfaced concern consolidation of land ownership patterns in this part of the State. An example is our exchanging lands with high economic, but low resource values for other lands of lower economic, but higher resource values. We are in the preliminary (scoping) stages of this RMP and welcome any comments or suggestions you may have toward resource management of lands in this area.

The All American Oil Pipeline, a concern over the last several years, was completed across Arizona in 1985. And as some of you may know, the construction route was surveyed prior to the start of work, to ensure avoidance of desert tortoise habitat on public lands.

The Phoenix District has identified a need for establishing desert tortoise monitoring plots in approximately eighteen areas. With present funding levels, monitoring will probably be contracted out for two sites. We have also proposed to inventory the remaining uninventoried areas in the district, some 1,080,000 acres in northwestern and central Arizona. Our priority is, however, to concentrate on monitoring known areas over identifying new habitat.

Also in the Phoenix District, we have completed the Hualapai Habitat Management Plan which provides for management prescriptions that would maintain or improve habitat needs for the tortoise on 75,000 public acres of crucial habitat. The Phoenix District is also beginning work on the Lower Gila South Habitat Management Plan. This HMP will include management prescriptions for nearly 50,000 acres of crucial desert tortoise habitat. Anyone interested in providing input on their plan should contact the Phoenix District.

STATEWIDE

We are working as part of the Arizona Interagency Desert Tortoise Team to build a statewide plan for research and management activities in the state. Intent of the plan is to coordinate management/research activities and funding with issues facing the desert tortoise.

Cecil Schwalbe will/has discuss/discussed the team in more detail. BLM intends to cooperate on the team and use its expertise. We intend to use the plan to implement needed research and habitat management techniques for maintenance or enhancement of tortoise habitat.

CONCLUSION

The BLM has progressed in its ability to inventory, monitor and manage the desert tortoise and its habitat in Arizona. With the continued cooperation of other Federal and State agencies as well as private interest groups, we hope to achieve even more for conservation of the desert tortoise in the years to come.

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1986 CALIFORNIA STATE REPORT ON DESERT TORTOISE MANAGEMENT FOR THE BUREAU OF LAND MANAGEMENT

Larry D. Foreman
Bureau of Land Management, California Desert District Office
Riverside, California

In the 1985 California State Report, I reviewed the management, monitoring, and research activities conducted by the Bureau over the past 10 years (Foreman 1985). For the symposium this year, the Bureau has been asked to review habitat management, monitoring, and research activities of the Bureau over the past year.

HABITAT MANAGEMENT ACTIVITIES

The Plan for the Chuckwalla Bench Area of Critical Environmental Concern (ACEC) was completed and signed within the past month. Implementation of this plan has commenced with the signing of routes of travel with a numerical designation. In the next few months routes designated in the ACEC for closure will be marked with vehicle closure signs. The ACEC plan designated 18 routes for year-round closure and 4 routes for seasonal closure. Other prescriptions designed to benefit tortoise habitat include limiting camping to within 100 feet of designated routes, interpretive signing, and refining tortoise density estimates.

The Bureau has received a draft ACEC plan for the Desert Tortoise Natural Area (DTNA). This draft plan was prepared by the Tortoise Preserve Committee. The draft has been reviewed by several staff members. It will be ready this spring for coordination with California Department of Fish and Game (CDFG) and then for formal public review. In the meantime, the Natural Area is being managed under the cooperative Habitat Management Plan signed by the Bureau and CDFG in 1978.

For the past year our Ridgecrest Resource Area staff has been negotiating a cooperative management agreement with the Tortoise Preserve Committee. This agreement will formalize their participation in monitoring, facility maintenance, and interpretive services.

Due to objections of a private property owner on the northwest edge of the Desert Tortoise Natural Area, it was necessary to remove 3/4 of a mile of fence and move the fence inside this private property. As a result, 240 acres of land (160 private/80 public) are being excluded form the fenced DTNA. Encouragingly, members of the American Motorcycle Association are assisting in the reinstallation of this fence segment as part of their compensation efforts for the Barstow-Vegas Motorcycle Race.

MONITORING AND RESEARCH ACTIVITIES

Again in 1986, Dr. Kristin Berry of the Bureau will be participating in the Southern California Edison research at Goffs with Dr. Fred Turner and others. Work will be continuing on juvenile survivorship, nest success, and nest predation. Dr. Turner has discussed elsewhere in the symposium the findings from 1983-1985. In addition Dr. Berry with Michael Weinstein will be validating a tortoise habitat model. Weinstein has described that model elsewhere in the symposium (Weinstein and Berry 1986).

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As reported in the 1985 State Report (Foreman 1985), the Bureau has selected 16 permanent tortoise trend plots for resurvey at the rate of four per year on a 4-year rotation. Last year contractors Woodman, Bohuski, Shields, and Juarez surveyed four plots. Three of these were contiguous plots near the Interpretive Center in the Desert Tortoise Natural Area; one additional plot near Fremont Peak was surveyed. These plots and those surveyed in 1982 have recently been analyzed by Dr. Berry. She has reported on these analyses elsewhere in the symposium (Berry 1986a, 1986b).

This year the Bureau is unable to fund the survey of four plots as planned; the number has been reduced to three. These survey plots are in Ivanpah Valley, Lucerne Valley, and Johnson Valley.

The Bureau is having great difficulty in maintaining the monitoring schedule. In 1983 and 1984 no plots were surveyed; this means that the plots currently being surveyed are now six years old. Four plots were surveyed in 1985, but now only three in 1986. This is a serious difficulty. Not only are trend analyses being delayed, but the survey method may become compromised. For example, marks made on the scute margins may become obscured and difficult to read over such a long period, and carcass remains may deteriorate so much that they cannot be found or the margin number cannot be read.

The tortoise permanent trend plot methodology appears to yield excellent information on adult tortoise population age structure and sex ratio and on minimum mortality since last survey based on carcasses. However, it is difficult to estimate population size and thus a mortality rate. This is because some tortoises use the plot only part of the time. In other words, their individual ranges overlap the plot. Since plot coverage is so complete, it is believed that a very high proportion of these part-timers are actually encountered on the plot and thereby counted as residents.

Various methods to compensate for this depend on tortoise range size. However, repeated sightings during plot surveys indicate that ranges of tortoises are highly variable from tortoise to tortoise. Furthermore, the ranges of individual tortoises may vary greatly from year to year. Thus, the density of tortoises calculated from a 60-day survey may not correlate well with actual population size. This is critical when trend analyses are based on only a few sampling replications many years apart.

I am concerned that the Bureau will not be able to afford continuation of the trend plot method on sixteen plots. I am concerned that difficulties in estimating population size will confuse trend results and obscure true mortality rates. In California, there is a broad spectrum of habitat types over a wide geographic area with several distinct populations as shown by others in this symposium (Lamb 1986, Buth 1986). Considerable funding is required to sample over this spectrum. As Federal budgets fall the Bureau needs a monitoring technique that is quick and cheap, or it needs alternative funding sources.

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DESERT TORTOISE PRESERVE COMMITTEE, 1985 STATUS REPORT

George E. Moncsko
Desert Tortoise Preserve Committee President
Ridgecrest, CA

The Desert Tortoise Preserve Committee (DTPC) is a private non-profit corporation formed in 1979. The principal purpose of the committee is to promote the welfare of the Desert Tortoise (*Gopherus agassizii*) in the wild in the southwestern United States and with the purpose of establishing and maintaining a Desert Tortoise Natural Area in the Western Mojave Desert. That Natural Area was formally established by the Bureau of Land Management (BLM) in 1980 as a Research Natural Area to protect the desert tortoise populations and habitat. The Natural Area was also designated as an Area of Critical Environmental Concern (ACEC) in the BLM's 1980 Plan for the California Desert Conservation Area. Also, as part of the 1980 Plan, the Western Rand Mountains ACEC was identified. This area is adjacent to the northeastern part of the Natural Area and was established to protect wildlife values including the desert tortoise and the state-listed rare Mojave ground squirrel.

The Natural Area is located in a part of California which historically included the highest density of tortoise populations in the United States. The region had tortoise populations estimated at 500 to 2,000 per square mile. At the time of establishment of the Natural Area the population was only 10 to 40 percent of the historical numbers.

This paper reports on the status and activities of the DTPC in 1985. The Committee has concentrated on Desert Tortoise Natural Area (DTNA) issues this year with some significant successes and a couple of setbacks. As part of our goals we have also supported education and conservation of the tortoise in a broader sense.

Under the steward-ship role for the DTNA our most pressing problems are acquisition of private land inholdings and the perimeter fence completion and maintenance. The DTPC raises funds for land acquisition and seeks out landowners who are willing to sell. The Nature Conservancy (TNC) often provides assistance in the land purchase activities. Through this process 10 acres were acquired this year with an offer made on another 70 acres. In addition to this we have been supporting the California Department of Fish and Game in their proposed acquisition of approximately 387 acres in the DTNA. These land acquisitions will be a significant step in reducing the 16 square miles of remaining inholdings and provide additional protection for the tortoise habitat. Further, we have supported the Department of Fish and Game in their acquisition of one full section of land in the Rand-Fremont Valley area near the DTNA. It is very gratifying to see the Department of Fish and Game taking such an active role again the in management and protection of non-game species.

The importance of completing the perimeter fence was again highlighted this spring. There was extensive sheep grazing trespass on the Natural Area. This grazing extended over five sections of land on the west side of the Natural Area. When this was reported to the Bureau of Land Management office responsible for the Natural Area they were unaware of the trespass, demonstrating that they had not been patrolling the perimeter or controlling the Natural Area.

Once the fence is installed, maintenance is necessary to repair deliberate damage and naturally caused breaks. This year the Committee raised the priority on fence maintenance as far as devoting manpower to the problem. Three fence repair work parties were held in conjunction with the Ridgecrest Resource Area office of the BLM; one was held in the spring and two were held in the fall. There were approximately 100 repair actions required this year of which about 85 percent were completed during the three weekends.

Another setback on the DTNA this spring was the removal of over a mile of perimeter fence on a key section (section 5) in the northwest part of the DTNA. This fence was installed outside the original easement and, on demand of the landowner, the BLM removed the fence. The fence is scheduled to be moved in the spring of 1986. When this is accomplished, the plans are to exclude the private lands in question and approximately 40 acres more to reduce the length of fence needing replacement. This will remove approximately 200 acres from the DTNA and the Area of Critical Environmental Concern protection. Hopefully, these lands will not be subdivided for resale and can be acquired in the future to again add to the DTNA.

As another part of our steward-ship responsibilities on the DTNA, the Committee has undertaken a comprehensive photo-monitoring program. This year a photo-monitoring habitat status baseline was completed and a report prepared. This is a significant milestone against which future activity can be referenced. The report covers eleven sections of DTNA land; 144 photos were taken at 57 sites in these sections. Copies of the report were provided to the BLM and The Nature Conservancy.

The habitat management plan (HMP) for the DTNA was issued by the BLM in October 1979 and is in need of updating. The DTPC volunteered to provide the BLM with a comprehensive draft management plan for their use, which was accepted. The Committee prepared a draft plan which included a proposed Management Situation covering the Resource Summary, current impacts to the resource and potential impacts in the near future. In addition, it contains a monitoring program, goals, planned actions and implementation actions. This draft was delivered in June for the BLM's use.

Study plots in three sections of the DTNA near the visitor center were baselined in 1979. Because periodic census data is necessary to better manage the tortoise population, the BLM issued a contract to redo the tortoise census on these plots during the spring of this year. This data will be applicable to the updated HMP.

The DTPC has worked to establish and maintain the DTNA for the past 11 years. The primary government agency we deal with is the BLM. Both parties agreed this year that a formal Cooperative Management Agreement (CMA) for the Natural Area would be beneficial. A draft CMA was negotiated and ready for signing late in the year when the BLM asked for further modifications. They proposed to insert language which would seriously jeopardize the ability of the DTPC to accomplish completion of the DTNA private inholdings acquisition. This proposal was rejected by the Committee and the CMA is now on indefinite hold. This illustrates the difficulty of working with a government bureaucracy to reach an agreement.

The Kern River Gas Transmission Company approached the DTPC for inputs on routing their proposed pipeline from Wyoming to Bakersfield, California, to minimize impact on the tortoise. This proposal is from one of six companies competing to supply natural gas to be used in the thermal-enhanced recovery of heavy crude oil in the Kern County oil fields.

The Committee reviewed their proposed routing alternatives and provided information on tortoise density through the various areas. Further alternative routings were suggested for high impact areas and tortoise mitigation philosophy was discussed. It was encouraging to be able to work with this company on a proposed project before the EIR is released. It remains to be seen if anything comes of it.

The spring of 1985 was not one of the better wildflower years due to lack of winter rains. However, the Committee members were active on the Natural Area in the spring. The interpretive trails around the visitor center were maintained and seven public tours were given by DTPC guides to 120 visitors. In addition, we presented 69 programs on the tortoise to 2,250 people and the BLM presented another 19 programs to 1,040 people. We attended two tortoise shows in San Diego and three in the Los Angeles area for publicity and to sell fund raising products. The Natural Area has received further publicity in area newspapers, magazines and radio programs. An especially nice article appeared in the National Wildlife Association's November issue of Range Rick magazine. This was targeted at young people and has generated approximately 200 letters to the Committee and the BLM.

Lastly, the Committee supported the tortoise petition under study by U.S. Fish and Wildlife Service this past year. The Committee position was to list the desert tortoise throughout its range as threatened and as endangered in the Western Mojave Desert. We were satisfied with the published findings and hope this can lead to listing of the tortoise in the near future.

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MINING IN THE CDCA AS IT RELATES TO DESERT TORTOISE HABITAT

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This presentation is from the perspective of the Barstow Resource Area where conditions are in some ways typical and other ways not typical of the California Desert Conservation Area (CDCA) as a whole. As shown on Map No. 4 of the 1980 CDCA Plan, the Barstow and Needles Resource Areas have large areas of crucial tortoise habitat. The Indio and Ridgecrest Resource Areas have smaller areas of crucial habitat, whereas El Centro Resource Area has relatively little crucial habitat.

The Bureau of Land Management (BLM) mining and minerals program is divided into three main categories: locatable, leasable and salable minerals. Locatable minerals are under the 1872 Mining Law. Regulations found in 43 DFR 3809 give BLM limited discretion to control mining on public lands. It is the policy of the Department of the Interior to encourage the development of federal mineral resources and reclamation of disturbed lands. Under the mining laws a person has a statutory right, consistent with Departmental regulations, to go upon the open (unappropriated and unreserved) federal lands for the purpose of mineral prospecting, exploration development, extraction and other uses reasonably incident thereto. This statutory right carries with it the responsibility to assure that operations include adequate and responsible measures to prevent unnecessary or undue degradation of the federal lands and to provide for reasonable reclamation. "Unnecessary or undue degradation" means surface disturbance greater than what should normally result when an activity is being accomplished by a prudent operator in usual, customary, and proficient operations of similar character and taking into consideration the effects of operations on other resources and uses outside the area of operations.

The 3809 regulations provide for three levels of use. A different set of limitations is applied to each level of use commensurate with the degree of surface disturbance associated with each. These levels of use and the requirements which apply to each are as follows:

(1) Activities ordinarily resulting in only negligible disturbance of public lands and resources are considered to be casual use. Falling under this category would be activities not involving the use of mechanized earth moving equipment or explosives and which do not involve the use of motorized vehicles in areas designated as closed or limited to off-road vehicles. The degree of disturbance caused by weekend prospectors and part-time miners would generally fall under this level of use. Casual use activities require no notice or plan of operations.

(2) Mining activities such as exploration causing a disturbance of five acres or less per year in a project area require only that notice be given to the BLM authorized officer (usually the Area Manager) at least 15 days before commencing operations (but see exceptions in Number 3 below). No approval by the BLM of the proposed operation is required. The 15 day period is designed to give the BLM adequate time to inform the operator of other resource values in the area to which impacts should be avoided if possible.

(In the case of endangered or threatened species the operator must take such action as necessary to prevent adverse impacts to these species and their habitat.)

(3) Exploration or mining operations which will disturb over five acres per year or which will be conducted in the CDCA, in an Area of Critical Environmental Concern (ACEC), in a Wild and Scenic River area, in areas designated as "closed" or "limited" to off-road vehicle use, or in areas withdrawn from mining where valid existing mineral rights are being exercised require the filing of a plan of operations prior to commencing operations. The plan must describe the entire operation. The normal response time to a plan is 30 days. With three important exceptions, the authorized officer has a maximum of 90 days (30 days plus an additional specified period not to exceed 60 days if more time is required for review) in which to respond to the plan. One of these three exceptions involves compliance with Section 7 of the Endangered Species Act (ESA) of 1973, as amended. If it is determined that the mining operations, as outlined in the plan of operations, will have a possible effect on a federally listed endangered or threatened species, the ESA requires that BLM initiate and complete a Section 7 consultation with the U.S. Fish and Wildlife Service prior to approval of the plan of operations.

The requirement of Section 7 of the ESA that BLM (along with all other federal agencies) ensure that any action the BLM authorizes, funds, or carries out is not likely to jeopardize the continued existence of any endangered or threatened species, seems to be the only legal mandate by which the BLM may reject a plan of operations. Department of the Interior Solicitors have quite clearly determined that the ESA has in effect amended the 1872 Mining Law.

Prior to the listing of the desert tortoise as endangered (August 4, 1989) the degree of protection we could impose under the 3809 regulations was limited to the prevention of unnecessary or undue degradation. An example of unnecessary degradation would be; an operator constructing an access road through a high concentration of tortoise burrows if an alternate route could have served nearly as well by avoiding the sensitive area. On the other hand, this standard does not require the operator to avoid every tortoise burrow or avoid mining in areas of high tortoise density.

Now that the tortoise is listed as endangered by the U.S. fish and Wild life Service (USFWS), the BLM policy in dealing with plans of operations and notices has changed. Regarding plans of operations, if the proposed activity is in tortoise habitat, the staff Wildlife Biologist or a technician will make an on-the-ground survey and determine if it may effect individual tortoises or their habitat. If the field survey results in a "may effect" decision, consultation with the USFWS is required. If the site is already highly disturbed, informal consultation by telephone may be sufficient. Otherwise, formal consultation is normally required. A draft environmental assessment (EA) is prepared and is included with the consultation letter. Consultation is expected to require a minimum of 90 days. The USFWS then issues a Biological Opinion as to whether the proposed action would jeopardize the tortoise. Since, as the surface managing agency, we are required to conserve the species, mitigation usually includes compensation from the project proponent. Under this procedure the operator is required to compensate for the lost habitat by purchasing and providing private land of like habitat. The ratio of acreage compensation is determined by a standard formula.

Regarding notices, the BLM still has little control. Notices are not considered a federal action since the BLM authorization is not required. For this reason, only a brief environmental checklist is prepared. If the proposed operation falls within a Category 1, 2, or 3 habitat for the desert tortoise, a letter is sent to the operator warning him/her of penalties for "take" (to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or attempt to engage in any such conduct). Additionally, any "take" would constitute "unnecessary and undue degradation" under the 3809 and 3802 regulations. "Take" has also been interpreted by the courts as the destruction of any habitat occupied or required by an endangered species. Notice operators are also furnished a list of mitigating measures to assist them in avoiding take, but with the caveat that simply following these suggestions does not relieve them of legal responsibility under the ESA.

The Barstow Resource Areas receives between 60 and 75 plans and notices each year. The stipulations below are used by the Barstow Resource Area, although not all of these are used on every plan.

(1) Confine access to a single road or trail to reduce impacts brought about by road proliferation.

(2) Limit the speed of vehicles along the access route to 15 MPH, in order to prevent any adverse impacts to the desert tortoise.

(3) Any ore or tailings that are stockpiled should be stored in previously disturbed areas.

(4) Construct 2 1/2-foot-high dirt berms around all open pits and trenches to restrict wildlife access, or construct an earthen ramp no steeper that 35 degrees to provide a wildlife escape route.

(5) Any pits which could trap a tortoise should be filled in at the end of the project and inspected at least twice daily while they remain open. Trapped tortoises should be removed but not transported more than 150 feet.

(6) Backfill or cap all drill holes made under this plan of operation as soon as the necessary geologic information has been obtained.

(7) Recontour all piles and disturbed areas to blend with the surrounding terrain upon completion of mining activities.

(8) Scarify all compacted soils (except desert pavement) upon completion of mining activities. This may be accomplished by rippers, discs, or rakes.

(9) If cultural or paleontological resources are discovered during the course of mining operations, all work at the point of discovery will cease and the Barstow Resource Area Manager will be notified. Surface disturbance within 100 feet of the point of discovery is not authorized until a written notice to proceed is received by the operator from the Barstow Resource Area Manager.

(10) Remove and properly dispose of all trash, equipment, and waste upon termination of mining activities.

(11) All trash and food items shall be promptly contained and regularly removed from the project site to reduce the attractiveness to ravens and other tortoise predators.

(12) Allow no sampling and trucking from March 1 - July 1, nor from September 1 - November 1 (each year) when tortoises are most active.

(13) All domesticated animals shall be on a leash or confined within a fenced area when at the subject site to provide for wildlife and public safety.

(14) The site is not to be used for the storage of inoperable appliances, autos, or equipment.

(15) All storage of equipment, supplies, materials, ore, or any residue of the mining operation will be accomplished in a manner which minimizes surface disturbance.

(16) All operators shall maintain the site, structures, and other facilities of the operations in a safe and clear condition during any non-operating periods. The other facilities of the operations in a safe and clean condition during any non-operating periods. The operator will be required, after an extended period of non-operation for other than seasonal operations, to remove all structures, equipment, and other facilities and to reclaim the site of operations, unless he/she receives permission, in writing, from the authorized officer to do otherwise. For the purpose of 443 DFR 3909.3-7, an extended period of non-operation is considered to be one year.

(17) Written notification will be provided to the BLM within 30 days of completion of operations and reclamation by the operator.

(18) The operator must comply with all County, State, and Federal standards and regulations.

(19) Any proposed activity not authorized by this plan shall not proceed without prior approval of a plan amendment by this office.

ADDITIONAL MINING MITIGATION

The following mitigation should be considered as site specific or special stipulations to be applied when the plan or notice being reviewed so requires their ameliorating potential.

(1) To discourage wildlife access, blade dirt berms 18 inches or higher on both sides of the constructed road except where it crosses washes.

(2) Secure all explosives or toxic materials used on the site so as to prevent access to humans and wildlife.

(3) After testing or mining has been completed, blade the pit walls to a slope no steeper that 2:1 (run:rise).

(4) Seal all underground workings made under this plan of operations within 15 days after they are no longer in use.

(5) Approval of this plan of operations does not authorize the cutting of firewood on public lands.

(6) Any trench or pit greater than three feet in depth which is left open during operations shall be posted with an appropriate warning sign.

Most plans and notices are for assessment work and exploration with surface disturbance of less than an acre. About 100 plans and notices have been filed within crucial habitat for desert tortoises in the Barstow Resource Area. The vast majority of these are either in areas that have been previously disturbed, or are for exploration causing a minimum of surface disturbance.

Unlike the 1872 Mining Law, leasing and mineral material sales are discretionary. Thus, the BLM has the latitude to apply a wide range of mitigation measures, or to deny a lease or sale if deemed in the public interest. With the exception of Searles, Bristol, Danby and Cadiz dry lakes, most of the leasing activity in the CDCA is for oil and gas. Oil and gas leases range in size from 640 to 10,240 acres with an average of 2,000 to 5,000 acres.

Leasing activities in tortoise habitat, which may cause any impact to tortoises or their habitat requires an environmental assessment and consultation with the USFWS. Mitigation, if the project is authorized, might include compensation for acreage of like habitat, seasonal use restrictions, or no occupancy.

Since September 1989 it has been the BLM policy to require an EA prior to leasing. The checklist approach (categorical exclusion review) is no longer acceptable. In the last 8 to 10 years, the Barstow Resource Area has not received any applications for permit to drill (APD), nor any development activity on oil and gas leases.

Mineral material disposals of salable (common variety) minerals fall into one of two categories, Free Use Permits (to government or nonprofit organizations) or Material Sale Permits. The Barstow Resource Area has 13 free use permits and four mineral material sales under current authorization. Of this total, five are used yearly, seven are used occasionally, and five are seldom used. Only two of the permits are within crucial habitat areas for desert tortoises. One of these is an old rock quarry. The other is a sand pit which was already highly disturbed when the permit was issued. Fourteen of the permits are within an area of less than 50 tortoises per square mile, one is within an area of 50-100 tortoises per square mile, and two are within an area of over 100 tortoises per square mile. Of the later two permits, one has not been used since it was issued, and the other is the old rock quarry.

The area of surface disturbance within the permit areas ranges from less than 10 acres to as much as 80 acres with the average being closer to the smaller value. Environmental assessments are prepared for mineral material disposals involving more than 10 acres or over 100,000 cubic yards. For operations beneath these threshold values, a categorical exclusion review is usually adequate.

The following special provisions are typical of those used for free use permits in the Barstow Resource Area:

(1) Keep all excavations parallel to the natural contour as indicated in Exhibit A.

(2) Maintain vegetation buffer between excavation pits (See Exhibit B). Excavation pits shall be a maximum of 200 feet wide. The intervening vegetative buffer strips shall be a minimum of 25 feet wide.

(3) Stockpile the top 6 to 10 inches of surface soil prior to mining. The associated vegetation may be left with the topsoil or hauled off the site at the discretion of the permittee.

(4) Reclaim areas within the permit area prior to periods of non-use of 4 months or longer. This would minimize erosion and its possible negative effect on maintenance of Camp Rock Road.

(5) Redistribute stockpiled topsoil evenly over the recontoured areas and scarify.

(6) Maintain asphalt stockpile in one pile or a series of low windrows, height not to exceed 5 feet.

(7) All project activities shall be restricted to those times of the year when tortoises are the least active. Acceptable periods would be from July 1 through September 1 and October 1 through March 11.

(8) A tortoise-proof fence shall be constructed around the project site. Such a fence shall extend 18 inches above ground and 12 inches below ground. Where rock is on the surface, the lower 12 inches shall be folded out against the ground and in a direction away from the excavation. There would be one entrance. At the entrance the fence shall parallel the road for 50 feet and then flare out away from the road for 20 feet. This would reduce the amount of tortoises being able to move into the project area.

In summary, the mineral sales and leasing regulations provide for ample mitigation and protection of sensitive species such as the desert tortoise. Operations under the 1872 Mining Law are subject to much less control by the surface managing agency. With the exception of the Endangered Species Act, cultural resource laws, and lands under wilderness review, the standard for mitigating this activity is limited to that of "unnecessary or undue degradation." The majority of activity under the 1872 Mining Law is in previously disturbed areas, or is for exploration work with less than an acre of surface disturbance per plan or notice.

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GENETIC VARIATION IN MITOCHONDRIAL DNA OF THE DESERT TORTOISE, *GOPHERUS AGASSIZII*, IN CALIFORNIA

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ABSTRACT - Twenty-seven desert tortoises representing seven populations in California were assayed for mitochondrial DNA (mtDNA) genotype. Levels of genetic variation and geographic differentiation were remarkably low in comparison to other terrestrial vertebrate species studied to date. Tortoises from the Chuckwalla, Arrowhead, Chemehuevi, Superior, Kramer and Fremont sites (six of seven) represent a mtDNA clone, which indicates that they have shared a common female ancestor at some time in the recent past. Tortoises from the Ivanpah Valley were characterized by a distinct XbaI genotype that differs from the aforementioned populations by a single restriction site gain. Differentiation in the Ivanpah population exemplifies a recurrent pattern in mtDNA variation where genetic "breaks" are concordant with geographic barriers.

INTRODUCTION

A major problem in the development of desert lands is the destruction of wildlife habitat. For example, the Southern California Edison Company has faced requirements for mitigation of adverse effects on the desert tortoise (*Gopherus agassizii*) posed by construction activities in the Mojave Desert. The tortoise is of considerable social and biological importance in California and recent efforts to have the species listed as endangered by the U.S. Fish and Wildlife Service can only serve to intensify concerns for its well-being.

Relocation of tortoises to other areas has often been suggested as a mitigating action, but the biological consequences of this procedure are not known. The most important problem in relocation is the identification of a suitable receiving site. If an area is already at carrying capacity, the addition of new tortoises will not succeed. Other problems include possibly deleterious social interactions between relocated and resident animals, transmission of disease to residents, and genetic consequences of interbreeding among relocated and resident tortoises.

Mixing of genes has been cited as a potential complication factor in tortoise relocation (Berry 1973, 1975; Diemer 1984), although there are few data indicating the prospective gravity of the problem or even whether a problem exists. The first step towards understanding and/or predicting genetic consequences of interbreeding is to measure the degree of genetic differentiation among desert tortoise populations. To genetically characterize the desert tortoise in California, I examined restriction-site variation in mitochondrial DNA for 27 individuals collected throughout the species' range in the state.

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BACKGROUND

The central role of deoxyribonucleic acid (DNA) in genetic inheritance has long been recognized. DNA is composed of nucleotides containing one of the following bases: adenine (A), guanine (G), cytosine (C), or thymine (T). Most of the DNA in eukaryotic cells is apportioned into discrete structures called chromosomes, which are housed in the nucleus. Thus nuclear DNA is the major source of genetic material inherited from each parent in the process of normal sexual reproduction. Additionally, small amounts of DNA are found in the cell's respiratory organelles, the mitochondria. Mitochondrial DNA (mtDNA) is composed of the same nucleotides found in nuclear DNA; similarly, particular arrangements (or sequences) of these nucleotides form genes that code for specific products, e.g., proteins, ribosomal RNAs, etc.

In other respects, mtDNA is quite different from nuclear DNA. For example, the molecule itself is a small, closed circular piece of DNA that, among vertebrates, averages around 17,000 base pairs in length. By comparison some of the smaller nuclear genomes (chromosome sets) in animals contain 25,000 times as much DNA. Furthermore, mtDNA evolves at a rapid rate--some 5 to 10 times faster than nuclear DNA (Brown 1983). One explanation proposed for this accelerated evolutionary pace is a noted absence of the complex edit and repair mechanisms that maintain nuclear DNA (Brown 1983).

MtDNA is also characterized by maternal inheritance, and is transmitted from the female parent to her offspring through the egg cytoplasm. In a sense, mtDNA genotypes are perfectly heritable, unaltered by the processes of segregation and recombination that characterize nuclear genotypes (Lansman et al. 1981). It is this trait, coupled with the molecule's small size and rapid evolutionary rate, that makes mtDNA an attractive system for studies in evolution.

Analysis of mtDNA involves relatively new molecular techniques that are gaining popularity in a number of biological disciplines. One such approach entails "sequencing" the molecule directly; upon establishing a given point on the molecule, the number, kinds and specific arrangement (or sequence) of nucleotide bases composing the DNA are precisely identified. However, this is a laborious and expensive procedure not feasible for most population or evolutionary studies.

The limitations imposed by sequencing procedures can be overcome by employing a series of enzymes known as restriction endonucleases, which provide an indirect assessment of mtDNA variation. These enzymes "recognize" specific base sequences along a DNA strand and digest or cut the molecule whenever these sites are encountered. For example, the enzyme Bam HI operates specifically on the base sequence GGATTC and will cut DNA at any such sequence. Some enzymes recognize less specific sequences in which either of the purines (A, G) or pyrimidines (C, T) may occupy a particular point in the base sequence. For example, the enzyme HincII will cut any of the following sequences: GTCAAC, GTTAAC, and CTTGAC.

If a restriction endonuclease recognizes only one sequence site along the entire ring-shaped mtDNA molecule, then the cut molecule becomes a single linear fragment of DNA. If two sequence sites exist, the two cuts result in two fragments. Three sequence sites yield three fragments, and so on. MtDNA variation can then be gauged by analyzing fragment sizes to assess the number of shared fragments versus those that are distinct. The resulting degree of similarity or dissimilarity provides insight as to differentiation and evolution of the mtDNA molecules being compared.

Initially, mtDNA research centered on characterization at the molecular level, including studies of gene content, arrangement and function (Brown 1983). More recently, researchers have employed mtDNA analysis to explore phenomena in organismal evolution, documenting variation both within and among species. High levels of conspecific variation and differentiation in mtDNA have been reported in a number of terrestrial, freshwater and marine animals (Avise and Lansman 1983, Avise 1985). Often, mtDNA variation assumes distinct geographic patterns within species. Such patterning, according to Saunders et al. (1986), "...argues that, for many species, dispersal and gene flow have not overridden historical influences on population subdivision."

In this study, mtDNA differentiation is examined in seven populations of the desert tortoise distributed over the range of the species in California. The purpose is to determine the degree to which these populations can be distinguished by mtDNA variation.

METHODS

Twenty-seven desert tortoises were collected at seven sites in California (Table 1). Appendix I provides further information as to specific collection localities. Animals were marked for individual recognition and shipped live to the Savannah River Ecology Laboratory in Aiken, South Carolina. Fresh heart and liver tissues from individual tortoises were combined to yield sufficient quantities of mtDNA. Tissues were prepared according to the procedure of Lansman et al. (1981), which is outlined, with some modification, herein.

Table 1. Site localities and samples sizes (n) for seven California populations of *Gopherus agassizii.*

Population	Site	n
1	Chuckwalla Mountains (Colorado Desert)	3
2	Arrowhead Junction (eastern Mojave Desert)	4
3	Chemehuevi Valley (eastern Mojave Desert)	4
4	Ivanpah Valley (northeastern Mojave Desert)	4
5	Superior Valley (central Mojave Desert)	4
6	Kramer Junction (western Mojave Desert)	4
7	Fremont Valley (western Mojave Desert)	4

Tissue samples were minced with scissors in 30 ml of MSB-EDTA-Ca^{++} buffer (pH 7.5) prior to final homogenization with a motor-driven glass teflon homogenizer. The buffered homogenate was subjected to two centrifugation spins at 700 x g for 5 min in a swinging bucket rotor to pellet unwanted cellular debris. Following the second spin, the supernatant was subjected to a 20-min centrifugation spin at 20,000 x g. This supernatant was then discarded and the pellet, containing primarily mitochondria, was washed by resuspension in 15 ml of MSB-EDTA and recentrifugation at 20,000 x g for 20 min.

Mitochondria were resuspended in 3 ml of STE and lysed by the addition of 0.15 ml of 25% SDS. Closed circular mtDNA was then purified by CsCl/ethidium bromide gradient centrifugation in a Beckman SW50.1 rotor at 40,000 rpm (160,000 x g) for 36 hr. CsCl, ethidium bromide and excess EDTA were removed by dialysis against 1M sodium acetate, 50 mM tris-HC1 and 10mM EDTA (pH 8.0) at room temperature for 24 hr. and then against TE for 24 hr. at 4° C. Dialyzed samples were stored at -70° C until subject to restriction endonuclease digestion.

Digestion were accomplished by 17 restriction endonuclease according to conditions recommended by the vendor, New England Biolabs (Table 2). For each enzyme, 4 ml of sample were used per digestion.

Table 2. Battery of the 17 restriction endonucleases (with their recognition sequences) employed in the mtDNA assay.

Restriction Endonuclease	Recognition Sequence
AvaI[1]	CPyCGPuG[2]
BamHI	GGATTC
BclI[1]	TGATCA
BglI[1]	CCCGGC
BglII[1]	AGATCT
BstEII	GGTACC
ClaI[1]	ATCGAT
EcoRI[1]	GAATTC
HincII[1]	GTPuPuAC[2]
HindIII[1]	AAGCTT
KpnI	GGTACC
NdeI[1]	CATATG
PstI	CTGCAG
PvuII[1]	CAGCTG
SacI[1]	GAGCTC
StuI[1]	AGGCCT
XbaI[1]	TCTAGA

[1] Denotes informative enzymes (those yielding more than one cut for populations surveyed).
[2] Py and Pu respectively denote that either pyrimidine (C or T) or either purine (A or G) are recognized at these given sites.

Digestion fragments were end-labeled with the appropriate α ^{32}P-labeled nucleotide(s) and electrophoresed through 1% agarose gels. Digestion profiles were revealed by autoradiography of vacuum-dried gels, and fragment sizes were compared against the 1-kilobase ladder standard available through Bethesda Research Laboratories.

The fraction of homologous fragments was calculated for all pairwise comparisons of the 27 individuals by $F = 2N_{XY} / (N_X + N_Y)$, where N_X and N_Y are the numbers of fragments in genotypes X and Y, and N_{XY} is the number of fragments shared. Values of F were converted to estimates of mtDNA nucleotide sequence divergence, *P*, following Nei and Li (1979).

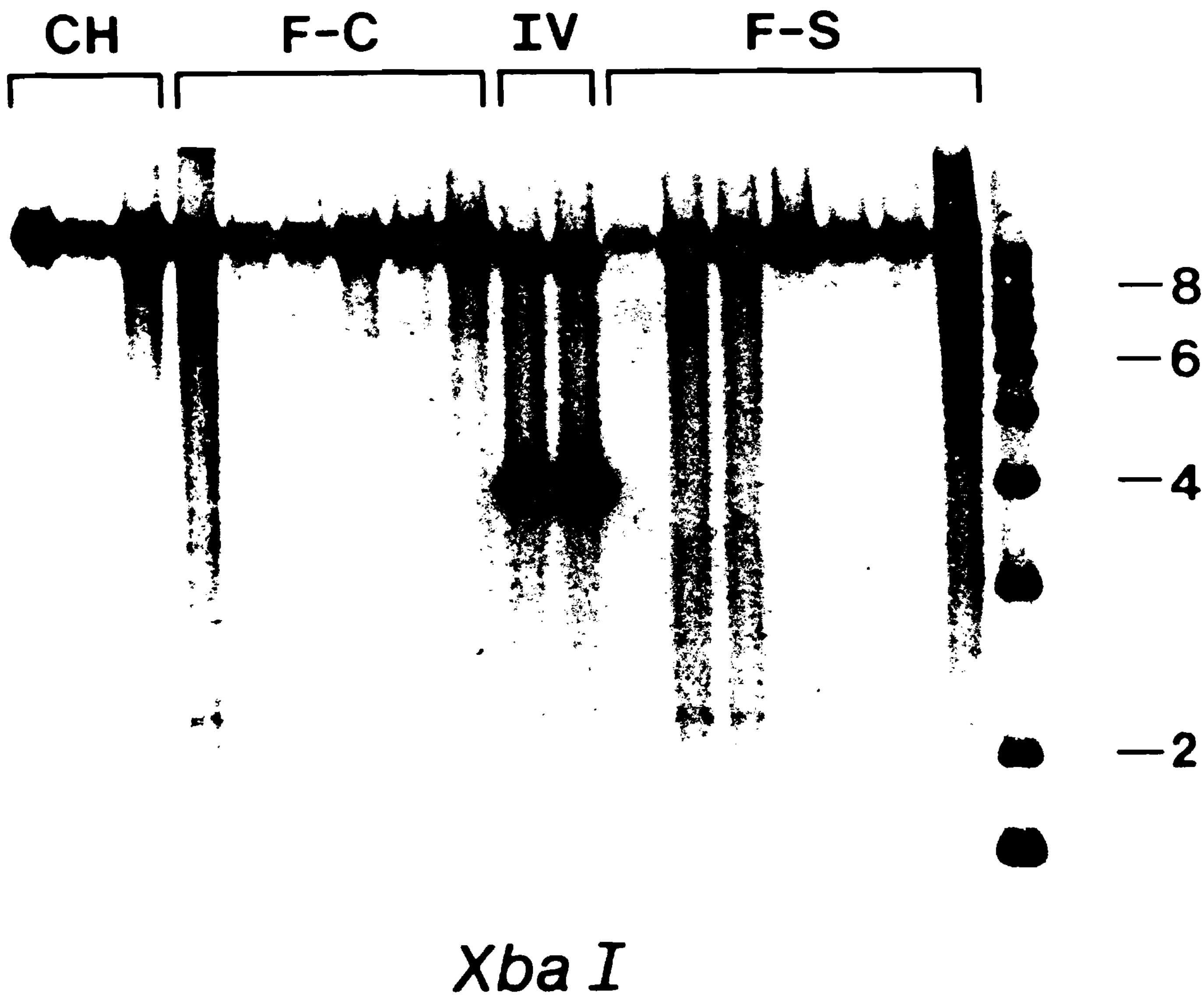

Figure 1. Autoradiograph of an XbaI digest of mtDNA from desert tortoises collected in the Chuckwalla area (CH), the Fenner-Chemehuevi area (F-C), Ivanpah Valley (IV), and the Fremont-Stoddard area (F-S). Each lane represents an individual tortoise except for the lane on the far right, which is a standard with fragments of known kilobase lengths. Note that the Ivanpah digestion pattern (XbaI "D") consists of two fragments and is distinct from the common, one-fragment pattern (XbaI "C").

RESULTS AND DISCUSSION

Digestion profiles of 13 informative restriction endonucleases yielded a total of 42 mtDNA restriction fragments (Table 2). The other enzymes (BamHI, BstEII KpnI and PstI) were uninformative in that they produced either one or no cuts in the mtDNA for all assayed individuals. Levels of fragment homology across populations were remarkably high. In fact, digestion profiles for 11 of the 13 informative enzymes were identical for all 27 individuals. Two digestion profiles were produced by XbaI, (Figure 1). Tortoises from Ivanpah Valley were characterized by a distinct profile designated XbaI "D", whereas the common profile, XbaI "C", was observed in the 23 remaining *Gopherus*. The XbaI "D" genotype (with a two-fragment digestion profile) differs from that of XbaI "C" (a one fragment profile) by a single restriction site gain. Variant genotypes may also exist for StuI, which yielded one or more multi-fragment digestion profiles. One tortoise from Superior Valley and another from Fremont Valley appear to differ from other individuals by a single restriction site gain (13 fragments vs. 11 fragments). Unfortunately, the fragments in question are quite small (< 500 base pairs in length) and subject to poor resolution. Therefore, interpretation of the StuI fragment data is at best equivocal.

Differentiation with regard to the Ivanpah population exemplifies a recurrent pattern in mtDNA variation where genetic "breaks" are concordant with geographic barriers (Avise 1985). The valley lies between the Ivanpah Mountains to the west and the New York Mountains to the southeast (Turner et al. 1984), which may function as genetic barriers to other populations west and south. Although the XbaI "D" genotype serves as a genetic marker that readily distinguishes Ivanpah tortoises from the other populations, the mtDNA genetic distance is still quite small ($p = 0.0021$). Nonetheless, the Ivanpah population appears to be a distinct assemblage, differing from other California populations in its matriarchal genealogy. This distinction was corroborated allozymically by Jennings (1985), who observed a rare allele of glucose phosphate isomerase (GPI) in the Ivanpah population and two adjacent Nevada samples.

Of interest is the high degree of similarity among the six remaining populations, where digestion profiles were identical for each restriction endonuclease employed. These digestion profiles, i.e., one per endonuclease, can be collectively viewed as a "composite genotype" for each animal. From this perspective the tortoises from Chuckwalla, Arrowhead, Chemehuevi, Superior, Kramer and Fremont sites represent a single mtDNA or genotype clone. Tortoises belonging to this clone must have shared a common female ancestor at some time in the past. That the Mojave and Colorado deserts likely formed continuous and relatively uniform habitats in historic times may have some bearing on the observed clonal pattern. However, low mtDNA variation should not be construed as genetic identity. MtDNA is a distinct, genetic system operating separately from nuclear DNA. Thus, low levels of mtDNA variability do not necessarily indicate low levels of nuclear genes that may impart adaption to local environments. For example, using allozyme analysis, Buth (pers. comm.) demonstrated that tortoises from Chemehuevi Valley and Kramer Junction (identical in mtDNA genotype) were significantly different in allelic frequencies and distribution.

Collectively, the allozyme and mtDNA data provide some insight as to proper management of tortoise populations in California. The Ivanpah population appears to be genetically distinct lineage and should be managed as such. Relocation of tortoises from one site to another within Ivanpah Valley would probably do little to disrupt genetic structure. However, the movement of tortoises into or outside the valley is not advised. Overall, prudence should be exercised in any relocation, and attempts made to relocate in suitable habitats adjacent to impacted areas. Although further mtDNA analysis would probably yield little information concerning relocation strategies in California, a nondestructive allozyme assay (involving blood samples) could be of value in attempting to screen rare alleles in populations considered for relocation.

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Appendix I. Tortoises collected for mitochondrial DNA analysis in California in 1985

General Locality	Date	Tortoises	Township	Range	Section
Fremont Valley, western Mojave Desert 11 km W Randsburg, San Bernardino County.					
	June 12	2 females	30S	39E	2
		1 female	29S	39E	27
		1 female	29S	39E	34
Kramer Junction, western Mojave Desert 27 km NW Victorville, San Bernardino County.					
	June 9	1 male 9N	5W	12	
		1 male 9N	5W	11	
		1 female	9N	5W	11
		1 female	9N	5W	14
Superior Valley, central Mojave Desert 24 km WNW Barstow, San Bernardino County.					
	June 13	1 female	32S	45E	35
		1 male 11N	3W	1	
		1 male 11N	3W	13	
		1 unsexed	11N	3W	1
Ivanpah Valley, northeastern Mojave Desert 24 km W Nipton, San Bernardino County.					
	June 8	1 male 17N	14E	26	
		1 female	15N	16E	8
		1 female	15N	16E	18
		1 unsexed	7N	14E	27
Arrowhead Junction, eastern Mojave Desert 29 km NW Needles, San Bernardino County.					
	June 6	1 female	10N	20E	13
		1 male 10N	20E	13	
	June 7	1 unsexed	10N	20E	13
		1 unsexed	10N	20E	13
Chemehuevi Valley, eastern Mojave Desert 24 km S Needles, San Bernardino County.					
	May 16	1 female	5N	22E	23
	May 22	1 female	6N	22E	17
	May 23	1 female	7N	21E	35
	May 29	1 male 6N	21E	1	
Chuckwalla Mountains, Colorado Desert 8 km S Desert Center, Riverside County.					
	June 5	3 females	5S	15E	31

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ENERGY, LIPIDS, AND REPRODUCTIVE OUTPUT IN THE DESERT TORTOISE (*GOPHERUS AGASSIZII*): A RESEARCH PROPOSAL

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ABSTRACT - Desert tortoises, (*Gopherus agassizii*), experience extreme seasonal changes in food and water availability. Without competitors, desert tortoises may still experience periods when energy is limited. Although many reptiles use lipid or fat reserves to ameliorate periods of low food availability, it is not known if this occurs in desert tortoises. However, knowledge of the importance and timing of lipid storage and allocation of this energy to reproduction and growth could be useful to our conservation efforts. I will determine the importance of lipid energy reserves to growth and reproduction, in an energy budget for female desert tortoises. Metabolic costs will be measured using the doubly labeled water method, and reproductive output will be determined from x-ray prints of gravid females. Lipid energy reserves will be measured using the absorption of cyclopropane gas. Fat-free somatic growth will be estimated using the relationship of fat-free somatic energy to carapace length.

INTRODUCTION

The concept that energy is a finite and limiting resource is central to the field of ecology and is the foundation of many biological theories (Congdon et al. 1982, Nagy 1983b). In deserts, the low primary productivity and unpredictable nature of food availability places an energetic stress on desert animals. This is especially true for large desert herbivores (Louw and Seely 1982) like the desert tortoise (*Gopherus agassizii*). Throughout much of the range of the desert tortoise, grazing livestock reduce the already low levels of forage available to the desert tortoise (Woodbury and Hardy 1948, Berry 1978, Luckenbach 1982). Mayhew (1966), Hoddenbach and Turner (1968), Turner et al. (1982, 1984) and many other researchers (see Turner et al. 1982) have shown that reproduction and growth in desert animals is partially dependent upon the amounts and distribution of annual precipitation. Yet, Turner et al. (1984) and Turner and Berry (pers. comm.) have evidence which suggests that after winters with little or no rainfall, the reproductive output of desert tortoises may not suffer as much as that of other desert reptiles. Desert tortoises could be storing lipids (fat) before winter and using this energy reserve for producing offspring during the ensuing spring (Turner et al. 1984). I will investigate the storage of lipids (fat) in desert tortoises and determine the energetic contribution lipid reserves make towards reproduction and growth.

Previous studies have investigated the desert tortoise's behavioral and physiological adaptions to survive food and water limitations (Dantzler and Schmidt-Nielsen 1966, Minnich 1982, Medica et al. 1980, Turner et al. 1984, Turner and Berry 1984, Nagy and Medica 1986, and many others, see Hohman, et al. 1980), but little is known about the importance of lipid energy stores to the survival and reproduction of desert tortoises. Using lipid reserves to buffer periods of

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fluctuating resources and harsh environmental conditions is not a new idea (see Derickson 1976 for review). Several studies have illustrated that reptiles can store lipids and may use these energy reserves later for over-wintering costs, reproductive costs, or both (Hahn and Tinkle 1965, Derickson 1976, Pond 1978, Congdon et al. 1982, Congdon and Tinkle 1982, McPherson and Marion 1982, Nagy 1983b, Long 1985). Although some aquatic and semi-aquatic turtles store up to 39% of their total dry mass as lipids (Congdon and Tinkle 1982, McPherson and Marion 1982, Rose and Judd 1982, Long 1985), tortoises seem to store less lipid. The Aldabran giant tortoise (*Geochelone gigantea*) and Berlandier's tortoise (*Gopherus berlandieri*) store, respectively, 2 and 3.5 percent of their dry mass as lipids (Hamilton and Coe 1982, Rose and Judd 1982).

Very little is known about the desert tortoise's ability to store and utilize lipids. Woodbury and Hardy (1948) suggested that desert tortoises store lipids during the spring and autumn for use during the summer and winter dormancy periods. However, data from energy budgets do not necessarily support this idea. Positive energy balance in an energy budget indicates that basic metabolic needs are met and surplus energy is available for lipid storage, reproductive production (or output), or fat-free somatic growth. Marlow (1979) found that western Mojave tortoises achieved positive energy balance only during the spring. Nagy and Medica (1986) found that eastern Mojave desert tortoises achieved positive energy balance only during the summer and fall months. The rainfall paradigm of the Mojave Desert may partially explain the differences in these energy budgets. The southeastern areas of the Mojave typically receive winter and summer rainfall whereas the western Mojave typically receives only winter rainfall (Luckenbach 1982). Nonetheless, these energy budgets have not measured the energy allocated to each of these components: storage, reproduction, and fat-free somatic growth. A complete energy budget provides quantitative information regarding the energy allocated to these components. This information is ecologically relevant and may be critical to our conservation efforts. When deciding whether or not to graze livestock in an area, relocate tortoises, or improve tortoise habitat, these energy requirements should be considered.

In this study, complete energy budgets of female desert tortoises will be measured to determine the importance of lipids to reproduction and growth. The metabolic rates of free ranging female tortoises will be measured using doubly labeled water (Nagy 1980, Nagy and Medica 1986). Reproductive output will be measured from x-ray prints of gravid females (Gibbons and Greene 1979, Turner and Berry 1984). Lipid energy reserves and somatic growth will be measured using in vivo body composition techniques. These body composition techniques minimize the need to sacrifice tortoises and provide detailed information regarding individual energy requirements.

From this energy budget, there are a few major questions which may be addressed:

(1) What time of the year do females store lipids as energy reserves?

(2) How much lipid energy is stored?

(3) How much energy is allocated to reproduction?

(4) What is the relative contribution by lipid energy reserves to reproductive output?

(5) Is there variation in the reproductive output and lipid storage of females?

From this basic information, we can determine the effects that grazing livestock have upon the energy requirements of tortoises.

MATERIALS AND METHODS

The rates of energy flux through the compartments of the energy budget will be measured. The energy budget will be partitioned as follows (Figure 1). Energy taken from the environment is termed ingested energy. Since organisms are not 100 percent efficient at assimilating and using the ingested energy, some energy returns to the environment as urine and feces. Ingested energy minus fecal and urinary energy efflux equals the metabolizable energy flow. Metabolizable energy is comprised of respiration costs (e.g. costs of maintenance, activity, temperature regulation, and digestion), changes in lipid (fat) content, reproductive output (as offspring), and fat-free somatic growth.

Rates of energy ingestion will be estimated from rates of sodium-22 turnover (Green 1978, Green and Eberhard 1979, Green et al. 1984), diet analyses, and field observations of feeding tortoises. Fecal and urinary energy flux will be estimated using the metabolic efficiency determined from feeding experiments. Metabolizable energy flow will be equal to the sum of respiration, reproductive, storage, and growth processes.

Respiration or metabolic costs will be measured using the doubly labeled water technique (Nagy 1980, Nagy and Medica 1986). The metabolic rates will be determined from the rates of tritium and oxygen-18 turnover of females. Oxygen-18 is a stable isotope and tritium is a relatively safe, soft-beta emitting isotope of hydrogen with a maximum radiation distance of less than 1 mm (Nagy 1983a, Nagy and Medica 1986). Every two weeks during the active season, a small volume (approximately 3.0 ml/kg) of labeled water will be injected intraperitoneally (Nagy and Medica 1986). After equilibration of the isotopes, a small blood sample (.2 ml) will be collected from a brachial or scapular vein (Ashley 1955, Avery and Vitt 1984). During the rest of the year, tortoises will be injected and blood samples will be taken on a monthly basis. The blood samples will be will be returned to UCLA for analysis of tritium and oxygen-18 levels. It will be necessary to remove six tortoises from populations nearby, to UCLA for feeding experiments. From these feeding experiments, assimilation efficiency, metabolic efficiency, and the factor for converting field metabolic rates (as carbon dioxide production) to rates of energy metabolism will be determined (Nagy 1983a, 1983b). Multiple regressions of field metabolic rates correlated with body size and growth rates will be used to measure the metabolic costs associated with reproductive production or growth (Nagy 1983b) and somatic growth.

Reproductive production includes the energy allocated to eggs. This energy requirement will be quantified from x-ray prints of gravid females, and measurements of egg composition and energy content.

Energy flux through lipid reserves will be measured as the difference in total lipid energy content of females, from one recapture to the next. Lipid content will be measured, <u>in vivo</u>, by monitoring the absorption of a lipid-soluble gas, cyclopropane. At relatively high concentrations (greater than 5 percent) cyclopropane is an anesthetic (Robbins 1958). However, concentrations below the anesthetic level will be used (less than 1 percent). A tortoise inside a chamber with a known amount of cyclopropane gas, will absorb some of the cyclopropane until the gas reaches equilibrium concentrations. A sample of the chamber gas is then analyzed for cyclopropane concentration from which the animal's lipid content will be determined. Solubility coefficients for lipid and non-lipid materials are necessary for this calculation. Lesser et al. (1952) used rats to demonstrate that this method is accurate to within 5 percent of the actual fat content.

Growth of somatic tissues will be measured as the energetic gain in fat-free somatic tissues over each recapture interval. A regression equation relating fat-free somatic energy to carapace length will be calculated from analysis of tortoise carcasses. The fat-free somatic energy content of live tortoises will be estimated from this regression and the carapace length of live tortoises.

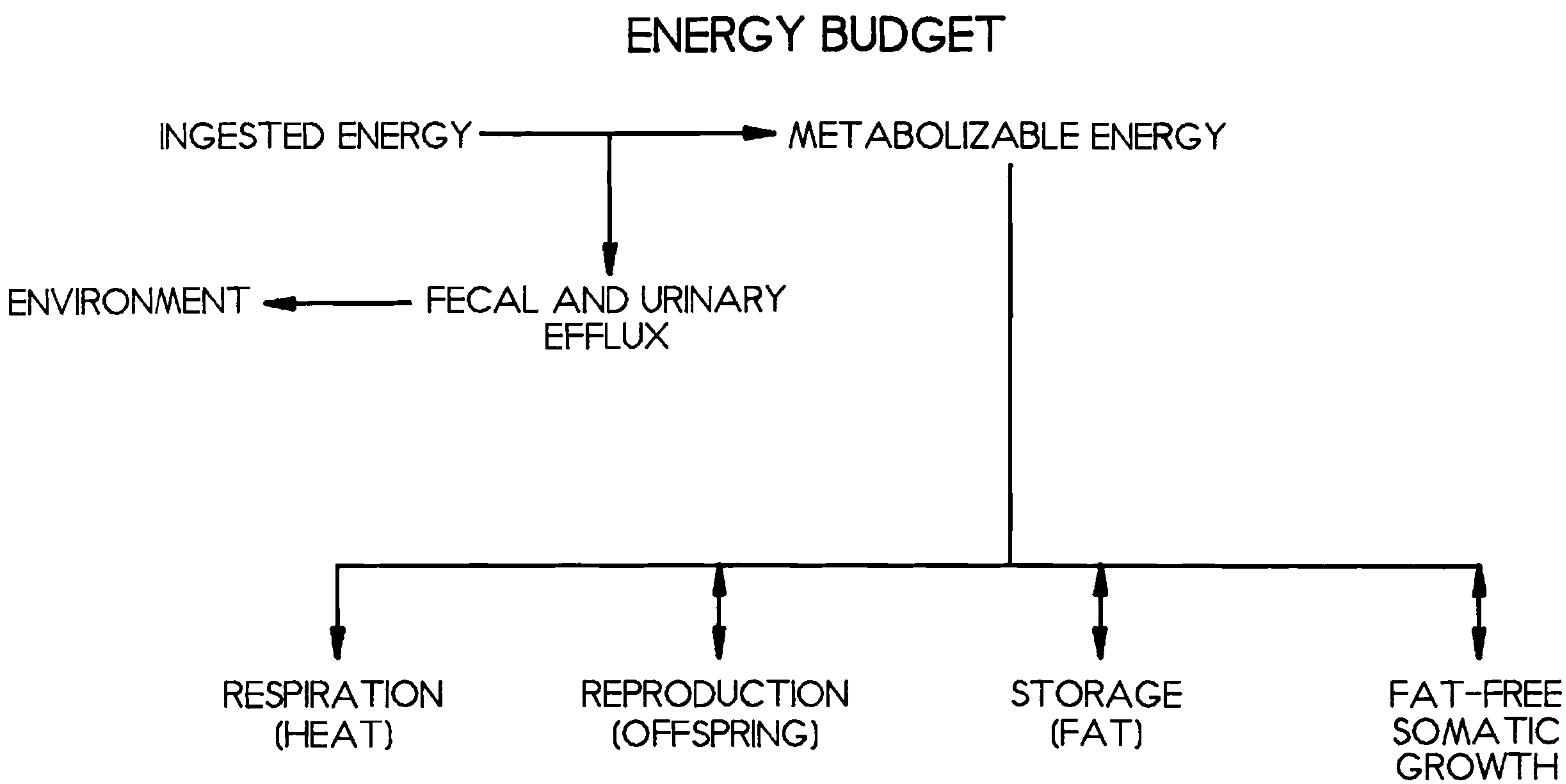

Figure 1. The energy budget is partitioned into the components shown. The energy flux through each compartment, except Environment, will be measured.

I have the remains of thirty-five tortoises from last year's genetic studies on desert tortoises. The energy content and solubility coefficients of tortoise tissues or materials (e.g. eggs and lipids) will be measured from these carcasses. Also, the regression of fat-free somatic energy to carapace length will be determined from these carcasses. However, to test for seasonal differences in the relationship of fat-free somatic energy to carapace length, it will be necessary to collect a minimum of six carcasses during the spring and six carcasses during the summer. Carcasses from road kills, or from tortoises which cannot be rehabilitated or released into the wild will be used before any live animals from areas nearby are collected for carcass analysis.

Although this project requires a commitment of tortoises to be sacrificed, the remainder of this project is noninvasive. If this energy budget were determined ten years ago, the standard procedure of measuring lipid content, reproductive output, and growth would require periodic collection of tortoises for carcass analysis. At a rate of ten carcasses every two weeks during the spring and 10 carcasses monthly for the other eight months, a minimum of 210 tortoises would have been sacrificed. However, using current in vivo techniques, the number of tortoises to be sacrificed is about 12. Additionally, current in vivo methods allow us to gather detailed information on the storage, reproductive, and growth requirements of individuals. The simple carcass analysis techniques provide only the average values of these energy requirements. This additional level of information will provide further insight into how desert tortoises cope with their environment.

Knowledge of these energy requirements of tortoises may be critical for the success of management techniques such as regulation of livestock grazing, relocation of tortoises, or habitat improvement. From the fundamental knowledge of the desert tortoise's energy requirements, we may begin to answer whether sufficient resources are available for their survival and reproduction.

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CHANGES IN DESERT TORTOISE POPULATIONS AT FOUR STUDY SITES IN CALIFORNIA[1]

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ABSTRACT - Data were collected on population attributes of desert tortoises (*Xerobates agassizii*) at four sites in California between 1977 and 1985. One site in the western Mojave Desert, Fremont Peak, was sampled three times (1977, 1980, and 1985) over a 9-yr period. The population density of adults and subadults declined from 27/km^2 in 1980 to 15/km^2 in 1985. The size-age class distribution shifted significantly ($P < 0.05$) between 1977 and 1985, to favor adults. The annualized mortality rate of subadults and adults was estimated at 4.8%/yr between 1973 and 1985. Gunshots, vandalism, and vehicle kills accounted for 20.0-23.1% of deaths between 1973 and 1985.

At Kramer Hills, a second site in the western Mojave Desert, the population was sampled once in 1980 and again in 1982. Densities did not change significantly. The annualized mortality rate of subadults and adults was estimated at 2.9%/yr for the 6-yr period between 1976 and 1982. Gunshots, vandalism, and vehicle kills accounted for 16.1-27.3% of deaths.

Chemehuevi Wash and Chuckwalla Bench, sites in the Colorado Desert, were sampled in 1979 and again in 1982. They also showed no significant changes in densities. Annualized mortality rates of subadults and adults were lower than for the western Mojave sites, 2.2% for the 7.5-yr period between 1975 and mid-1982 for Chemehuevi Wash and 2.3% for the 9.5-yr interval between 1973 and mid-1982 for Chuckwalla Bench. Gunshot and vehicle kills were reported at both sites but were lower in frequency than at the western Mojave Desert sites.

[1] A few figures for population densities, study plot size, and mortality rates have changed slightly for several reasons, including corrections to the computer program for estimating densities, re-evaluation of plot size, and discovery of additional carcasses. The figures herein are 1990 corrections.

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Mortality rates were higher for all study sites than at Goffs, a relatively undisturbed site in the eastern Mojave Desert (Turner and Berry 1984b). All four sites experienced damage from unauthorized off-road vehicle use.

INTRODUCTION

Between 1977 and 1980, the U.S. Bureau of Land Management (BLM) established 25 baseline study sites to determine attributes of desert tortoise (*Xerobates agassizii*) populations in California (Berry 1984a). In 1980, 16 of the sites were selected for a long-term monitoring program (Foreman et al. 1986). The original plan was to survey each site at three-year intervals and to collect data on population densities, age-class structure, sex ratios, and mortality rates, and on changes in habitat. Due to budget limitations, intervals between surveys shifted to five or more years.

This paper describes results of initial baseline and monitoring studies at four sites--Fremont Peak, Kramer Hills, Chemehuevi Wash, and Chuckwalla Bench. The Fremont Peak and Kramer Hills sites are in the western Mojave Desert in the Fremont-Stoddard desert tortoise crucial habitat (U.S. BLM 1980, Berry 1984a). Chemehuevi Wash is in the northeastern Colorado Desert in the Fenner-Chemehuevi crucial habitat, and Chuckwalla Bench is in the Colorado Desert in the Chuckwalla crucial habitat.

METHODS

Locations and site descriptions of the four study sites--Fremont Peak (Site 5), Kramer Hills (Site 7), Chemehuevi Wash and Valley (Site 20), and Chuckwalla Bench (Site 23)--are in Berry (1984b). Sites generally were surveyed using 30- and 60-day census techniques (Berry 1984c) at two- to three-year intervals (Table 1). For the low density population at Fremont Peak, three censuses were selected for analysis: 15-day census in 1977, 30-day census in 1980, and 60-day census in 1985. Only one Fremont Peak plot, Site 5 in Sec. 34, was used for the analysis (data from the two Fremont Peak plots, Sites 5 and 6, were combined and analyzed as a unit in Berry [1984a, 1984c]). Because the other three sites have moderate to high density populations, only 60-day censuses were used in the analysis. Considerable survey time is necessary to adequately cover plots with such densities (Berry 1984c). With the exception of numbers of census days, data were collected in the same way on each site. Each tortoise encountered was marked, measured for carapace length (CL), weighed, and its location plotted by date on grids 161 m x 161 m. All remains were collected, assigned a number, and their locations plotted on the grids. Data were recorded on human uses (visitor use, hunting, shooting, vehicle use, sheep grazing, etc.) and on signs of such use.

Live and dead tortoises were assigned to six size-age classes: juvenile 1 (< 60 mm CL), juvenile 2 (60-99 mm CL), immature 1 (100-139 mm CL), immature 2 (140-179 mm CL), subadult (180-207 mm CL), and adult (≥ 208 mm CL) (Turner and Berry 1984a). For purposes of Chi-square analysis of size-age class distribution, tortoises were grouped in four classes: juvenile, immature, subadult, and adult. Densities for the Fremont Peak site were estimated using the simplified Lincoln Index, because the sample sizes were very low. Densities for Kramer, Chemehuevi Wash, and Chuckwalla Bench were estimated with the Stratified Lincoln Index (SLI) (Overton 1971). For the SLI, tortoises were grouped into five size-age classes: juvenile, immature 1, immature 2, subadult, and adult. Then they were sorted by capture-recapture events into three groups:

captured only in the first 30 census days, captured only in the second 30 census days, and captured in both 30-day census periods. Sex ratios were evaluated using the Z statistic (Turner and Berry 1984b). Statistical tests were considered significant at $P < 0.05$.

Table 1. Surveys undertaken on four desert tortoise study sites in California (from Berry 1984c).

Site no.	Site name	Year	Plot size (km^2)	Census type
5	Fremont Peak	1977	2.59	ca. 15 day-spring census
		1978	2.59	3-4 days in spring
		1979	2.59	10-day fall census
		1980	2.59	30-day spring census
		1985	2.59	60-day spring census
7	Kramer Hills	1980	2.59	60-day spring census
		1982	2.59	60-day spring census
20	Chemehuevi Wash	1977	5.2	30-day spring census
		1978	5.2	7 days in spring
		1979	4.7	60-day spring census
		1979	4.7	20-day fall census
		1982	4.7	60-day spring census
23	Chuckwalla Bench	1977	2.59	30-day spring census
		1978	2.59	7 days in spring
		1979	3.37	60-day spring census
		1979	3.37	20-day fall census
		1982	2.59	60-day spring census

For each carcass, estimates were made of time of death and carapace length. Time of death was estimated using keys and figures for carcass deterioration in Berry and Woodman (1984) and Woodman and Berry (1984), respectively. Only tortoises considered dead $\leq$ 4 years at time of collection were used in the analysis. Carapace lengths for partial or disarticulated remains were estimated using one or more of 25 regression equations of scute size on carapace length (Berry and Woodman 1984). Annualized mortality rates were calculated for adults and subadults using the formula:

$$M = 1 - e^{-ta} \qquad (1)$$

where t is number of years and a is annual survivorship. Estimates of annualized mortality rates were confined to subadults and adults, because carcasses of these size classes persist longer than those of smaller tortoises (Woodman and Berry 1984). Where possible, each carcass was assigned a cause of death, e.g., vehicle kill, gunshot, predator (canid, raven), etc. See Berry (1985, 1986) for methods of determining raven and gunshot deaths, respectively.

Data were collected on cover of annual plants using the canopy coverage method of Daubenmire (1959). Annuals were sampled with 0.1 m^2 quadrats along one or more transect lines. Data on biomass (dry weight) were collected for some, but not all years.

RESULTS

Fremont Peak Study Site

Population Attributes

Although survey days increased from 15 in 1977 to 30 in 1980 and 60 in 1985, numbers of tortoises registered/survey day declined for each census year. Thirty-two tortoises (2.1/survey day) were registered in 1977, 43 (1.4/survey day) in 1980, and 37 (0.61/survey day) in 1985. Using the simple Lincoln Index, densities of subadults and adults were estimated at 27/km^2 in 1980 compared with 15/km^2 in 1985 (densities were not estimated for 1977 because of insufficient survey time and plot coverage).

Table 2. Size-age class distribution of registered desert tortoises at the Fremont Peak study site in 1977, 1980, and 1985.

Size-age class	Number of registered tortoises (% of total registered) 1979	1980	1985
Juvenile 1 and 2	1 (3.1)	5 (11.5)	0 (0)
Immature 1 and 2	14 (43.8)	11 (25.6)	4 (10.8)
Subadult	5 (15.6)	5 (11.6)	0 (0)
Adult 1 and 2	12 (37.5)	22 (51.2)	33 (89.2)
Totals	32 (100.0)	43 (99.9)	37 (100.0)

Table 3. Results of Chi Square tests comparing size-age class distributions for four desert tortoise study sites in different years. Data from each site were grouped into four size-age classes for the analysis--juvenile, immature, subadult, and adult.

Site no.	Site name	Years	X^2	$P < 0.05$
5	Fremont Peak	1977, 1980	4.45	no
		1980, 1985	15.10	yes
		1977, 1985	21.10	yes
7	Kramer Hills	1980, 1982	8.12	yes
20	Chemehuevi Wash	1979, 1982	2.31	no
23	Chuckwalla Bench	1979, 1982	8.15	yes

Between 1977 and 1985, the size-age class distribution of the population shifted significantly (Tables 2 and 3). Comparisons were made between size-age class structure in 1977 and 1980, 1977 and 1985, and 1980 and 1985. Differences were significant between 1977 and 1985 and 1980 and 1985, but not between 1977 and 1980. The trends showed increasing proportions of adults in the 1980 and 1985 samples. When proportions of adult (≥ 208 mm CL) and nonadult tortoises were compared for the three census years using Chi-square analysis, significant differences also were apparent (Table 4). Sex ratios for adults and subadults did not differ significantly from expected 1:1 ratios in any of the three census years (Table 5), however.

Table 4. Comparisons of proportions of adult (≥ 208 mm carapace length) and nonadult tortoises at four desert tortoise study plots in different years.

Site name	Year	No. adults (%)	No. nonadults (%)	X^2	$P < 0.05$
Fremont Peak	1977	12 (37.5)	19 (62.5)	1.12 (1977, 1980)	no
	1980	22 (51)	21 (49)	13.39 (1980, 1985)	yes
	1985	33 (89)	4 (11)	19.2 (1977, 1985)	yes
Kramer Hills	1980	62 (42)	84 (58)		
	1982	73 (39)	112 (61)	0.31	no
Chemehuevi Wash	1979	54 (36)	97 (64)		
	1982	70 (34)	137 (66)	0.15	no
Chuckwalla Bench	1979	130 (51)	135 (49)		
	1982	144 (55)	118 (45)	1.84	no

Remains of 117 tortoises were collected between 1977 and 1985. Of the total, 77 were judged to have been recent deaths, i.e. dead ≤ 4 years at time of collection (Table 6). Of the 65 tortoises dying between 1973 and 1979, 13 (20%) probably died of gunshot wounds, and two (3%) from raven kills. Of the 12 tortoises dying between 1980 and 1985, two (16.7%) probably died of gunshot wounds and one (8.3%) from a vehicle kill. The annualized mortality rate for adult and subadult tortoises was estimated at 7.4%/yr between 1973 and 1979, at 1.9%/yr between 1980 and mid-1985, and at 4.8%/yr between 1973 and mid-1985.

Annual Plant Productivity

Data are available on cover and biomass for two sample years, 1980 and 1985 (Table 7). Cover and biomass values in 1985 were about 1/100 of those for 1980.

Table 5. An analysis of sex ratios of adult and subadult tortoises at four study sites using the Z statistic.

Site no.	Site name	Year	Numbers of females, males	Z value	$P < 0.05$
5	Fremont Peak	1977	8, 9	0.2424	no
		1980	12, 15	0.5780	no
		1985	20, 13	-1.2195	no
7	Kramer Hills	1980	42, 42	0.0	no
		1982	47, 48	0.1033	no
20	Chemehuevi Wash	1979	57, 43	1.400	no
		1982	61, 38	-2.3101	yes
23	Chuckwalla Bench	1979	74, 79	0.4035	no
		1982	98, 80	-1.3493	no

Table 6. Numbers of tortoises dying at the Fremont Peak study site between 1973 and mid-1985.

Size-age class	Numbers of tortoises dying in interval	
	1973-1979	1980 to mid-1985
Juvenile 1	1	0
Juvenile 2	4	1
Immature 1	11	1
Immature 2	10	3
Subadult	11	3
Adult 1	15	3
Adult 2	13	1
Totals	65	12

Levels of Human Use

The plot is 1.7 km from Highway 395, and is cut in an east-west direction by a 1.6 km length of the well-used, graded Cuddeback-Fremont Peak Road. An additional 2.8 km of dirt roads and 0.74 km of old railroad bed cross the plot. The southern boundary is another 1.6-km long road. During surveys in 1977, 1978, 1979, 1980, and 1985 field workers reported almost daily or daily use of vehicles along the Cuddeback-Fremont Peak Road. U.S. Air Force vehicles may use the road daily; in 1985 at least two large gravel trucks passed through per day. On weekends, campers and other recreational vehicles used the road and traffic was particularly heavy on such three-day weekend or long holidays as Memorial Day and Easter week, e.g., 40-50

Table 7. Annual plant production at the Fremont Peak desert tortoise study site in 1979 and 1982.

Measurements of productivity		1979	
	March	April	May
No. transects	1	2	2
No. quadrats (0.1 m^2)	25	100?	100?
Mean cover (cm^2/m^2, %)	(6508, 65.1)	(373.3, 3.7)	(55.7, 0.6)
(range)		(335.9-410.7)	(28.7-82.8)
Mean biomass (g/m^2)	17.02	1.66	0.19
(range)		(1.63-1.69)	(0.17-0.21)

vehicles with dirt bikes/day in 1985. Some vehicles traveled cross-country off dirt roads. Shooting occurred during all field surveys. People were observed to shoot indiscriminately at animals while on foot or from moving vehicles. Campers occasionally stayed overnight. People also used the plot for picnics, photography, and viewing wildflowers. Sheep grazed every spring, bedding and/or watering for several days. Sheep used the plot on more than one occasion during 1985. Aircraft flew low over the plot during each census, creating frequent and loud sonic booms. Spent ordnance and trash were evident.

Changes in Habitat Condition

Human uses obviously are heavy, but we have no way to measure changes in habitat condition without comparing low-level aerial photographs from, for example, the 1970's with the 1980's. We assume that uses are not declining and that road traffic may be increasing. We estimate that habitat condition is static or declining.

Kramer Hills Study Site

Population Attributes

Densities did not change significantly between 1980 and 1982 (Table 8). Note that density estimates of tortoises ≥ 140 mm CL were similar between years. Any increases in numbers appear to be attributed to changes in juvenile and immature 1 size classes (< 140 mm CL), but are not significant. Size-class structure changed significantly between the two census years (Tables 3 and 9), but ratios of adults to nonadults did not change significantly (Table 4). Sex ratios did not differ significantly from the expected 1:1 ratio (Table 5).

Table 8. A comparison of estimated densities at the Kramer Hills study site in 1980 and 1982 using the Stratifies Lincoln Index.

Size Classes	Numbers / km^2 (95% confidence interval) 1980	1982
All size classes	86 (64-115)	121 (94-155)
Only those ≥ 140 mm long (immature 2, subadult, adult)	53 (39-73)	52 (40-68)
Only those ≥ 180 mm long (subadult, adult)	42 (30-59)	44 (33-59)
Only those ≥ 208 mm long (adult)	29 (20-41)	30 (22-41)

Remains of 140 tortoises were collected in 1980 and 1982. Of the total, 53 were judged to be recent deaths, i.e., dead ≤ 4 years at time of collection (Table 10). Of the 31 tortoises dying between mid-1976 and mid-1980, four (12.9%) appeared to have been shot, one (3.2%) was run over by a vehicle, one (3.2%) may have been egg bound, and two (6.5%) were killed by ravens.

Of the 22 dying between mid-1980 and mid-1982, two (9.1%) were killed by gunshots, three (13.6%) by vehicles, one (4.6%) by vandalism, and seven (31.8%) by ravens. For the 6-yr period, 11 (20.8%) died from gunshots, vehicle kills, or vandalism. The annualized mortality rates for adults and subadults between mid-1976 and mid-1982 was 2.9%/yr, 3.4%/yr between 1976 and 1980, and 2.6%/yr between 1980 and 1982.

Table 9. Size-age class distribution of registered desert tortoises at the Kramer Hills study site in 1980 and 1982.

Size-age class	Number of registered tortoises (% of total registered) 1980	1982
Juvenile 1 and 2	26 (17.8)	57 (30.8)
Immature 1 and 2	36 (24.7)	33 (17.8)
Subadult	22 (15.1)	22 (11.9)
Adult 1 and 2	62 (42.5)	73 (39.5)
Totals	146 (100.1)	185 (100.0)

Table 10. Numbers of tortoises dying at the Kramer Hills study site between 1976 and mid-1982.

Size-age class	Numbers of tortoises dying in interval 1976-1979	1980 to mid-1982
Juvenile 1	2	2
Juvenile 2	3	11
Immature 1	9	2
Immature 2	3	1
Subadult	1	4
Adult 1	7	2
Adult 2	6	0
Totals	31	22

Annual Plant Productivity

Values for percent cover of annuals differed within and between years (Table 11). For April and May of 1980 figures were 52.7% and 24.5%, respectively. In 1982 the figure for April was 28.1%, about half the figure for April 1980. Data on biomass were collected only during 1982.

Table 11. Annual plant production at the Kramer Hills desert tortoise study site in 1979 and 1982.

Measurements of productivity	1979 March	1979 April	1979 May
No. transects	3	3	3
No. quadrats (0.1 m^2)	150	150	150
Mean cover (cm^2/m^2, %)	(5270, 52.7)	(2453, 24.5)	(2814, 28.1)
(range)	(4363-5989)	(1599-3018)	(1814-4453)
Mean biomass (g/m^2)	—	—	22.5
(range)			(12.6-35.6)

Levels of Human Use

The site is relatively accessible. It lies 4.8 km from Highway 395, 2.1 km from Shadow Mountain Road and 7.2 km from Route 66, Helendale, and towns along the Mojave River. An old homesite (no remaining structures) is on the plot, and two other sites with collapsed structures are 0.6 and 0.7 km north. About 2.4 km of graded dirt roads border the plot and an additional 3.2 km of ungraded roads are within plot boundaries. In 1980, 12.0 km of vehicle trails 40 cm or wider were evident. Vehicle use may have increased between 1980 and 1982. In 1980 vehicle use averaged 0.5 car/weekday and 1-4/day on weekends. In 1982, many motorists drove through the plot on their way to and from the abandoned buildings in Buckthorn Wash, a favorite shooting spot. Some people rode dirt bikes off-road. In 1982, tracks of All Terrain Crawlers (ATCs) were evident in several areas for the first time. During the Memorial Day weekend, a small group of ATCs apparently used the plot for a flagged race or as a flagged course.

Shooting appeared to increase between 1980 and 1982. In 1980 motorists who stopped on the site often engaged in shooting, and in one instance were observed shooting at live animals from a vehicle. Plinking at trash was another activity. By 1982, numbers of bullet casings and trash used as targets had increased substantially. The site sometimes is used as a dump for large quantities of trash.

Sheep have grazed and/or bedded heavily on a 3 ha area in the past. In 1980, sheep grazed for 12 days on and nearby the plot, using three watering sites and creating 17 bedding areas (Nicholson and Humphreys 1981). Sheep grazed on 73% of the plot, using 4% for bedding sites. Sheep damaged 10% of 164 marked tortoise burrows and destroyed 4%. One juvenile was buried alive in its burrow.

Changes in Habitat Condition

Habitat condition is declining. Vehicle use off-road appeared to increase between 1980 and 1982. Unfortunately vehicle trails were not mapped in 1982, so the rate of increase cannot be calculated. New road spurs were created when sheepherders drove water trucks off the dirt roads to new locations to water sheep. Highly disturbed and compacted areas developed with new watering and bedding sites. Dumping of trash increased, as did refuse from plinking and shooting.

Chemehuevi Wash Study Site

Population Attributes

Densities and size-age class structure did not change significantly between 1979 and 1982 (Tables 3, 12, 13). The proportions of adult (≥ 208 mm CL) and nonadult tortoises did not change either. However, sex ratios shifted between 1979 and 1982 (Table 5). In 1979, the sex ratio was not significantly different than the expected 1:1 ratio, whereas in 1982, significantly more females than males were in the sample.

Between 1977 and 1982, 107 carcasses were collected. Of these, 36 were judged to be recently dead, i.e., ≤ 4 years, at time of collection (Table 14). Of the 17 tortoises dying between 1975 and 1979, one (5.9%) was definitely shot, a second may have been shot, and six showed signs of canid predation. Of the 19 dying between 1980 and mid-1982, two (11%) probably were killed by ravens and nine (47%) showed evidence of canid predation. Paul Schneider (field notes) suggested that two (11%) may have been vehicle kills. The annualized mortality rate for adults and subadults was 2.2%/yr for the 7.5-yr interval between 1975 and mid-1982, 3.5%/yr for 1975 to 1979, and 1.5%/yr for 1980 to mid-1982.

Annual Plant Production

Data on percent cover were collected only for 1979 (Table 15). No quantitative data were available for 1982. Schneider (1982 field notes) wrote that annual production did not seem as "good" as in 1979, but was not "poor."

Table 12. A comparison of estimated densities at the Chemehuevi Wash study site in 1979 and 1982 using the Stratifies Lincoln Index.

Size Classes	Numbers / km^2 (95% confidence interval) 1979	1982
All size classes	60	74
	(42-75)	(58-94)
Only those ≥ 140 mm long	27	27
(immature 2, subadult, adult)	(20-37)	(21-36)
Only those ≥ 180 mm long	18	22
(subadult, adult)	(13-25)	(17-29)
Only those ≥ 208 mm long	12	15
(adult)	(8-17)	(11-21)

Table 13. Size-age class distribution of registered desert tortoises at the Chemehuevi Valley study site in 1979 and 1982.

Size-age class	Number of registered tortoises (% of total registered) 1979	1982
Juvenile 1 and 2	27 (17.9)	49 (23.7)
Immature 1 and 2	43 (28.5)	59 (28.5)
Subadult	27 (17.9)	29 (14.0)
Adult 1 and 2	54 (35.7)	70 (33.8)
Totals	151 (100.0)	207 (100.0)

Levels of Human Use

The site lies adjacent to Highway 95 and is protected from the highway for about 0.72 km by a 6 to 7 m berm immediately adjacent to the road. A dirt road, parallel to and immediately north of Chemehuevi Wash, extends from the highway 2.08 km through the plot. In 1979 signs of human use included piles of garbage, campsites and many vehicle tracks in Chemehuevi Wash, mining pits, and many large caliber brass shell casings. Some signs of human use were probably from the annual off-road vehicle event, the Parker Score 400 (see Woodman 1983 for background). By spring 1982, impacts from the Parker 400 race were more obvious than in 1979. Most impacts were from vehicles which strayed from the course, primarily the dirt road. Vegetation was damaged in several areas for distances up to 7 m from the road center. In December 1981, about one-third of the plot was staked with placer claims. During the spring survey in 1982, few people (other than tortoise field workers) used the site: one person camped for a few days, four vehicle-oriented recreationists traveled on dirt roads and cross-country, and Caltrans employees removed numerous loads of sand in dump trucks.

Table 14. Numbers of tortoises dying at the Chemehuevi Wash study site between 1975 and mid-1982.

Size-age class	Numbers of tortoises dying in interval	
	1975-1979	1980 to mid-1982
Juvenile 1	0	1
Juvenile 2	1	10
Immature 1	7	5
Immature 2	2	0
Subadult	6	2
Adult 1	0	1
Adult 2	1	0
Totals	17	19

Changes in Habitat Condition

Slight deterioration has occurred, probably associated with the Parker 400 races and the newly staked placer claims. Increased vehicle traffic on the dirt road was evident, and vegetation was damaged in several sites by vehicles which apparently strayed from the race course. Recent vehicle tracks throughout the plot could have been made by the people staking placer claims, as well as recreationists traveling off-road.

Chuckwalla Bench Study Site

Population Attributes

The size of the plot is estimated at about 2.75 km^2. Comparisons of densities between census years are shown in Table 16. Densities did not differ significantly between 1979 and 1982. Size-age class structure changed significantly between the two census years (Tables 3, 17), but proportions of adults to nonadults did not differ significantly (Table 4). Sex ratios did not differ significantly from a 1:1 ratio (Table 5).

Table 15. Annual plant production at the Chemehuevi Wash desert tortoise study site in 1979 and 1982.

Measurements of productivity	1979 March	1979 April	1979 May
No. transects	3	3	3
No. quadrats (0.1 m^2)	---	---	---
Mean cover (cm^2/m^2, %)	(2560, 25.6)	(4610, 46.1)	(4890, 48.9)
(range)	(760-4100)	(4010-5480)	(3980-6340)
Mean biomass (g/m^2)	---	---	---
(range)	---	---	---

Between 1977 and 1982, 238 carcasses were collected. Of the total, 120 were judged to be recently dead, i.e., ≤ 4 years, at time of collection (Table 18). Of the 69 tortoises dying between 1975 and 1979, two (2.9%) probably were shot. Of the 51 tortoises dying between 1980 and mid-1982, 13 (25.5%) were probably killed by ravens. Causes of death for the others are unknown. The annualized mortality rate for adults and subadults was 2.3%/yr for the 9.5-yr interval between 1973 and mid-1982, 3.4%/yr for 1973-1979, and 1.2%/yr for 1980 to mid-1982.

Table 16. A comparison of estimated densities at the Chuckwalla Bench study site in 1979 and 1982 using the Stratifies Lincoln Index.

Size Classes	Numbers / km^2 (95% confidence interval) 1979	1982
All size classes	223 (177-283)	153 (120-195)
Only those ≥ 140 mm long (immature 2, subadult, adult)	97 (75-125)	100 (79-127)
Only those ≥ 180 mm long (subadult, adult)	75 (56-98)	87 (68-112)
Only those ≥ 208 mm long (adult)	59 (44-79)	61 (47-78)

Table 17. Size-age class distribution of registered desert tortoises at the Chuckwalla Bench study site in 1979 and 1982.

Size-age class	Number of registered tortoises (% of total registered) 1979	1982
Juvenile 1 and 2	44 (16.6)	40 (15.2)
Immature 1 and 2	68 (25.6)	44 (16.8)
Subadult	23 (8.7)	34 (12.9)
Adult 1 and 2	130 (49.0)	144 (55.0)
Totals	265 (99.9)	262 (99.9)

Annual Plant Production

Annual plant production, as measured by percent cover, was probably similar in 1979 and 1982 (Table 19).

Levels of Human Use

The plot probably was used more in the 1940's and 1953 for military maneuvers than it is today (Berry 1984a). The Bradshaw Road, a graded dirt road, crosses the southern part of the plot for about 1.6 km, and may average one car/day. Most traffic was on weekends. A 0.4 km dirt road runs from the Bradshaw Road to about the plot center. Occasional vehicles used the wash and/or traveled cross-country. Plot visitors were campers, rockhounds, hunters, and shooters. Shooting was heard three times at night during the 1982 survey. The southern edge of the plot is in the Chocolate Mountains Aerial Gunnery Range and is used for low level aircraft flights. Canisters of two phosphorous flares from aerial maneuvers were on the plot.

Changes in Habitat Condition

Habitat appears to be a static condition. Vehicle tracks from off-road travel are gradually increasing.

Table 18. Numbers of tortoises dying at the Chuckwalla Bench study site between 1973 and mid-1982.

Size-age class	Numbers of tortoises dying in interval 1973-1979	1980 to mid-1982
Juvenile 1	0	5
Juvenile 2	7	22
Immature 1	15	14
Immature 2	3	0
Subadult	12	3
Adult 1	27	3
Adult 2	5	4
Totals	69	51

DISCUSSION

Population attributes can change as a result of natural causes or human-induced changes in the environment. Some population attributes, such as size-class distribution, may appear to change with local weather conditions and low forage production. For example, Turner and Berry (1984b, 1985, 1986, unpub. data) conducted annual surveys of tortoises in eastern California between 1983 and 1986. In years of low forage production, proportions of small tortoises ($\leq$ 140 mm CL) were substantially lower in samples, than in years with high forage production.

To measure population trends, three or more samples taken at evenly spaced intervals and using similar or identical methods are desirable. Only one of the four plots, Fremont Peak, has data from three censuses spanning nine years. The census method changed, with the length increasing from 15 to 60 days. In spite of the increase in census length, numbers of tortoises registered and densities declined. Other attributes suggesting declines were statistically significant shifts in size class distributions to favor adults, and high annualized mortality rates (4.8%/yr over a 12-yr period) of adults and subadults. Mortality rates were probably higher than recorded, especially for the 1980-1985 period, because of the longer interval between censuses and carcass deterioration. Carcasses of tortoises killed by vehicles on dirt roads probably were no longer evident (Berry and Woodman 1984).

Table 19. Annual plant production at the Chuckwalla Bench desert tortoise study site in 1979 and 1982.

Measurements of productivity	1979 March	1979 April	1979 May	1982 ----
No. transects	5	5	5	5
No. quadrats (0.1 m^2)	100	100	100	---
Mean cover (cm^2/m^2, %)	(870, 8.7)	(1690, 16.9)	(630, 6.3)	(2150, 21.5)
(range)	(430-1440)	(1460-2090)	(440-810)	(1480-2920)
Mean biomass (g/m^2)	---	---	---	---
(range)				

One might argue that the low numbers and high proportions of adults registered in the last census year, 1985, were the result of low annual plant productivity, findings similar to those reported by Turner and Berry (1985, 1986) for the study site at Goffs. However, while Turner and Berry (1985, 1986) found that tortoises took more effort to locate in years with poor annual forage production, they still recorded 26 to 28% small tortoises ($\leq$ 140 mm CL) in their samples, compared with 8.1% at Fremont Peak in 1985. Because the increased length of the 1985 Fremont Peak census provided ample search time for the smaller size classes, we view the declines in numbers registered and densities and the high proportions of adults, as real measures of the status of the population, not as artifacts of sampling in a dry year. Declines are probably related to human influences--shooting, vehicle kills, and possibly deteriorating habitat.

Data for the Kramer Hills, Chemehuevi Wash, and Chuckwalla Bench sites are limited to two censuses spaced two to three years apart. None of the sites shows significant changes in densities or in proportions of adults and nonadults in the populations. Annualized mortality rates for adults and subadults ranged from 1.2%/yr for a 3.5-yr interval at Chuckwalla Bench to 3.5%/yr for a 4.0-yr period at Chemehuevi Wash. These figures are similar to or higher than the 2%/yr estimate for the Goffs study site in eastern California, one of the least disturbed tortoise study sites in the state (Turner and Berry 1984b). Of particular concern is the long-term effect of the 3.2% mortality rate on the Kramer Hills population. A high proportion (16.1-27.3%) of deaths were attributed to gunshots, vandalism, and vehicle kills, figures similar to those for Fremont Peak. Habitat was also deteriorating, primarily from unauthorized off-road vehicle use.

Problems with mortality rates, vandalism, and deteriorating habitat were less acute at the Chemehuevi Wash and Chuckwalla Bench sites. These two sites have slightly lower annualized death rates than Kramer Hills, and a lower proportion of deaths was attributed to shooting and vehicles.

Data from these four study sites can be compared to data from the two sites on the Desert Tortoise Natural Area (Berry et al. 1986) and the Goffs site (Turner and Berry 1984b, 1985, 1986). Four of the seven sites occur in the western Mojave Desert or Fremont-Stoddard Crucial Habitat--two sites on the Desert Tortoise Natural Area, Fremont Peak, and Kramer Hills. Populations at two of these sites, the interpretive center at the Desert Tortoise Natural Area and Fremont Peak, are obviously declining. Populations at the interior Natural Area plot, a protected site, and Kramer Hills site had not declined in density between 1979 and 1982, the last census year, but are unlikely to remain so for any length of time. The high rate of vandalism at the interior Natural Area plot may threaten population stability. The high rates of vandalism and vehicle kills and continuing habitat deterioration at Kramer Hills are a serious threat to the continued well-being of this population. In contrast, data from Goffs in the eastern Mojave Desert and Chemehuevi Wash in the northeastern Colorado Desert (Fenner-Chemehuevi Crucial Habitat) indicate little change. Goffs, especially, has received few human impacts. No tortoises have been found shot or run over by vehicles. The Chemehuevi Wash site shows indications of greater human impacts. The Chuckwalla Bench in the southern Colorado Desert and the Chuckwalla Crucial Habitat Colorado deserts also shows little change.

Berry (1986), using data collected on BLM study plots through 1982, reported significantly higher incidence of gunshot deaths in the western Mojave or Fremont-Stoddard Crucial Habitat than elsewhere in California. The 1985 data from Fremont Peak and the Desert Tortoise Natural Area Interpretive Center (Berry et al. 1986) continue to support this finding. The higher concentrations of people and all kinds of human use are probably responsible for this source of mortality, as well as the declining populations.

RECOMMENDATIONS

(1) More efforts must be made to collect data on annual plants in the manner specified in contracts. Some field workers did not collect data at all or only collected data on percent cover of annuals. Some field workers apparently used only a few quadrats.

(2) Frequent sampling of plots is essential to determining trends. Initially, the BLM planned to sample the plots at three-year intervals. Because of budget cuts, the interval has changed to five to seven years. With such extended intervals, valuable data on mortality rates and causes of death are lost. Shells deteriorate, can be buried in rain storms, carried off by people or predators, eaten by rodents, or ground into fine pieces by vehicles (Berry and Woodman 1984). The Kramer Hills, Chemehuevi Wash, and Chuckwalla Bench plots are overdue for sampling by two years. Unless special funds are forthcoming, they may not be sampled until 1988 or 1989. Alternative sources of funding should be sought.

(3) The loss of tortoises to gunshot deaths, vandalism, and vehicle kills on all four plots indicates a need for better control of people. Obviously the problem is greatest in the western Mojave, but it is growing in the Chemehuevi Valley and Chuckwalla Bench areas. Measures should be developed to reduce the problem.

(4) Unauthorized off-road vehicle use was evident on all plots. Such use contributes to habitat deterioration and in some cases may be the principal source of habitat loss. The problem needs attention, through signs, law enforcement, and education.

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ESTIMATED DENSITY AND DISTRIBUTION OF THE DESERT TORTOISE AT FORT IRWIN, NATIONAL TRAINING CENTER AND GOLDSTONE SPACE COMMUNICATIONS COMPLEX

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ABSTRACT - Two hundred fifty-five 1.5 mile long strip-transects were walked at Fort Irwin National Training Center (NTC) and Goldstone Space Communications Complex (Goldstone) with the purpose of estimating the density and distribution of the desert tortoise (*Gopherus agassizii*). A survey of military use on the 800 mi^2 study site was also conducted to ascertain what impacts are occurring and potential effects on the desert tortoise. About 10 percent of the study site (both the NTC and Goldstone) had estimated densities of 20-250 tortoises per mi^2. The remainder of the study site had estimated densities of less than 20 tortoises per mi^2. Major tortoise concentrations were located in two regions, one near the southern border and one near the center of the NTC. Both populations were believed to have approximately 35 mi^2 of contiguous habitat with estimated densities of more than 20 tortoises per mi^2. Both concentrations were determined to have very small "core" areas where densities were estimated to be greater than 50 tortoises per mi^2.

An inverse relationship between tortoise density and measured degree of impact was found. The impacts judged to be of primary concern were due to military off-road vehicles (MORV) and activities along roadways. About one quarter (26 percent) of the strip-transects were found to have more than 200 sets of MORV tracts, and nearly one half (44 percent) were found to have 50-200 sets of MORV tracts.

Cite as: Woodman, A. P., S. J. Juarez, E. E. Humphreys, K. Kirtland, and L. F. LaPre. 1986. Estimated density and distribution of the desert tortoise at Fort Irwin, National Training Center and Goldstone Space Communications Complex. Proc. Symp. Desert Tortoise Council. 1986:81-99.

INTRODUCTION

Fort Irwin National Training Center (NTC), and Goldstone Space Communications Complex (Goldstone) are comprised of approximately 800 mi^2 (2100 km^2) in the central Mojave Desert (Figure 1). Located 27 miles (43 km) northeast of Barstow, San Bernardino County, California, the NTC and Goldstone are within the known range of the desert tortoise, (*Gopherus agassizii*). The desert tortoise is granted full protection by the California Department of Fish and Game (CDFG), although it is not designated as a rare or endangered species. Provisions of California Fish and Game Code (Sec. 5000) prohibits collection, transport, sale, or deliberate actions causing harm to individual tortoises. No provisions of state law specifically protect desert tortoise habitat. In addition, the desert tortoise is currently under status review for federal listing by the U.S. Fish and Wildlife Service (USDI 1982) for possible listing as either threatened or endangered in accordance with the amended Endangered Species Act of 1973. The Beaver Dam Slope population in Utah has already been listed as threatened by the federal government (Dodd 1980). In California, the Bureau of Land Management (BLM) has designated the desert tortoise as a "sensitive" species (USDI 1980), a designation which affords the species additional consideration in the environmental planning process.

Concern about declining desert tortoise populations in California prompted the NTC to request that a tortoise survey be conducted on post. The U.S. Army Corps of Engineers funded this field study to estimate the distribution, density and military-related impacts to the desert tortoise at the NTC. Previous field studies of the desert tortoise in the California desert have covered BLM-managed lands containing suitable habitat, including areas to the south, east, and west of the NTC (Luckenbach 1982, Berry and Nicholson 1984). Military lands represent a gap in the current knowledge of the distribution and estimated desert tortoise densities in California. Therefore, this study is intended to provide additional information about the tortoise on federal lands that have not been investigated at the same level of detail as the surrounding areas of public domain managed by the BLM.

SITE DESCRIPTION

Fort Irwin was actively used as a training and test center by the U.S. Army from 1940 to 1971. From 1971 to 1981, Fort Irwin was relatively inactive, although some major exercises (e.g., Bold Eagle and Gallant Eagle) occurred. Since 1981 the Fort's status has been that of a National Training Center and activity has greatly increased. One battalion is permanently stationed at the NTC and each of 10 rotational units conduct annual maneuvers. Tanks, personnel carriers, supply trucks, jeeps and infantry are used in these exercises. Due to the nature of these maneuvers, vehicles do not always remain on established roads.

Five "Impact Areas" are distributed throughout the NTC comprising approximately 265 mi^2 (700 km^2). They are Leach Lake, Gary Owen, Nelson, Lucky Fuse, and Langford (Figure 1). These areas are designated as Impact Areas by the Army and are not to be confused with impacts to the environment which we discuss in this paper. Impact Areas are areas which contain one or more target sites. The target sites are fired upon by the military from the perimeter of the Impact Area. The remainder of each Impact Area is relatively undisturbed and its only human-oriented use is as a buffer zone.

Goldstone is situated on the west side of the NTC. It is operated jointly by the National Aeronautics and Space Administration (NASA) and the Jet Propulsion Laboratory for the purpose of tracking vehicles in deep space. Six radar sites are located on the facility. Other than the radar sites and associated access roads, there is little disturbance to the lands at Goldstone.

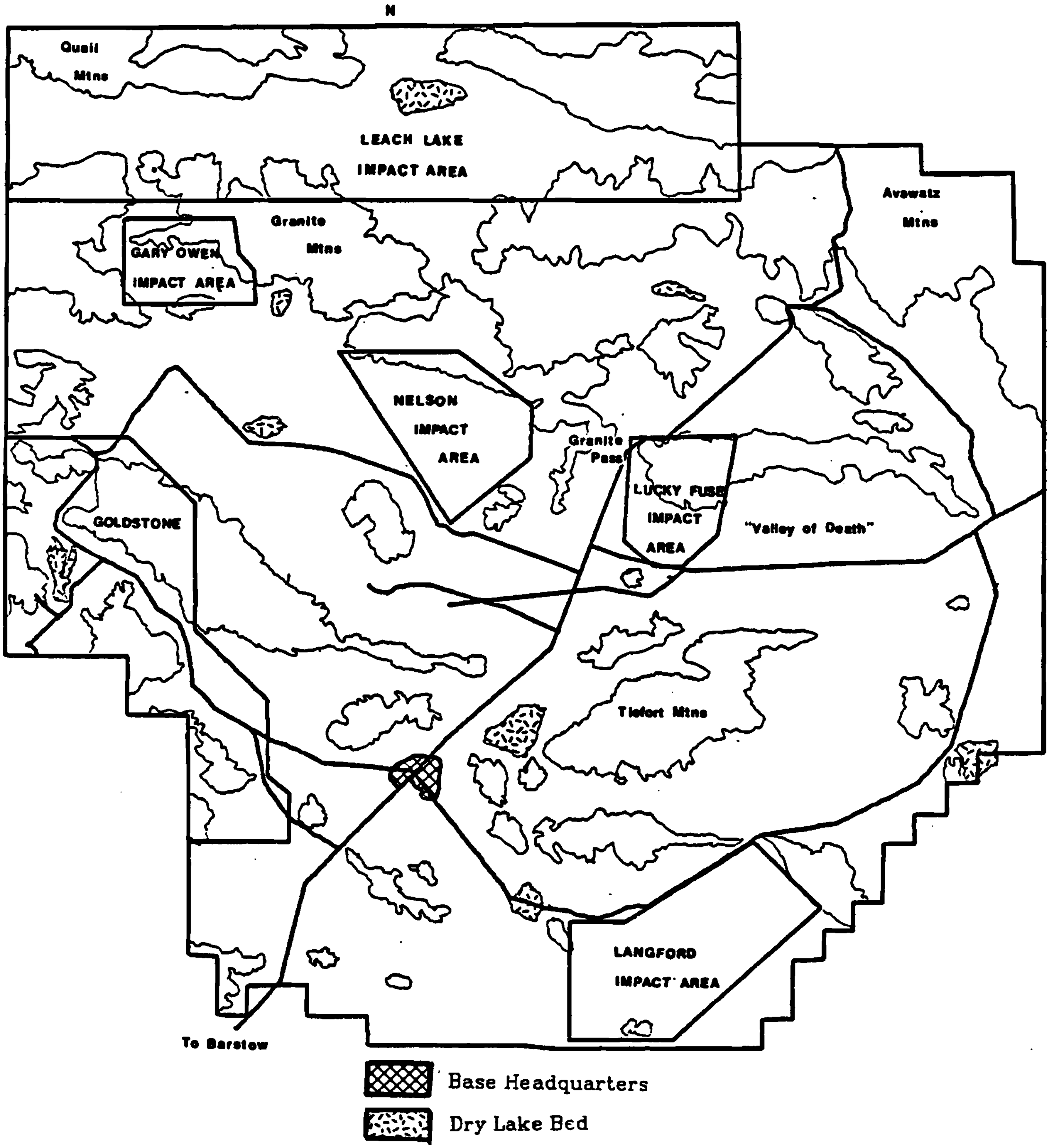

Figure 1. Fort Irwin National Training Center and Goldstone Space Communications Complex, San Bernardino County, California. Major roads are indicated with heavy lines.

Nearly half of the 800 mi^2 (2070 km^2) which comprise the NTC and Goldstone, approximately 390 mi^2 (1020 km^2), were available for the tortoise survey. The unavailable lands were either declared off-limits by the Army due to hazardous conditions (primarily the above mentioned Impact Areas) or were judged unsuitable as tortoise habitat and excluded from the study.

METHODS

Historical Data

Interviews were conducted with Ted Rado, Wildlife Biologist for the BLM in Barstow, Calif., Bob Vernoy and Frank Hoover of the CDFG, and eight civilian NTC personnel to obtain information on historical sightings and abundance. Two of the civilian NTC employees worked for the Range Control Dept. and spent much of their time in the field. The other six interviewees were security guards who patrolled the NTC ranges. All NTC personnel interviewed had been employed for one to ten years. Patterson's literature review (1976) was also utilized for previous sightings and museum records.

Field Techniques

Density and distribution of tortoises within the NTC and Goldstone were estimated using a strip-transect technique developed by Berry and Nicholson (1984). This method involves recording the numbers and types of tortoise sign (e.g., burrows, scats, live tortoises, shell remains, tracks, and courtship rings) on a transect 1.5 miles (2.4 km) long and 10 yards (9.2 m) wide. These sign counts are then adjusted to remove ambiguous sign. The adjusted sign counts (ASC) are then compared to the ASCs of a calibration plot (an area which previously has had tortoise density estimated by mark-recapture methods).

Only burrows and scats were used in the determination of adjusted sign from which tortoise densities were estimated because: (1) finding live tortoises was dependent on too many variables (such as season, temperature, or presence of rain), (2) shell-remains have been removed from the BLM study plots where the calibration transects were done, and (3) tracts and courtship rings were not equally discernible on all soil types. One other adjustment was made to scat and burrow counts. An associated group of sign that could be attributed to one tortoise was tallied as one ASC. For example, if three adult tortoise scats of similar size and age were found near an adult tortoise burrow, the unadjusted sign count of four would be adjusted to one ASC. The adjusted signs were summed to determine the ASC for each transect.

The length of a transect, not its shape, is critical to the mathematical calculations. Deviations from the standard triangular shape (Berry and Nicholson 1984) were to facilitate sampling of homogenous habitat, or to more efficiently use available time.

To correlate observed ASC to absolute tortoise density, we relied on the results of past studies which have dealt with the relationship between ASC and tortoise density. Densities of desert tortoises are rarely homogenous throughout the one mi^2 BLM study plots. Thus, Berry and Nicholson (1984) used strip-transects from six BLM study plots to show that adjusted sign counts were positively correlated with the number of live tortoises marked in a 30 day census in the 0.25 mi^2 containing the transect. Estimates of absolute density for the six BLM plots were determined using a mark-recapture analysis (Turner and Berry 1984).

For the purpose of calibration, each researcher walked six similarly formatted strip-transects on each of two BLM study plots (Figure 2). The results of these transects are shown in Table 1. The two plots chosen for calibration were Fremont Peak, censused for 30 days in 1980, and Kramer, censused for 60 days in 1980 (BLM contract files). These sites were selected because of their proximity to the NTC and their range of densities. Using the original data from these plots, and the mark-recapture data of Turner and Berry (1984), we calculated that Fremont Peak had an estimated density of 87 tortoises per mi^2 and Kramer had an estimated density of 185 tortoises per mi^2.

Tortoise density was estimated by multiplying ASC by a correlation coefficient. The correlation coefficient is a value that can be dependent on the environment in which the sign were sampled, as well as the individual observing the sign. For this reason, a correlation coefficient was determined (using least squares fitting) for each field worker based on the individual field worker's ASCs from the 12 calibration transects. The correlation coefficient, at 95 percent confidence, for each field worker was: SMJ = 14.1, KK = 13.7, and APW = 12.8. The results of the least squares fitting are shown in Figure 3 and are tabulated in Table 1.

Field work at the NTC and Goldstone took place between July 26 and August 11, 1983. Two hundred fifty-five transects were walked by Woodman (88 transects), Kirtland (84 transects), and Juarez (83 transects) on the NTC and Goldstone, (Figure 4). Two hundred forty-six transects were walked in the shape of an equilateral triangle, six in the shape of a "Z," and three in the shape of a rectangle. Transects were deliberately walked in homogenous habitat and soil type to prevent ambiguity with ecotonal areas. Approximately one transect per 1.5 mi^2 of potential tortoise habitat was walked. Representative photographs were taken of each transect and live tortoise encountered. Transects were mapped onto USGS 15' topographic maps and 1:50,000 scale maps provided by the military. These maps are deposited with the U.S. Army Corps of Engineers, Los Angeles District.

The distribution and intensity of human impacts were sampled. Four types of human impacts were counted or noted: (1) military tank and four-wheel vehicle tracks (MORV for "military off-road vehicles"), (2) roads, (3) debris, which included garbage, live and practice ordnance, and 20 mm, 30 caliber, and 50 caliber bullet casings, and (4) uncommon uses such as bivouac sites, burned areas, and presence of domestic and/or feral animals. When MORV use was sufficiently light, individual tracks were counted, and when use was heavy, percent track was estimated. A count of 250 tracks was estimated to be equivalent to 50 percent coverage. Since only a simple measure of impact was desired, we did not distinguish tread marks from wheeled vehicle marks, age of tracks, or describe the various types of debris.

Vehicle track density (VTD) was placed in one of three disturbance categories. A VTD of one (0-50 tracks per transect) represented a relatively undisturbed area, a VTD of two (51-200 per transect) represented a moderately disturbed area, and a VTD of three (over 200 tracks per transect) represented a highly disturbed area.

To determine the relation between tortoise density and human impact, a common scale for the different impacts was devised. This common scale was obtained by assigning the "normalized" value 1.0 to the median value of an impact type. The normalized impact values were then plotted verses ASC (Figure 5). The median values for the various impact types were: tracks = 5 - 10 percent or about 40 sets of tracks, debris = 12, and road count = 2. indicated with heavy lines.

Table 1. Adjusted sign counts of the calibration transects for each field worker and estimated tortoise densities for the 0.25 mi^2 containing the transect.

Researcher	Adjusted sign count	Estimated density of quarter section
	Fremont Peak	
Karen Kirtland	1	79
Stephen Juarez	1	79
Peter Woodman	5	79
Karen Kirtland	9	140
Stephen Juarez	3	140
Peter Woodman	11	140
Karen Kirtland	4	96
Stephen Juarez	6	96
Peter Woodman	4	96
Karen Kirtland	1	44
Stephen Juarez	1	44
Peter Woodman	1	44
Karen Kirtland	6	44
Stephen Juarez	3	44
Peter Woodman	4	44
Karen Kirtland	8	120
Stephen Juarez	5	120
Peter Woodman	7	120
	Kramer	
Karen Kirtland	14	140
Stephen Juarez	17	140
Peter Woodman	15	140
Karen Kirtland	12	208
Stephen Juarez	14	208
Peter Woodman	13	208
Karen Kirtland	17	200
Stephen Juarez	13	200
Peter Woodman	14	200
Karen Kirtland	16	200
Stephen Juarez	11	200
Peter Woodman	19	200
Karen Kirtland	13	170
Stephen Juarez	15	170
Peter Woodman	19	170
Karen Kirtland	10	192
Stephen Juarez	10	192
Peter Woodman	9	192

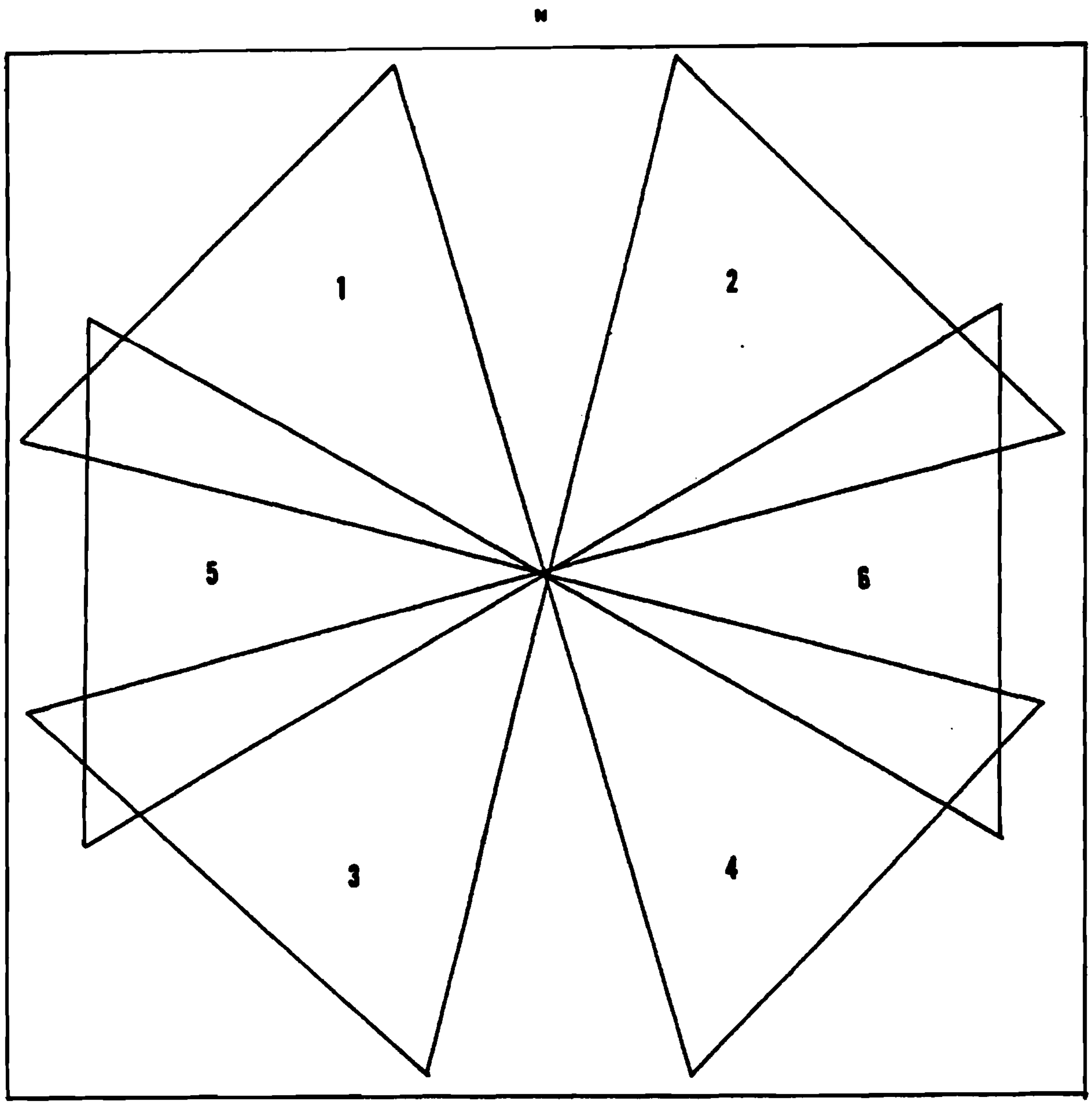

Figure 2. Format used for walking the calibration transects on both calibration plots.

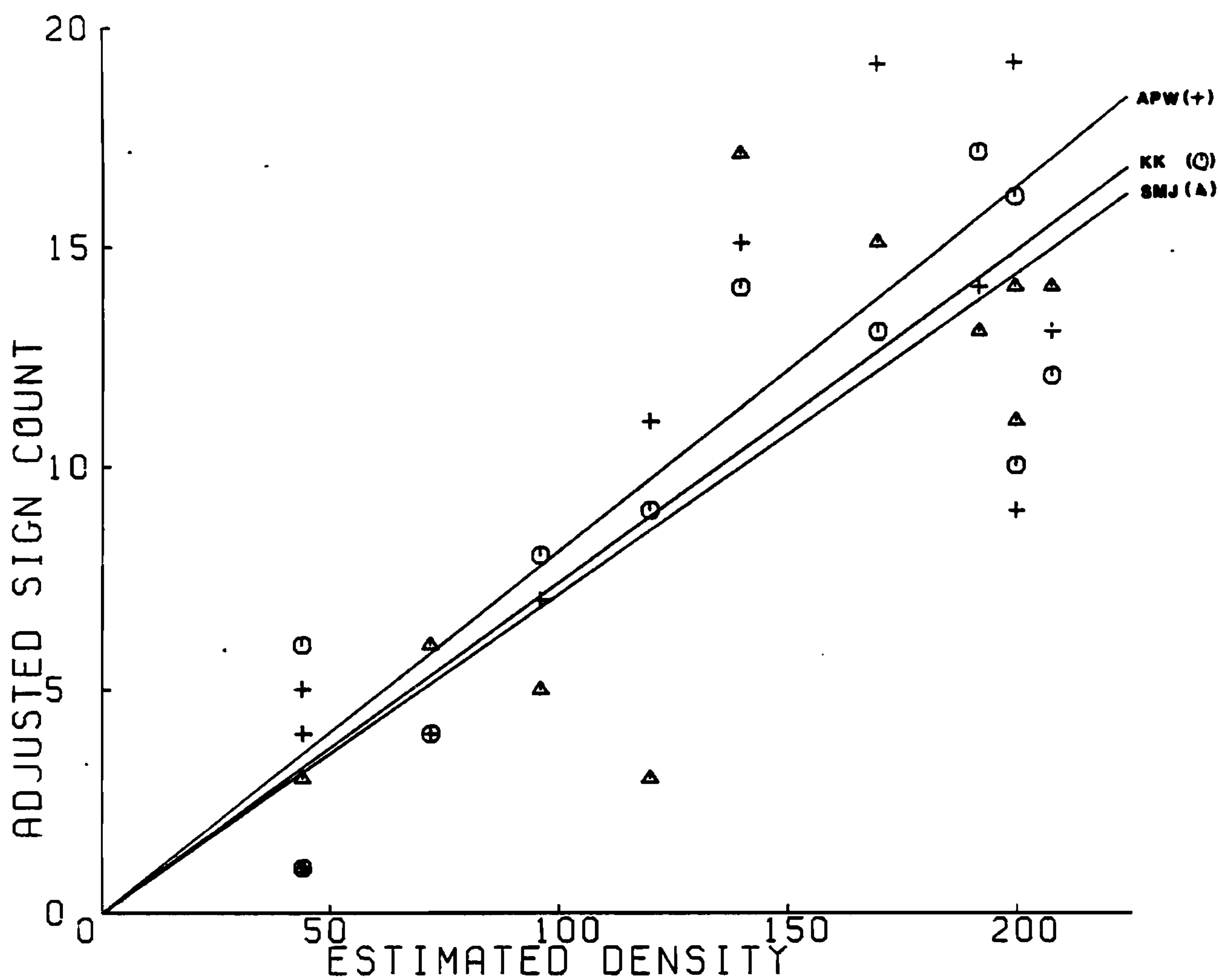

Figure 3. Graph of line of best fit slope relating adjusted sign count to previously estimated tortoise density for the calibration plots for each of the three field workers.

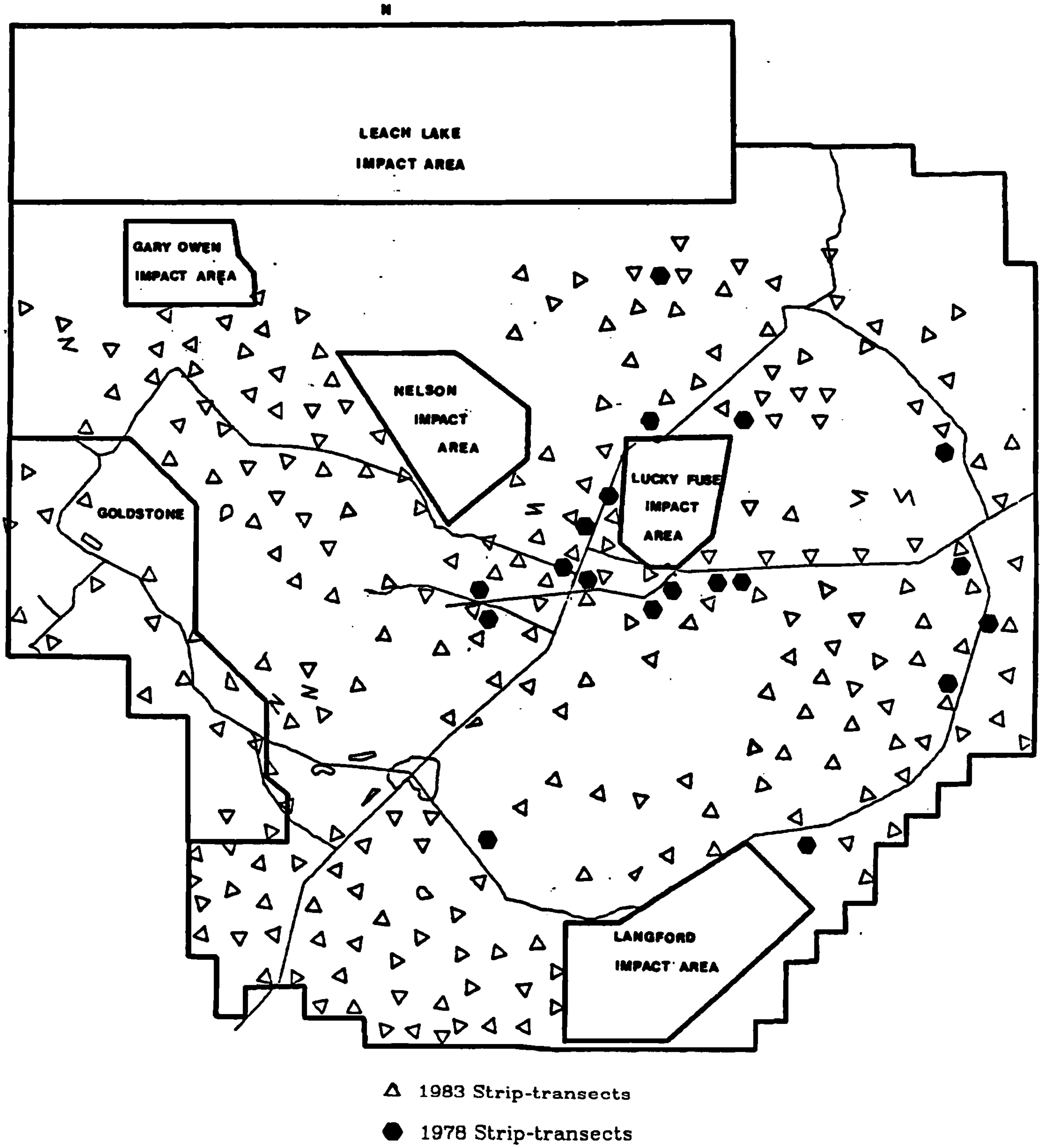

Figure 4. Distribution of tortoise transects at Fort Irwin National Training Center and Goldstone Space Communications Complex.

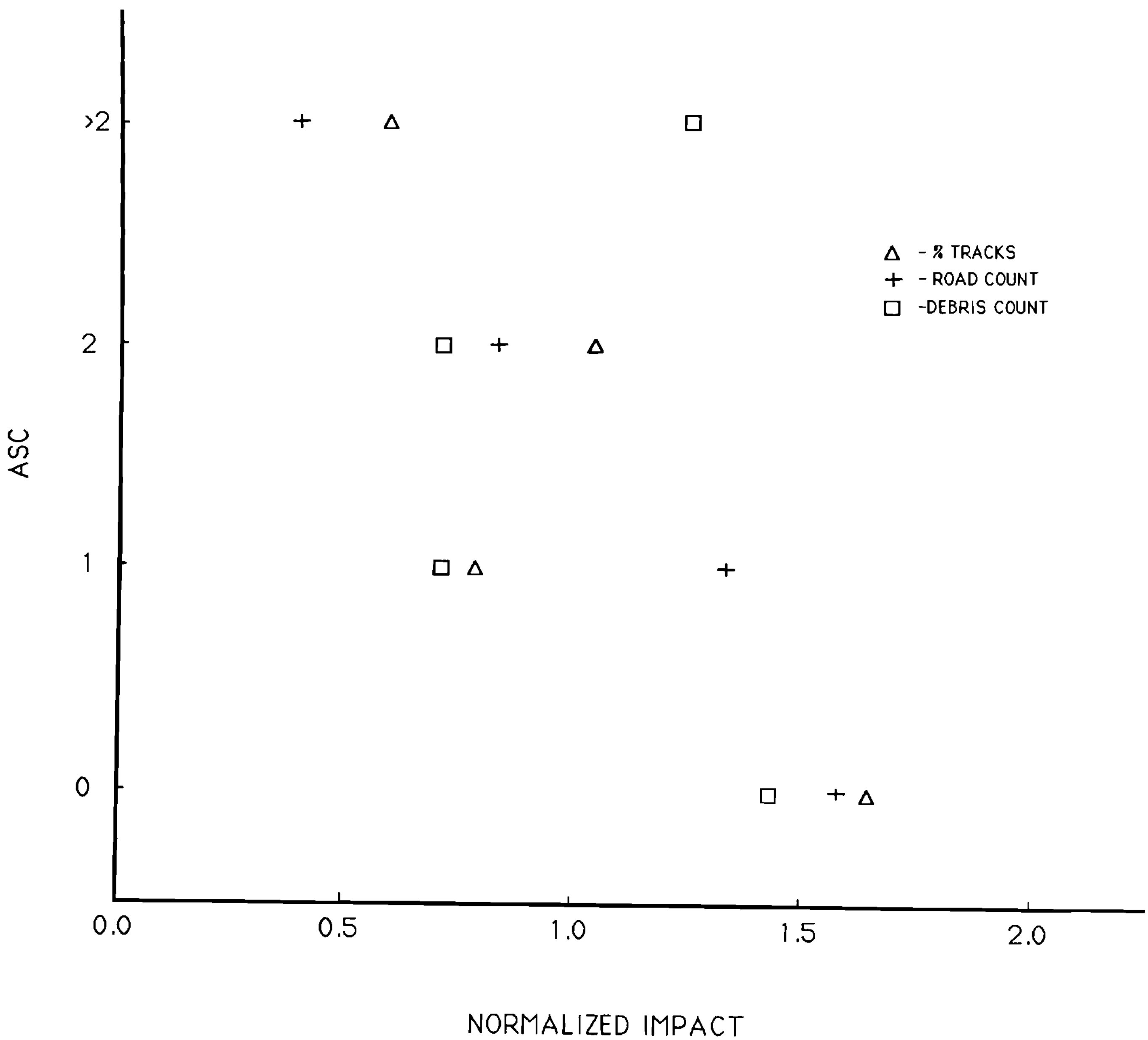

Figure 5. Plot of adjusted sign count (ASC) as a function of normalized impact. The value 1.0 is equal to the median value of an impact type. The median value for the various impact types were: percent tracks = 5-10 percent (40 tracks), road count = 2, and debris count = 12.

RESULTS

Previous Studies and Other Data

Patterson's literature review (1976) did not indicate tortoise sightings on or near the NTC. The closest recorded observation of a live tortoise was in the Calico Mountains, about 10 miles (15 km) southwest of the NTC.

Nineteen transects were walked in 1978 on the NTC by one to three people. Ten transects were done in May 1978 and nine in September 1978. The location of the 1978 transects was matched with the closest location of a transect from this study. The ASCs from the two studies were then compared (Table 2). On four transects our ASCs indicated densities of 20-50 tortoises per mi^2 while the transect results from 1978 indicated densities of 0-20 tortoises per mi^2. All other comparable transects showed similar densities.

Table 2. Comparison of the geographically closest strip-transects and adjusted sign counts in 1978 and 1983.

Transects done in 1978		Transects done in 1983	
Number	Adjusted sign count	Number	Adjusted sign count
1	1	176, 178	0, 0
2	1	141	1
3	4	143	6
4	1	34	0
5	0	39	3
6	0	54	3
7	0	89	0
8	0	175, 176	0, 0
9	1	18	0
10	0	137	0
11	0	4, 6	0, 0
12	1	148	0
13	1	141	0
14	4	143	6
15	1	34	0
16	0	39, 40	3, 2
17	0	54	3
18	0	89	0
19	1	18	0

The nearest BLM permanent study plot (Calico Mountains) was studied for 30 days in the spring of 1978 (Turner and Berry 1984). It was located three miles (5 km) west of the NTC. In that study the researchers estimated the population to be 20-50 tortoises per mi^2.

Of the BLM and CDFG personnel interviewed, only Frank Hoover of the CDFG was able to comment on the tortoise population at the NTC. Hoover participated in 12 of the 19 transects done in 1978. He believed that tortoise densities were low and was told by NTC employees that Granite Pass was the area with the most tortoises. No live tortoises were seen during the 1978 survey.

All eight NTC employees reported they saw a few tortoises a year, never more than ten. The areas consistently mentioned as having tortoises were Granite Pass, the region southeast of Granite Pass in the "Valley of Death" (Figure 1), and the areas north, south and west of Langford Dry Lake. One of the eight NTC employees mentioned a decline in the number of tortoises observed from 1982 to 1983.

Distribution and Estimated Densities

None of the density estimates from this study indicate high density tortoise populations. The highest density estimates from this study (100-250 tortoises per mi^2) indicate moderate densities as defined by Luckenbach (1982). Any designation of "high density" in this report is relative only to the study site and not the California desert in general.

Most transects in Goldstone and the NTC yielded few or no sign. Figure 6 shows the tortoise distribution and density classes for the areas studied. Sixteen percent of the 390 mi^2 that were surveyed had estimated densities of 20-50 tortoises per mi^2. Three percent had estimated densities of 50-100 tortoises per mi^2 and less than one percent had an estimated density of 100-250 tortoises per mi^2. The remaining 80 percent was estimated to have densities of 0-20 tortoises per mi^2.

Few tortoise sign were found in predominately rocky areas, hard pan, or loose, sand soils. The better tortoise habitat, based on ASC, was found on firm sandy-loam to gravelly soils of alluvial fans or bajadas. Twenty-five transects were walked in less suitable habitat: seventeen were walked in rocky areas, two of which had one ASC each: five on hardpan, one of which had one ASC; and three on loose, sandy soils, none of which had tortoise sign.

Vegetation in the better tortoise habitat, based on ASC, was typical creosote scrub plant community (Munz 1974) dominated by creosote bush (*Larrea tridentata*), burro bush (*Ambrosia dumosa*), desert senna (*Cassia armata*), goldenhead (*Acamptopappus sphaerocephalus*), and Cooper goldenbush (*Happlopappus cooperi*). The elevation range of habitat with the higher estimated tortoise densities (20-250 tortoises per mi^2) was 1600 to 3600 feet (490 to 1100 m).

Two tortoise concentrations were found on the NTC. One was immediately south of Granite Pass (the Granite Pass population) and the other was west of the Langford Impact Area (the Langford population). The Granite Pass population consists of an estimated 33 contiguous mi^2 (85 km^2) of habitat with estimated densities of 20-100 tortoises per mi^2, of which two mi^2 had estimated densities of 50-100 tortoises per mi^2. This area may be larger than 33 mi^2, but as it abuts Lucky Fuse Impact Area, seven mi^2 of potential habitat could not be surveyed.

The Langford population had 16 mi^2 (41 km^2) with estimated densities of 20-50 tortoises per mi^2, six mi^2 with estimated densities of 50-100 tortoises per mi^2 and one mi^2 with an estimated density of 100-250 tortoises per mi^2. Approximately 10 mi^2 (26 km^2) of potential habitat could not be surveyed because this population, like the Granite Pass population, abuts an Impact

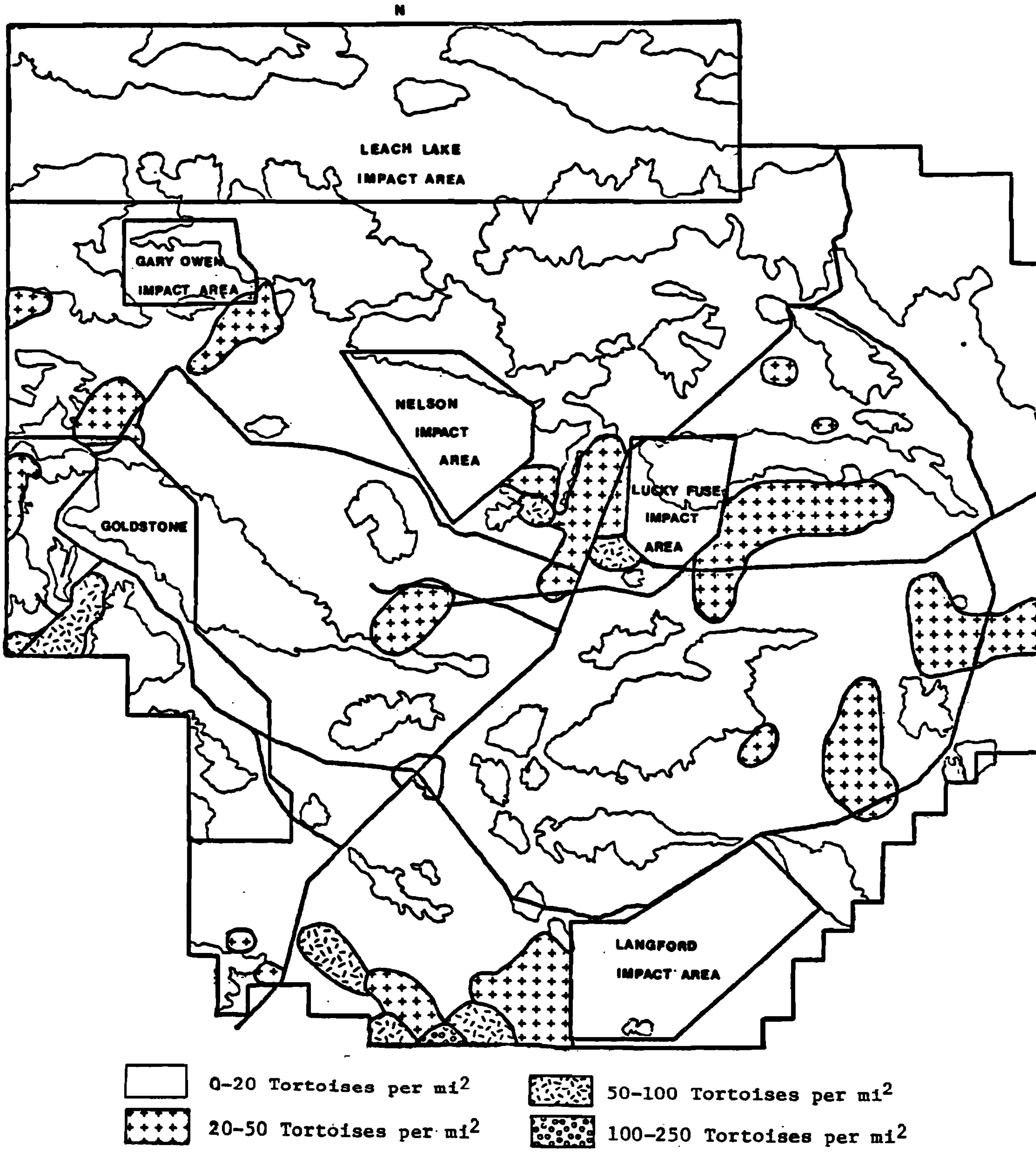

Figure 6. Distribution and estimated densities of the desert tortoise on Fort Irwin National Training Center and Goldstone Space communications Complex. Mountainous terrain and Impact Areas were not surveyed.

Area, in this case the Langford Impact Area. Habitat with more than 20 tortoises per mi^2 probably continues south of the NTC onto BLM lands, however these lands have not been surveyed (Berry and Nicholson 1984).

In addition to the Granite Pass and Langford populations, two areas with estimated densities of 20-50 tortoises per mi^2 on more than seven contiguous square miles were located on the NTC. Both areas were southeast of the "Valley of Death". The larger of the two areas was estimated to be 11 mi^2 (18 km^2), and the smaller area had an estimated eight mi^2 (13 km^2) of contiguous habitat. Approximately three mi^2 in the west-central portion of Goldstone had a density estimate of 50-100 tortoises per mi^2. Berry and Nicholson (1984) indicate an additional contiguous two mi^2 with estimated densities of 50-100 tortoises per mi^2 in Goldstone.

Impacts

Figure 7 shows the VTD rating and location of MORV tracks on the NTC and Goldstone. Sixty-six transects (26 percent) had a VTD rating of three, 45 transects (18 percent) had a VTD rating of two and 144 transects (56 percent) had a VTD rating of one. A map of most of the roads on the NTC and Goldstone is shown in Figure 8. Although an effort was made to avoid major roads, only 78 transects (31 percent) did not contain roads.

Trash and/or ordnance was observed on 222 transects (88 percent) and were not observed on 32 transects (12 percent). Bivouac sites were noted on five transects. Bivouac sites are camping areas, roughly 0.75 acres (0.3 ha) each, with most smaller shrubs removed. Sheep scat was noted on three transects, all of which were near the western edge of the NTC. All observed sheep scat appeared to be several years old, and grazing is not a current land use on the study site.

Goldstone was relatively free from impacts. The major potential impact to the population of 50-100 tortoises per mi^2 is a paved road at the northern limit of the population. A radar site, surrounded by approximately one acre (0.4 ha) of cleared land, near the population center is an additional source of potential impact. If personnel refrain from collecting tortoises, the impact will be limited to the effects of traffic to and from the site.

DISCUSSION

Life History Characteristics

The desert tortoise is particularly vulnerable to perturbation because it is a K-selected species, i.e. one that is characterized by a long life-span and low reproductive potential (Berry 1978). Sexual maturity in the desert tortoise is reached in 15 to 20 years and its life-span may be 100 years or more (Woodbury and Hardy 1948, Berry 1978). Tortoises forage almost exclusively on annual forbes, annual and perennial grasses, and some cacti (Berry 1978, Bickett 1980). Tortoises are dependent on perennial shrubs for use as cover from sun, escape cover from predators, and burrow sites (Burge 1978).

Estimated Density and Distribution

The density estimates of Berry and Nicholson (1984) for the NTC, Goldstone, and the surrounding areas were basically consistent with the findings of this study. However, the higher concentration of transects allowed us to more accurately delineate density gradients and to locate small, isolated populations.

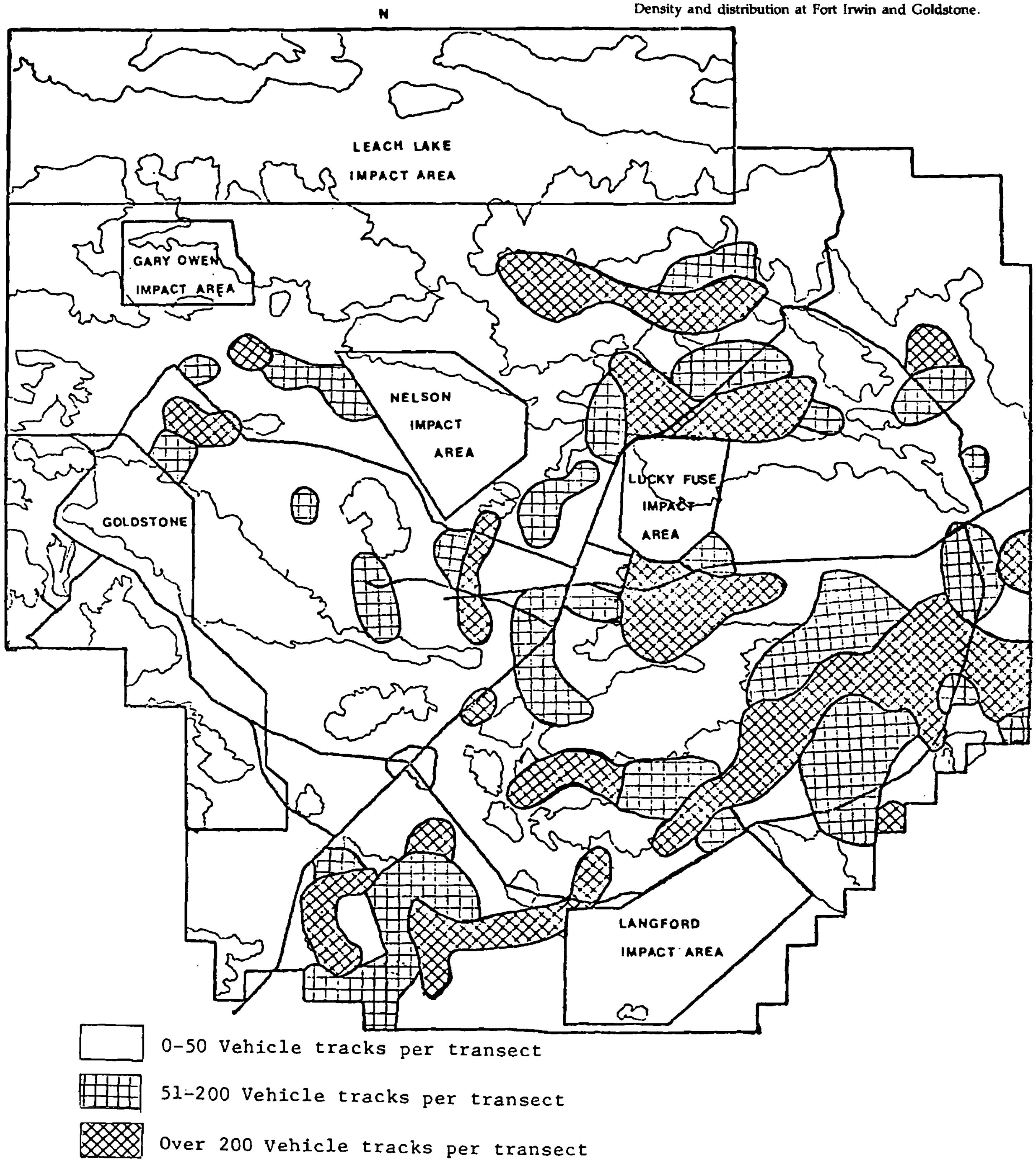

Figure 7. Distribution and estimated densities of military off-road vehicle tracks on Fort Irwin National Training Center and Goldstone Space Communications complex. Mountainous terrain and impact areas were not surveyed.

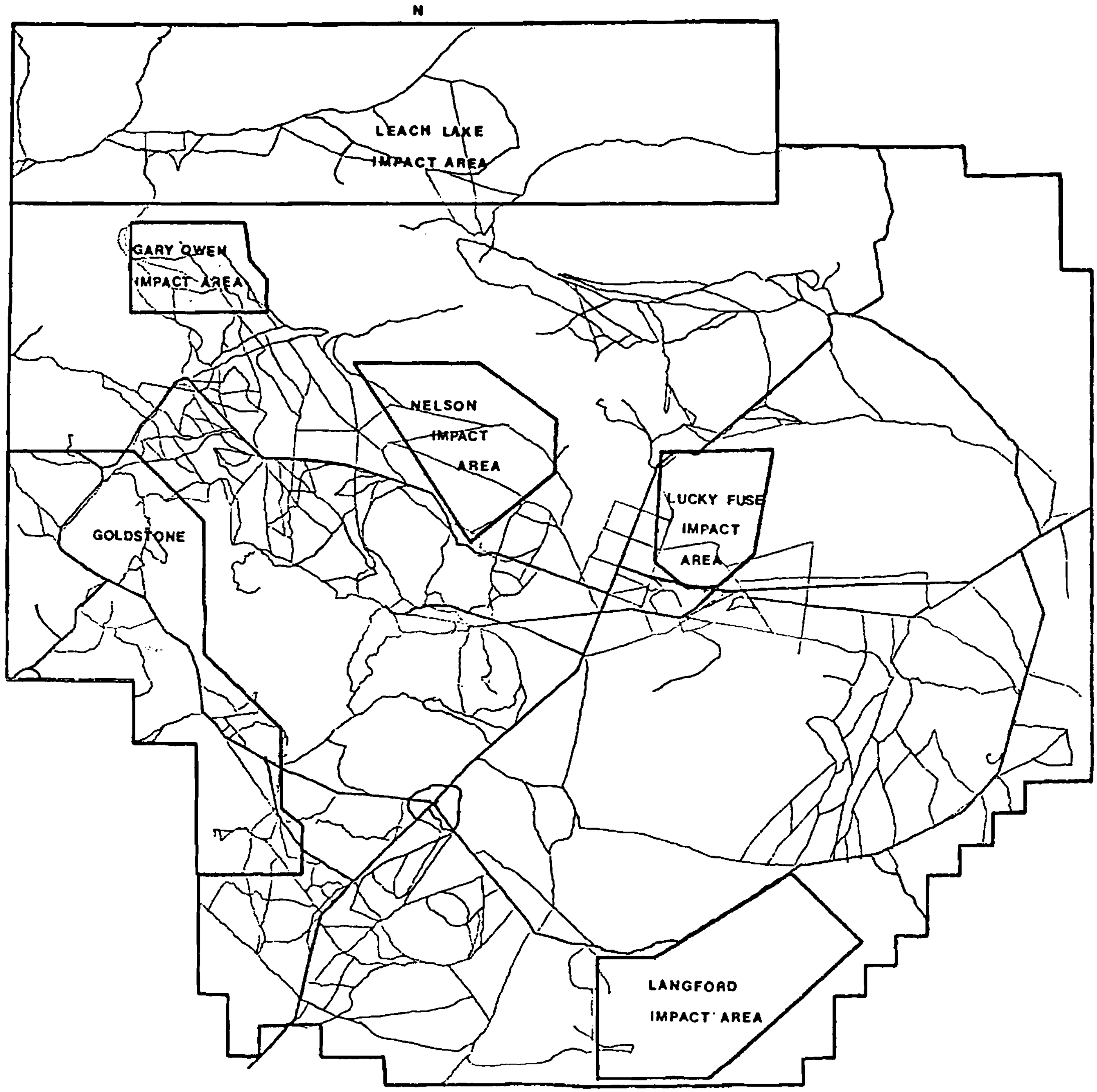

Figure 8. Paved and most unpaved roads on Fort Irwin National Training Center and Goldstone Space Communications Complex.

At the time of the study, two major and several lesser concentrations of tortoises existed on the NTC and Goldstone. Since much of the terrain that was surveyed is suitable tortoise habitat (alluvial fans and bajadas), it is likely that the now fragmented concentrations were once part of a single, larger population (Luckenbach 1982). The population, presumably, has since been fragmented by military activities which destroy individuals and habitat.

It is possible that some unknown factor is preventing the tortoise from more fully exploiting the bajadas and alluvial fans. However, an inverse relationship with impacts (roads and percent tracks) and ASC can be shown (Figure 5). Damage to the desert environment from off-road vehicles (ORVs) has been well documented. ORVs physically destroy the vegetation, resulting in reduced density and canopy cover (Keefe and Berry 1973, Lathrop 1978). Luckenbach (1975), Duck (1978), Bury et al. (1977), Wilshire et al. (1978), and Hall (1980) have shown that disturbed areas show reduced density and diversity of vegetation. The degree of loss is dependent on the intensity of use (Duck 1978, Lathrop 1978). Recovery rates for density and cover of vegetation in areas used by the military have been estimated at up to 112 and 212 years respectively (Lathrop 1983). Wildlife populations show declines in both density and diversity in disturbed areas (Bury et al. 1977, Berry 1984). Depending on the severity of the impacts, desert soils and vegetation may require more than 100 years to recover (Webb and Wilshire 1980).

Roads have been shown to negatively impact desert tortoises. Tortoise populations may be seriously reduced in a one kilometer corridor (0.5 km on each side) along a paved road (Nicholson 1978, Humphreys in prep.). Nicholson also speculates that the impact from major unpaved roads may have similar effects.

The impacts to soil and, by inference, to vegetation and wildlife from military activities at the NTC have been extensive and severe. The most heavily impacted areas of the NTC were in the southern and western portions. The highest tortoise densities were also found in these same general areas, although tortoise density and degree of impact were locally exclusive. For example, the high density "core" concentrations were in regions with a VTD rating of one, but were surrounded by areas of higher VTD rating.

In addition, the major population centers are adjacent to Impact Areas which are relatively undisturbed except for the target centers. The Granite Pass population occurs between Nelson Impact Area and Lucky Fuse Impact Area. This population could continue through the Lucky Fuse Impact Area. The Langford population is adjacent to Langford Impact Area and the southern border of the NTC. We strongly suspect that the combination of mountainous terrain and the proximity of Impact Areas have afforded protection to these tortoise populations.

The Langford population was bordered on the north by an area with a VTD rating of three and the northwest tip of the population (50-100 tortoises per mi^2) extended into VTD three area. If current use levels continue, we anticipate a continued drain on the population. Stochasticly, one would anticipate MORVs and infantry to encounter tortoises. While soldiers could be advised of the legal status of the desert tortoise, the driver of a MORV may not see or be able to react in time to prevent crushing a tortoise or its burrow.

The Granite Pass population, in addition to being threatened with MORVs is bisected by a major well-used road. The road and the MORVs have high potential to contribute to the loss of tortoises.

The two areas southeast of the "Valley of Death" with estimated densities of 20-50 tortoises per mi^2 lie within regions with VTD ratings of two and three. Again, the heavy military use of these areas has high potential to destroy habitat and populations.

Significance of the Desert Tortoise Population

Fort Irwin is at the northeast edge of the large Fremont-Stoddard population (Berry and Nicholson 1984). Only two areas with estimated tortoise densities over 20 per mi^2 border the NTC (Berry and Nicholson 1984). The rest of the perimeter has estimated densities of 0-20 tortoises per mi^2. The other previously surveyed area is at the southwest corner of the NTC.

Tortoise densities on the NTC and Goldstone make up a very small portion of the habitat with tortoise densities greater than 20 per mi^2. In consideration of biological resources within the NTC boundaries, the two high-density areas are of importance.

ACKNOWLEDGMENTS

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CHANGES IN DESERT TORTOISE POPULATIONS AT THE DESERT TORTOISE RESEARCH NATURAL AREA BETWEEN 1979 AND 1985

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ABSTRACT - Desert tortoise (*Xerobates agassizii*) populations were sampled with 60-day spring censuses at two plots on the Desert Tortoise Natural Area, eastern Kern County, California. The first plot at the interpretive center (7.7 km^2) was sampled in 1979 and 1985. The plot included protected habitat inside the Natural Area fence, as well as habitat outside the fence experiencing moderate to intensive human use. The second plot, the control (2.85 km^2) was 4.0 km away in the Natural Area interior. It was censused in 1979 and 1982. It received little human use.

During the six-year interval between censuses at the interpretive center plot, population densities declined 32.1% inside the fence (from 131/km^2 to 89/km^2) and 54.4% outside the fence (from 114/km^2 to 52/km^2). The changes were significant at the 95% CI. In contrast, during the three-year interval between censuses at the control plot, densities decreased from 147/km^2 to 129/km^2, but the decrease was not statistically significant. At both plots, statistically significant changes occurred in the size-age class distribution of the populations. Proportions of juvenile, immature, and subadult classes decreased.

At the interpretive center plot, 20.3% of deaths were attributed to gunshot, mutilation, and vehicle kills, compared with 14.9% for gunshot only on the control plot. Common Ravens (*Corvus corax*) probably were responsible for 29.6% of deaths on the interpretive

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center plot and 44.9% on the control. Of the dead tortoises ≤ 103 mm in carapace length, 66.7% probably were killed by ravens at the interpretive center and 74.5% at the control. Significantly more tortoises were killed by ravens on the two Natural Area plots than at 13 other tortoise plots in California. The high proportions of raven kills may account for decreases in proportions of juveniles, immatures, and subadults in the two samples.

At the interpretive center plot, unauthorized releases of captive tortoises and turtle species occurred, and attempted collections of wild tortoises were observed. Visitors signing the log at the interpretive center increased from 832 in 1982 to 1,964 in 1985. Inside the fence, an estimated 2.17 ha were disturbed between 1979 and 1980 by development of interpretive facilities. Outside the fence, 525 vehicles/yr were estimated to occur on the plot in 1982 and 1983. Denuded habitat increased from 10.4 to 14.1 ha between 1979 and 1985. Vehicle trails ≥ 1 m increased 130% in length and 157% in area. Areas denuded of vegetation by vehicle use, camp sites, and sand extraction increased 31%. At the control plot, habitat condition remained stable or improved. Only a few fresh vehicle tracks were observed.

INTRODUCTION

Desert tortoise populations (*Xerobates agassizii*) have declined in parts of the geographic range for decades (Berry 1984a). In December 1985, the U.S. Fish and Wildlife Service recognized that declines had reached the point where federal listing was warranted (U.S. Fish and Wildlife Service 1985).

More than 10 years earlier, the U.S. Bureau of Land Management (BLM) and the Desert Tortoise Preserve Committee, a private nonprofit conservation corporation, realized that tortoise populations and habitat were in trouble in the western Mojave Desert. They established the Desert Tortoise Research Natural Area in eastern Kern County, California (Hird et al. 1979, U.S. BLM 1980). The first efforts at protection were initiated in fall of 1973, when the Natural Area was posted as closed to unauthorized vehicle use (Stockton 1984). In 1977 and 1978 the BLM constructed a fence around the Natural Area perimeter to prevent entry by off-road vehicles and sheep. In 1979 the BLM developed a management plan for the Natural Area with three objectives: (1) maintain and protect natural populations and habitat for the desert tortoise and other animals and plants; (2) gather baseline data on tortoise population attributes and compare the data with other tortoise populations in similar habitat elsewhere in the geographic range; and (3) develop a natural history program to increase public awareness of the tortoise and other desert animals and plants (Hird et al. 1979). During 1979 and 1980, an interpretive center was constructed with kiosk, nature trails, parking lot, access road, and sanitary facilities. Protective signs were placed at 160 m intervals on the fence.

In 1979 the BLM established two study plots to monitor tortoise populations at the Natural Area. One plot was at the interpretive facilities and included protected lands inside the Natural Area fence, as well as land receiving considerable human pressure outside the fence. The second plot, a control, was in the interior. Objectives of the studies were to determine effects of visitor use on tortoise populations and habitats, and to compare data from the control plot with data gathered from other tortoise plots in the Southwest. This paper (1) summarizes changes in tortoise populations and habitat at the Natural Area between 1979 and 1985, (2) compares the findings with data from other studies, and (3) outlines implications for future management.

METHODS

The two study plots are designated the interpretive center and the control. The interpretive center plot is 7.7 km^2, is on the southeastern boundary of the Natural Area, and is 8.5 km north and 9.9 km east of California City, Kern County, California (Figure 1). Fifty-eight percent of the plot occurs within the fenced boundaries of the Natural Area, while 42% is outside the fence (Figure 2). Visitor use began to increase in the mid-1970s with tours led by the Desert Tortoise Preserve Committee and has continued to grow. The interpretive kiosk, nature trails, parking lot, and toilet facilities are at the plot center. The portion of the plot outside the fence has a heavily used dirt road, borrow pit, a network of dirt roads and off-road vehicle (ORV) trails, and unimproved camp sites. For parts of the data analysis, the interpretive center plot was divided into two subplots by the fenced boundary: inside the fence, and outside the fence.

The control plot is 2.85 km^2 and occurs in the interior of the Natural Area (Figure 1). The southern boundary is 4.0 km north of the northern boundary of the interpretive center plot. The southeast corner of the plot touches a corner of the fence, but elsewhere the plot is 2.6 to 10.4 km inside the fence. Visitor use has declined since late 1973, when the Natural Area was closed to recreational vehicle use and the closure was posted along Natural Area boundaries. Visitor numbers declined further after construction of the boundary fence.

The interpretive center plot was surveyed in 1979 (March 5 to May 29) and 1985 (March 25 - June 3) by three people, each of whom worked for 60 days. In 1979 field workers had no prior field experience with tortoises surveys, whereas the 1985 team had from two to eight years of experience. In 1979, one field worker occasionally followed tour groups and recorded the tortoises they found. Each tortoise encountered was marked, measured for carapace length (CL), weighed, and its location plotted by date on a 300-quadrat grid (quadrat = 0.0259 km^2). In 1979, carcass remains were labeled in situ, but data were not collected on time of death nor carapace length. In 1980 and 1981, five specimens were collected by Campbell (1982, 1983) and L. Stockton (pers. comm.). In 1985, all remains were collected, assigned a number, and their locations were plotted on the grid. Data were recorded on human uses (e.g., visitor use, hunting, shooting, vehicle use, sheep grazing etc.) and on signs of such use.

The control plot was surveyed in 1979 and 1982 with similar techniques and coverage, except that the 1979 census occurred earlier in spring than the 1982 census (March 8 to May 30 vs. April 5 to June 9). Experience of field workers for 1979 and 1982 was similar: each had undertaken one previous census. The 1982 census had more survey hours than the 1979 census, because the 1982 field worker received assistance on parts or all of 28% of the census days. Carcasses were collected during the 60-day spring censuses in 1979 and 1982, and also in fall of 1978 and 1979.

Live and dead tortoises were assigned to six size-age classes: juvenile 1 (< 60 mm CL), juvenile 2 (60-99 mm CL), immature 1 (100-139 mm CL), immature 2 (140-179 mm CL), subadult (180-207 mm CL), and adult (≥ 208 mm CL) (Turner and Berry 1984). For the purposes of statistical analysis of size-age class distribution, tortoises were grouped in four classes: juvenile, immature, subadult, and adult. Densities were estimated using the Stratified Lincoln Index (SLI) (Overton 1971). For the SLI, tortoises were grouped into five size-age classes: juvenile, immature 1, immature 2, subadult, and adult. Then they were sorted by capture-recapture events into three groups: captured only in the first 30 days, captured only in the second 30 days, and captured in both 30-day census periods. Sex ratios were evaluated for subadults and adults using the $\underline{Z}$ statistic (Turner and Berry 1984). For each carcass, estimates were made of time of death

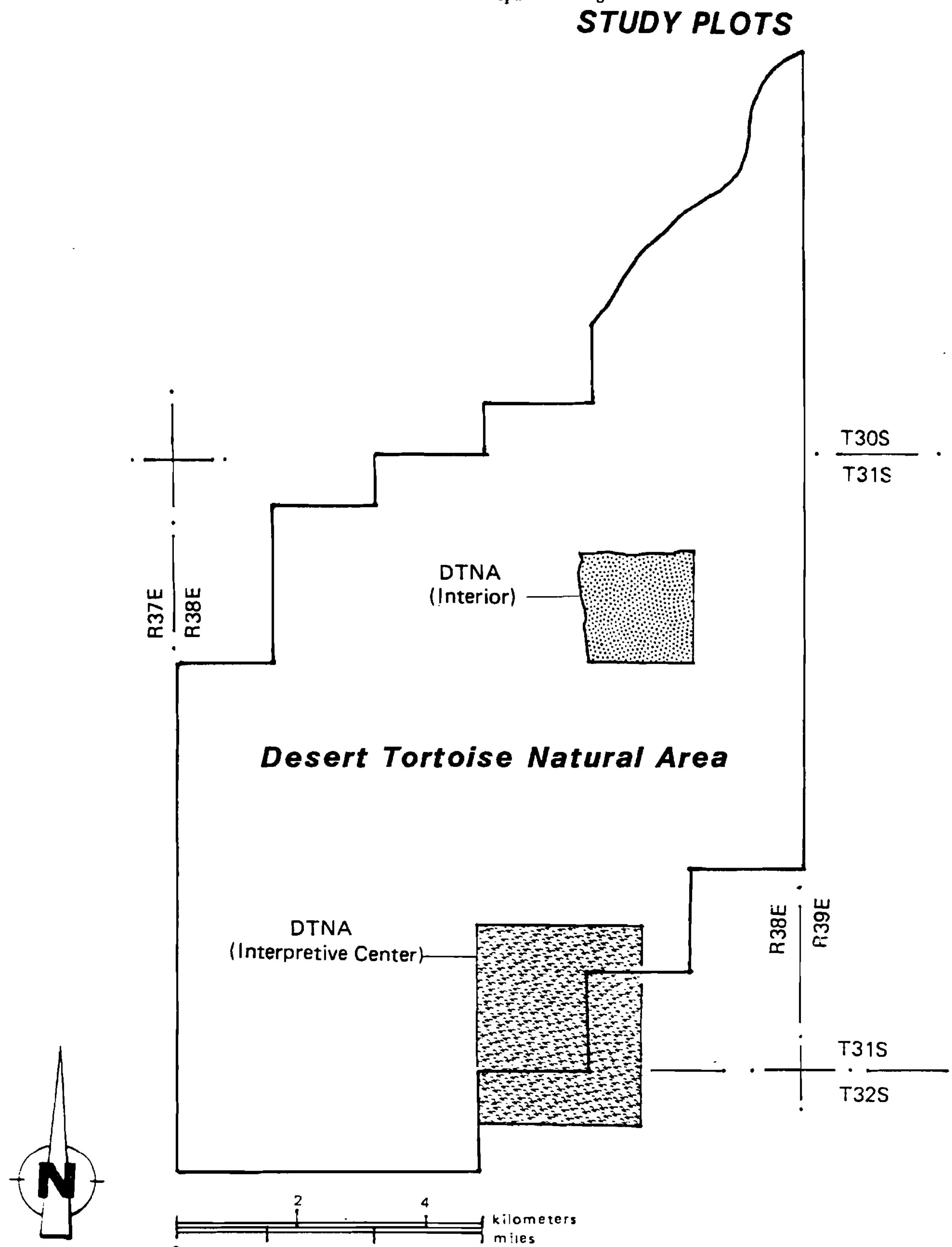

Figure 1. Locations of the interpretive center and interior study plots at the Desert Tortoise REsearch Natural Area, eastern Kern County, California.

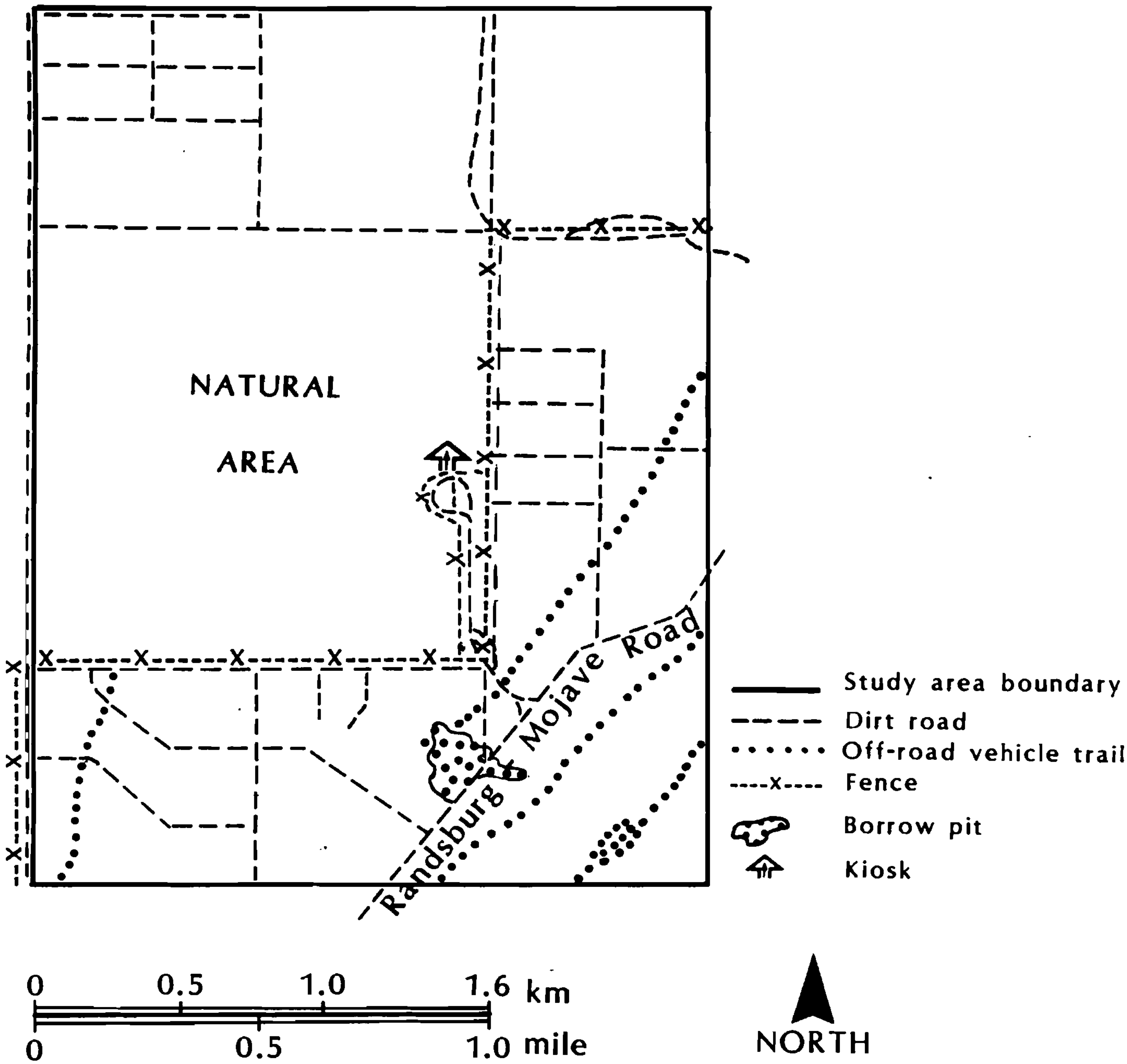

Figure 2. The Desert Tortoise Research Natural Area interpretive center plot of 7.7 km^2, including 4.53 km^2 inside the fence and 3.24 km^2 outside the fence.

statistic (Turner and Berry 1984). For each carcass, estimates were made of time of death and carapace length. Time of death was estimated using keys and figures for carcass deterioration in Berry and Woodman (1984) and Woodman and Berry (1984), respectively. Only tortoises considered dead ≤ 4 years at time of collection were used in the analysis. Carapace lengths for partial or disarticulated remains were estimated using one or more of 25 regression equations of scute size on carapace length (Berry and Woodman 1984). Annualized mortality rates were calculated for adults and subadults using the formula:

$$M = 1 - e^{-ta} \qquad (1)$$

where t is number of years and *a* is annual survivorship. Estimates of annualized mortality rates were confined to subadults and adults, because the carcasses of these size classes persist longer than those of smaller tortoises (Woodman and Berry 1984). Where possible, each carcass was assigned a cause of death, e.g., vehicle kill, gunshot, predator (canid, raven), etc. See Berry (1985, 1986) for methods of determining raven and gunshot deaths, respectively. Tortoises were considered captive releases if painted or had holes drilled in their shells.

Data were collected on cover of annual plants using the canopy coverage method of Daubenmire (1959). Annuals were sampled with 0.1 m^2 quadrats along five or more transect lines. Data on biomass (dry weight) were collected for 1982 and 1985 only.

Visitor use was estimated from visitor logs, aerial flights, and ranger patrols from the Ridgecrest and Riverside BLM offices, from Desert Tortoise Preserve Committee records, and California Department of Fish and Game reports. Human impacts to tortoise habitat were summarized using aerial photographs, on-site measurements, and field notes.

RESULTS

Interpretive Center Plot

Population Attributes

Density Estimates. Estimates of density were made for four size groups of tortoises: (1) all sizes, (2) only those ≥ 140 mm CL, (3) only those ≥ 180 mm CL, and (4) only those ≥ 208 mm CL (Table 1). In 1979 densities were higher on the subplot inside the fence than on the subplot outside, but these differences were not significant at the 95% Confidence Interval (CI). However, by 1985 density estimates were significantly lower outside the fence (95% CI) than inside. In the six-year interval between 1979 and 1985, densities inside and outside the fence also had declined significantly (95% CI). Declines were 32.1% inside the fence and 54.4% outside the fence. Declines were in the juvenile and immature 1 size classes. If, for example, densities of tortoises ≥ 180 mm inside the fence in 1979 are compared with densities of the same size group inside the fence in 1985, no significant difference is apparent. The same is true for tortoises ≥ 208 mm CL.

Sex Ratios. Sex ratios of subadults and adults (≥ 180 mm CL) differed significantly from expected 1:1 ratios in 1979 and 1985 (Table 2). When data were analyzed by subplot (inside or outside the fence), sex ratios differed significantly from the expected 1:1 ratios for tortoises inside the fence but not for those outside the fence.

Table 1. Estimated densities at the Desert Tortoise Research Natural Area interpretive center plot in 1979 and 1985 using the Stratified Lincoln Index. Estimates are for parts of the plot inside and outside the fence.

Size classes	Year	Numbers/km² (95% confidence interval) Inside	Outside
All size classes	1979	131 (111-155)	114 (90-146)
Tortoises ⩾ 140 mm CL	1979	87 (73-104)	73 (57-94)
Tortoises ⩾ 180 mm CL	1979	70 (58-84)	53 (41-69)
Tortoises ⩾ 208 mm CL	1979	56 (46-68)	39 (29-52)
All size classes	1985	89 (77-101)	52 (42-65)
Tortoises ⩾ 140 mm CL	1985	76 (66-78)	43 (34-54)
Tortoises ⩾ 180 mm CL	1985	69 (60-79)	40 (32-52)
Tortoises ⩾ 208 mm CL	1985	61 (53-71)	37 (28-47)

Table 2. An analysis of sex ratios of adults and subadults combined at the interpretive center and control plots on the Desert Tortoise Research Natural Area.

Study plot and year	Data group	Number of females, males	Z	Significance level
Interpretive center plot				
1979	All	225, 177	-2.3976	95%
	Inside fence	160, 114	-2.7781	99%
	Outside fence	70, 77	0.577	n.s.
1985	All	224, 164	-3.0433	99%
	Inside fence	171, 130	-2.3646	95%
	Outside fence	66, 56	-0.9051	n.s.
Control plot				
1979	All	73, 65	-0.6808	n.s.
1985	All	93, 89	-0.2965	n.s.

Size-age Class Structure. Size-age class structures of tortoises registered in 1979 and 1985 are shown in Tables 3 and 4, respectively. The same data were subdivided into two groups by capture location: tortoises inside the fence, and tortoises outside the fence (Tables 5 and 6). Some marked tortoises were first captured inside the fence and subsequently recaptured outside the fence or vice versa (4.4% in 1979 vs. 7.7% in 1985).

Tortoises were grouped into four size-age classes (juveniles, immatures, subadults, and adults) for X^2 analyses by year (Table 7). Size-age class structure changed significantly ($P < 0.001$) between 1979 and 1985, both when plot data were treated as a single unit and when the data were analyzed by subplot (inside or outside the fence). In almost all cases, proportions of juveniles, immatures, and subadults declined between 1979 and 1985.

When the proportions of adult (≥ 208 mm CL) and nonadult tortoises in the 1979 and 1985 samples were compared using X^2 analyses, significant differences ($P < 0.001$) were apparent (Table 8). The proportion of adults increased between 1979 and 1985 in all samples.

Recapture Rates Between Censuses. Significantly more tortoises marked inside the fence in 1979 were recaptured in 1985 than those that were marked outside the fence. Fifty percent of adult and subadult tortoises marked inside the fence were recaptured after the six-year interval, compared with 30% of this size group outside the fence ($P < 0.025$. 1 df, $X^2 = 5.16$). For tortoises of all size classes, 35% were recaptured inside the fence vs. 21% outside the fence ($P < 0.025$, 1 df, $X^2 = 6.52$). More females (≥ 180 mm CL) marked in 1979 were recaptured in 1985 than males but the differences were not significant ($X^2 = 2.20$, 1 df).

Recapture rates were analyzed as a function of visitor use levels. The plot was divided into three parts: A (low use), B (moderate use), and C (high use) (Figure 3). Recapture rates were 55% in A, 44% in B, and 24% in C. Differences in the proportions of recaptures in the three areas were significant ($X^2 = 7.33$, 2 df, $P < 0.025$).

Mortality. Remains of 107 tortoises were collected. Of these, 54 were judged to have been recent, i.e., dead ≤ 4 years (Table 9). At least 26.4% of the recent deaths were of obviously marked tortoises. The annualized mortality rate for subadult and adult tortoises was estimated at 1.3% per year between 1981 and 1985. Of the 54 recent deaths, 1 tortoise died from vandalism, 1 possibly from being overturned by sheep, 3 from gunshots, 5 from vehicles, 2 from either gunshot or vehicles, and 16 from predation by the Common Raven (*Corvus corax*). Causes of death for the remaining 26 are unknown. Vandalism, gunshots, and vehicles accounted for 11 or 20.4% of deaths. There was no significant difference between numbers of tortoises dying from these causes inside or outside the fence ($X^2 = 0.13$, 1 df). Among the 54 carcasses of tortoises dying prior to 1981 (dead ≥ 4 years), 7 (12.9%) probably were shot and 4 (7.4%) appeared to have been hit by vehicles. About 29.6% of recent deaths were attributed to ravens (66.7% of all carcasses ≤ 103 mm CL showed signs of raven predation). The level of raven predation on small tortoises (≤ 103 mm CL) at the interpretive center and control plots did not differ significantly ($X^2 = 2.54$, 1 df). However, raven predation at either or both sites exceeded levels at 13 other sites in California (Table 10) (see also Berry 1985). When data from the Natural Area plots were pooled and compared with pooled data from seven other tortoise sites in the western Mojave Desert, the differences were highly significant ($X^2 = 81.66$, 1 df, $P < 0.001$). When the pooled Natural Area data were compared with pooled data from 13 other tortoise sites in California, the differences also were highly significant ($X^2 = 106.82$, 1 df, $P < 0.001$).

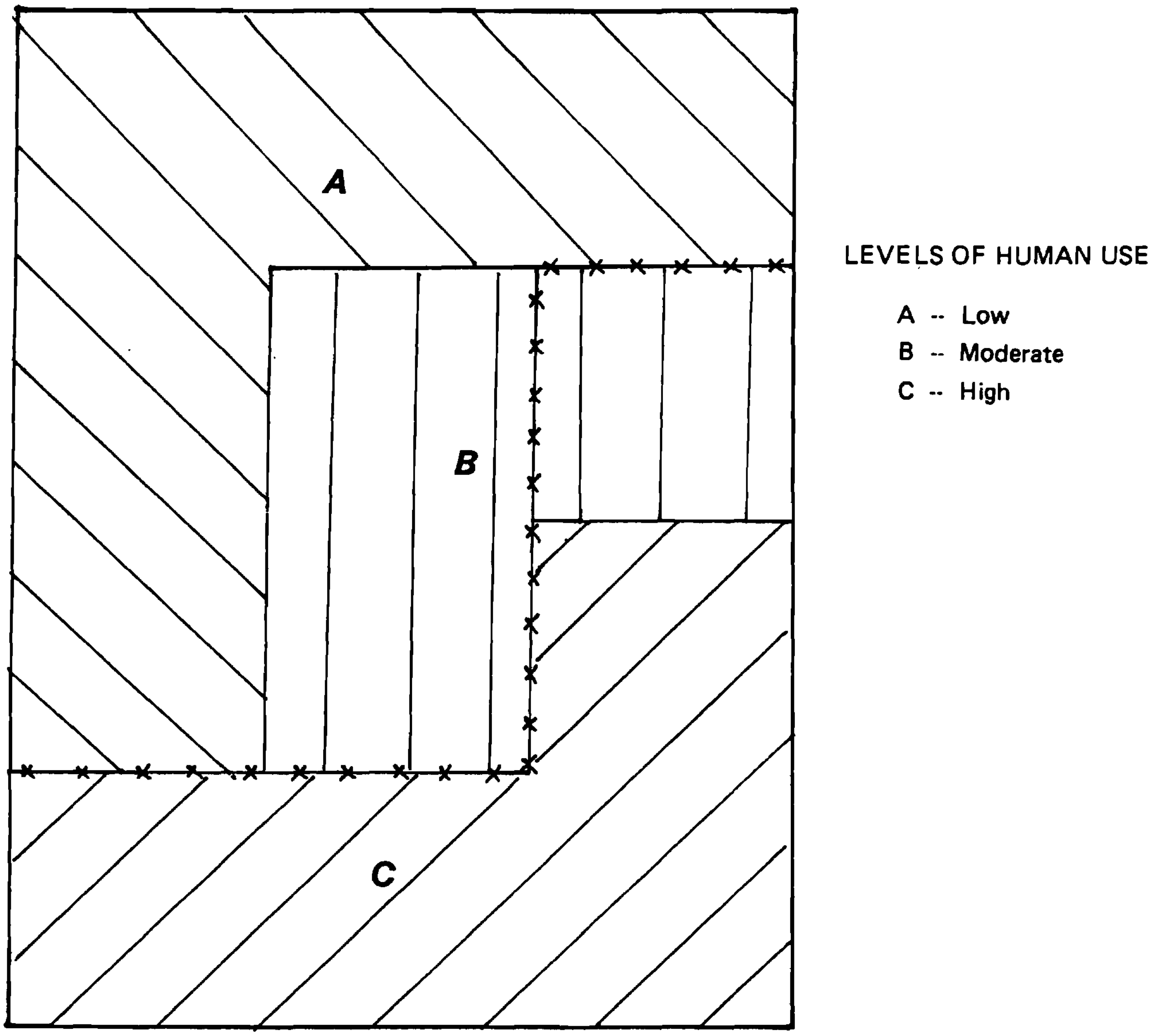

Figure 3. The interpretive center plot at the Desert Tortoise Research Natural Area was divided into three parts, based on levels of human use, for a Chi-square analysis of recapture rates. A has the least human use and C has the greatest human use.

Table 3. Size-age class structure of marked desert tortoises at the Desert Tortoise Research Natural Area interpretive center plot in 1979.

Size-age class	Unid.	Sex Male	Female	Total	% Recaptures
Juvenile 1	18			1	3.0
Juvenile 2	28			28	4.7
Immature 1	65			65	10.9
Immature 2	80			80	13.5
Subadult		47	30	77	12.9
Adult 1		36	135	171	28.8
Adult 2		94	60	154	25.9
Totals	191	177	225	593	99.7

Table 4. Size-age class structure of marked desert tortoises at the Desert Tortoise Research Natural Area interpretive center plot in 1985.

Size-age class	Unid.	Sex Male	Female	Total	% Total	% Recaptures
Juvenile 1	6			6	1.2	0
Juvenile 2	21			21	4.4	0
Immature 1	38			38	7.9	2.6
Immature 2	28			28	5.8	14.3
Subadult		19	19	38	7.9	23.7
Adult 1		40	116	156	32.4	39.1
Adult 2		105	89	194	40.3	53.1
Totals	93	164	224	481	99.9	37.0

Table 5. A comparison of numbers of marked desert tortoises inside and outside the fence at the Desert tortoise Research Natural Area interpretive center plot in 1979.

Size-age class	Inside		Outside		No. tort. in both
	Total	% Total	Total	% Total	
Juvenile 1	12	3.0	6	2.7	-
Juvenile 2	18	4.5	9	4.1	-
Immature 1	42	10.6	24	10.9	-
Immature 2	51	12.8	34	15.5	5
Subadult					
male	25	6.3	24	10.9	2
female	20	5.0	9	4.1	-
Adult 1					
male	19	4.8	23	10.5	6
female	94	23.7	46	20.9	5
Adult 2					
male	70	17.6	30	13.6	7
female	46	11.6	15	6.8	1
Totals[1]	397	99.9	220	100.0	26

[1] These totals include tortoises which were found both inside and outside the fence (26 tortoises were counted twice). These totals do not match the total in Table 3.

Table 6. A comparison of numbers of marked desert tortoises inside and outside the fence at the Desert Tortoise Research Natural Area interpretive center plot in 1985.

Size-age class	Inside		Outside		No. tort. in both
	Total	% Total	Total	% Total	
Juvenile 1	6	1.6	0	0	-
Juvenile 2	10	2.7	11	7.2	-
Immature 1	26	7.2	13	8.5	1
Immature 2	22	6.0	7	4.6	1
Subadult					
male	15	4.1	6	3.9	2
female	14	3.8	6	3.9	1
Adult 1					
male	29	7.9	15	9.8	4
female	79	21.6	43	28.1	6
Adult 2					
male	86	23.6	35	22.9	16
female	78	21.4	17	11.1	6
Totals[2]	365	99.9	153	100.0	37

[2] These totals include tortoises which were found both inside and outside the fence (26 tortoises were counted twice). These totals do not match the total in Table 3.

Table 7. Results of Chi Square tests comparing size-age class structures of tortoise populations on two plots at the Desert Tortoise Research Natural Area. Tortoises were grouped into four size-age classes (juvenile, immature, subadult, and adult) for the analyses.

Plot name and data set	Years	X^2	*P*
Interpretive center			
All data	1979, 1985	17.64	< 0.001
Inside fence	1979, 1985	24.47	< 0.001
Outside fence	1979, 1985	17.53	< 0.001
Control			
All data	1979, 1985	8.88	< 0.05

Table 8. A comparison of proportions of adult (≥ 208 mm carapace length) and nonadult tortoises on two plots at the Desert Tortoise Research Natural Area.

Plot name and data set	Year	No. adults	No. nonadults	X^2	*P*
Interpretive center					
All data	1979	325 (55%)	268 (45%)		
	1985	350 (73%)	131 (27%)	36.69	< 0.005
Inside fence	1979	229 (58%)	168 (42%)		
	1985	272 (75%)	93 (25%)	23.94	< 0.005
Outside fence	1979	114 (52%)	106 (48%)		
	1985	110 (72%)	43 (28%)	15.16	< 0.005
Control					
All data	1979	102 (54%)	87 (46%)		
	1985	156 (67%)	78 (33%)	7.06	< 0.01

Table 9. Size-age class structure of tortoises dying between 1981 and 1985 at the interpretive center plot on the Desert Tortoise Research Natural Area.

Size-age class	Sex Unid.	Male	Female	Total	% Total
Juvenile 1	4			4	7.4
Juvenile 2	19			19	35.2
Immature 1	3			3	5.65
Immature 2	3			3	5.6
Subadult		1	1	2	3.7
Adult 1 and 2	1	14	8	23	42.6
Totals	30	15	9	54	100.1

Table 10. Tortoises (≥ 110 mm carapace length) probably killed by ravens at 15 tortoises study plots in California (Berry 1985).

Desert region Plot name	Numbers of carcasses Raven kills	 Other	% raven kills[1]
Western Mojave			
Desert Tortoise Natural			
Area interpretive center	16	8	66.7
Area control	73	19	79.4
Fremont Valley	11	26	29.7
Fremont Peak	3	5	
Kramer	9	11	
Calico	1	0	
Stoddard Valley	14	15	48.3
Lucerne Valley	4	2	
Johnson Valley	8	9	
Eastern Mojave Desert			
Ivanpah Valley	3	10	
Goffs	2	5	
Colorado Desert			
Ward Valley	1	2	
Chemehuevi Valley	1	35	2.8
Chuckwalla Bench	13	35	27.7
Chuckwalla Valley	0	4	

1 Percent not calculated when samples were less than 24.

Collection of Wild Tortoises and Release of Captives

While working on the plot in 1979, one field worker (BLM field notes) stopped a motorcycle rider from collecting a tortoise. In 1982 Warren and Elizabeth Forgey (pers. comm.) encountered people intent on releasing captives near the interpretive center kiosk. In one case the Forgeys took three captives from a person attempting to release them. In a second case, they introduced a person with captives to a person who was planning to collect. Stockton (1984) reported finding a diseased captive and captives with paint on their shells and holes drilled in carapaces. Notes from the visitor registers at the interpretive center indicate that visitors have released at least 12 tortoises. California Department of Fish and Game wardens are another source of tortoises. They bring captives and confiscated wild tortoises to the Natural Area for release, in spite of a departmental policy prohibiting such releases (e.g., pers. comm. M. Henry, F. Tharp).

Three released captives were found dead. One was a desert tortoise with extensive fiber-glass repairs to the shell (1985). Two others were species not found in the desert: a Texas tortoise (*Xerobates berlandieri*) in 1979 (fresh in 1977), and a box turtle (probably *Terrapene* sp.) in 1985. In 1985, one released captive was alive and part of the marked resident population.

Changes in Habitat Condition

Abundance of Annual Plants. Cover of annuals was lower in 1985 than in 1979 both inside and outside the fence (Table 11). Biomass values were available only for 1985. Shields, who worked on the plot in both census years, noted that annual production was a little less in 1979 than in 1985.

Inside the Fence. The contrast between habitat condition inside and outside the fence has become increasingly marked since the fence was erected. In 1979, 9.6 km of old dirt roads existed on the subplot inside the fence (Figure 2). In 1979 and early 1980, additional surface disturbance occurred with construction of the interpretive center, which includes a kiosk, two outhouses, one wide loop trail, two nature trails, an access road, and parking lot. The total disturbed surface area was estimated at 2.17 ha. In April 1979 a herd of sheep (unauthorized) entered the Natural Area and grazed inside the fence near the interpretive center probably for a day or more. Between 1979 and 1985, the old dirt roads received little use--an occasional track from a two- or four-wheel vehicle. In contrast, the fenced access road became a corridor for ORV use. Trails from two-wheeled vehicles developed on either side of the 0.8 km road. The parking lot received similar use, with trails and vehicle tracks proliferating in the vegetated area between the designated parking lot and the fence. Occasionally two-wheeled vehicles entered the Natural Area (estimated occurrence = once/month) through the gate intended for visitors. Old and fresh tracks were evident near the interpretive center and nature trails. Sounds of gunfire were frequently heard both inside and outside the fence during the censuses, particularly during Easter week and over the three-day Memorial Day weekend.

Outside the Fence. A comparison of the surface area denuded of vegetation by vehicles and campers in 1979 and 1985 is shown in Table 12. No change occurred in graded roads. However, habitat lost to ORV camps and the borrow pit increased 23% in area and ORV trails ≥ 1 m wide increased 130% in length and 157% in area. Overall, 3.71 ha of tortoise habitat was lost from vehicle-related activities in 6 years. (This figure does not include damaged or denuded trails < 1 m wide.) Since 1979, the borrow pit has been used increasingly as a camp site and as a starting and ending point for ORV activities. Some races occur near and along the Natural Area fence.

Sheep grazed almost annually, in violation of California City ordinances. They were present in both 1979 and 1985. In late March and early April of 1985 a flock of 300 grazed for two weeks, making several passes and bedding at several sites. During strong winds, the sheep excavated depressions in the lee of shrubs, decreasing annual plant productivity. Many trampled tortoise burrows were observed, and an overturned juvenile was found dead within hours after the flock had passed.

Levels of Human Use

During the 1970s, the BLM identified recreational activities within concentrated use zones in the California deserts and measured numbers of visitor-use-days (VUDs) (U.S. Bureau of Land Management, 1979. Summary of Recreation Use in the California Desert. Riverside, Calif.). For the general area in the vicinity of the interpretive center, the figure was 100 VUDs/km^2/yr. Figures increased markedly in the 1980s. Visitor counts taken from the register at the interpretive center ranged from 832 in fiscal year 1982 to 1,964 in 1985 (J. Aardahl, pers. comm.). Most people signing the register probably used the interpretive facilities inside the fence. Outside the fence, vehicular-oriented recreation also has increased markedly. Uptain (1983) estimated that about 7,000 vehicles/yr were in the vicinity of the Natural Area during 1982 and 1983 and that 7.5% of the use (525 vehicles) was in the portion of the plot outside the fence or nearby. Desert Tortoise

Table 11. Annual plant production at the Desert Tortoise Research Natural Area interpretive center plot in 1979 and 1985.

Location and measures of productivity	1979 March	1979 April	1979 May	1985 April	1985 May
Inside the Fence					
No. transects	9	9	9	5	5
No. quadrats (0.1 m^2)	180	180	180	250	250
Mean cover (cm^2/m^2, %)	840, 8.4	2680, 26.8	1910, 19.1	754, 7.5	274.8, 2.7
(range)	(510-1900)	(2200-3200)	(810-2250)	(385-1192)	(172-503)
Mean biomass (g/m^2)	—	—	—	4.7	0.96
(range)				(3.9-5.9)	(0.52-1.81)
Outside the Fence					
No. transects	6	6	6	3	3
No. quadrats (0.1 m^2)	120	120	120	150	150
Mean cover (cm^2/m^2, %)	1210, 12.1	1718, 17.8	1490, 14.9	678, 6.7	513, 5.1
(range)	(580-1320)	(1310-2770)	(950-1990)	(433-951)	(378-672)
Mean biomass (g/m^2)	—	—	—	4.1	1.3
(range)				(2.9-5.5)	(1.1-1.7)

Table 12. Vehicle-related impacts to the portion of the Desert Tortoise Research Natural Area interpretive center plot occurring outside the fence.

Source of habitat loss	Year 1979	1985	% Change
Graded roads			
length (m)	6,500	6,500	0
area (m^2)	36,200	36,200	0
Off-road vehicle camps and borrow pit (m^2)	43,000	53,000	23.3
Off-road vehicle trails (⩾ 1 m)			
length (m)	7,268	16,723	130.1
area (m^2)	11,218	28,878	157.4
Total area (m^2)	90,418	118,078	30.6

Preserve Committee tour guides (Laura Stockton and Elizabeth and Warren Forgey, pers. comm.) reported that vehicle-oriented recreationists at least doubled between 1979-80 and 1985 in this same area.

Control Plot

Population Attributes

Density estimates. Density estimates for the entire population showed a decrease in the three-year interval between 1979 and 1982, but the decrease was not statistically significant (95% CI) (Table 13). Decreases did not occur in all size-age classes. The decrease was in the smaller size-age classes, those tortoises < 140 mm CL. In the larger size-age classes, densities increased, but not significantly so. Sex ratios of adults and subadults did not differ significantly from expected 1:1 ratios in either census year (Table 2).

Size-age class structure. Size-age class distributions of tortoises registered in 1979 and 1982 are shown in Tables 14 and 15, respectively. Tortoises were grouped into four size-age classes for X^2 analysis by year (Table 7). About 54% of tortoises captured in 1979 were recaptured in 1982 (Table 15). Figures ranged from a low of 25% for the immature 1 size class to a high of 78.8% for the adult 2 size class. The size-age class structure changed significantly ($P < 0.05$) between 1979 and 1982. Proportions of immatures and subadults declined, while adults increased. When proportions of adult and nonadults in the 1979 and 1982 samples were compared using X^2 analysis, significant differences ($P < 0.01$) were also apparent (Table 8). Adults increased while nonadults decreased.

Mortality. Between fall of 1978 and June of 1979, remains of 202 tortoises were collected. One hundred thirty-seven of these were classified as recent deaths (dead ⩽ 4 years). Juveniles and adults (56.2% and 33.5%, respectively) composed the majority of the remains (Table 16). Seventy percent of the juveniles probably were killed by ravens. Deaths of 20 tortoises (14.6%) probably can be attributed to gunshots. One adult was found dead in a mining pit, probably from

Table 13. A comparison of estimated densities at the Desert Tortoise Research Natural Area control plot in 1979 and 1982 using the Stratified Lincoln Index.

Size classes	Numbers/km^2 (95% confidence interval) 1979	1982
All size classes	147 (113-192)	129 (102-165)
Tortoises ≥ 140 mm CL (immature 2's, subadults and adults)	74 (57-97)	104 (81-133)
Tortoises ≥ 180 mm CL (subadults and adults)	59 (45-78)	92 (71-119)
Tortoises ≥ 208 mm CL (adults)	44 (32-59)	70 (53-91)

Table 14. Size-age class structure of marked desert tortoises at the Desert Tortoise Research Natural Area control plot in 1979.

Size-age class	Unid.	Sex Male	Female	Total	% Total
Juvenile 1	12			12	6.3
Juvenile 2	3			3	1.6
Immature 1	14			14	7.4
Immature 2	22			22	11.6
Subadult		17	19	36	19.1
Adult 1		11	32	43	22.8
Adult 2		37	22	59	31.2
Totals	51	65	73	189	100.1

Table 15. Size-age class structure of marked desert tortoises at the Desert Tortoise Natural Area control plot in 1982.

Size-age class	Unid.	Sex Male	Female	Total	% Total	% Recaptures
Juvenile 1	15			15	6.4	0
Juvenile 2	5			5	2.1	0
Immature 1	8			8	3.4	25.0
Immature 2	22			22	9.4	40.9
Subadult	2	16	10	28	12.0	37.0
Adult 1		17	54	71	30.3	54.9
Adult 2		56	29	85	36.3	78.8
Totals	52	89	93	234	99.9	54.3

exposure. Another adult probably died from an act of vandalism. The tortoise had been placed in a five gallon can in the center of a 2.4 m-deep mining pit and died while trying to lay eggs, within a day of removal from the pit. Causes of death for the other tortoises are unknown.

In 1982, remains of 32 tortoises were collected. Thirty were judged to have died since the fall of 1979 (Table 16). Six of the 30 (20%) were marked. Twenty-one (70%) of the 30 were juveniles and eight were (27%) adults. Nineteen (90%) of the 21 juveniles probably were killed by ravens. One immature and three adults (13%) probably were killed by gunshots. One adult female appeared to have died from a prolapsed uterus and problems associated with egg laying. The estimated annualized mortality rate for adults and subadults between January of 1974 and June of 1982 was 2.6%. Figures were 4.7% for January of 1974 through 1979 and 1.3% from January of 1980 to June of 1982.

Table 16. Numbers of tortoises dying at the Desert Tortoise Research Natural Area control plot between Junuary 1974 and June 1982.

Size-age class	Number of tortoises (% of sample) Time interval 1974-1979	1980-1982.5
Juvenile 1	31 (22.6)	15 (50.0)
Juvenile 2	46 (33.6)	6 (20.0)
Immature 1	8 (5.8)	0 (0.0)
Immature 2	2 (1.5)	1 (3.3)
Subadult	4 (2.9)	0 (0.0)
Adult 1	31 (22.6)	3 (10.0)
Adult 2	15 (10.9)	5 (16.7)
Totals	137 (99.9)	30 (100.0)

Changes in Habitat Condition

Abundance of Annual Plants. Cover values for the 1979 and 1982 samples were similar (Table 17).

Human-Induced Changes. During the 1979 spring census, fresh vehicle tracks were observed on one road. Three mining excavation pits in the northwest quarter were too deep for tortoises to escape. One pit held a dead tortoise. During the 1979 spring census, two pits were fenced to prevent further deaths. Fresh shell casings from shotguns were present. In fall of 1979 several fresh vehicle tracks were on the dirt road and in washes.

During the 1982 census, few signs of vehicle tracks on- or off-road were evident. Two vehicles were observed on the plot. Both entered the Natural Area from the western side, at least 6.4 km away. One vehicle contained sightseers and the other a man who stated that he was looking for a way to herd his sheep through the Natural Area, from the area of Highway 395 on the east to the Mendiburu ranch on the west. He drove on roads, as well as cross-country. Sounds of gunfire were heard on several occasions. Fresh shotgun casings were also present.

DISCUSSION

Population attributes can change as a result of natural causes or human-induced changes in the environment. Some population attributes, such as size-class distribution, may appear to change with local forage conditions and low forage production. For example, Turner and Berry (1984b, 1985, 1986, unpub. data) conducted annual surveys of tortoises in eastern California between 1983 and 1986. In years of low forage production (7.1-150.3 cm^2/m^2; 0.02-6 g/m^2), proportions of small tortoises $\leq$ 140 mm CL were substantially lower in samples than in years with moderate to high forage production (1100-1700 cm^2/m^2; 40 g/m^2).

To measure population trends, three or more samples taken at evenly spaced intervals and using similar or identical methods are desirable. In our case, we have only two samples and they do not cover the same time period. Methods were very similar but not identical. The greater expertise of field workers at the interpretive center plot in 1985 and the additional field work conducted at the control plot in 1982 should have contributed to a higher capture rates of all tortoises, particularly those $\leq$ 140 mm CL, in those census years. We should keep these factors in mind when considering interpretations of the data.

Did annual production affect the sampling outcome at the two study sites? The annual plant data do not provide a clear answer, partly because biomass data were not collected in 1979 at either site. Biomass figures for 1985 at the interpretive center were in the range cited by Turner and Berry (1984b, 1985, 1986) for a low forage production or poor year. However, cover values were considerably higher and were in the range of a moderate to high production year! At the control site, cover values were lower for 1982 than 1979, but still within the range of a moderate to high production year. Biomass figures were comparable to the low production year. For the purposes of this analysis, we will rely on the judgment of the field workers and assume that annual plant production was similar during the study years and that forage production was not particularly poor.

Tortoise densities at the interpretive center plot declined significantly both inside and outside the fence in the six-year interval between censuses. Data on 1985 recaptures of tortoises registered in 1979 indicate that declines were in a gradient, with the lowest levels occurring inside the fence at the greatest distances from the interpretive center and the highest levels outside the

Table 17. Annual plant production at the Desert Tortoise Research Natural Area control plot in 1979 and 1982.

Measurements of productivity	1979			1982
	March	April	May	----
No. transects	5	5	5	5
No. quadrats (0.1 m^2)	300?	300?	300?	300?
Mean cover (cm^2/m^2, %)	(1050, 10.5)	(3670, 26.7)	(2960, 29.6)	(1450, 14.5)
(range)				(820-1810)
Mean biomass (g/m^2)	---	---	---	51.4
(range)				(34.5-78.4)

fence. These same recapture data provide circumstantial evidence that declines were greater in areas with more human use and contact, because significantly more tortoises marked in 1979 were recaptured in 1985 in areas with low levels of human use inside the fence than in areas of moderate to high human use both inside and outside the fence.

Since declines occurred both inside and outside the fence, the sources of declines might be similar in both areas. Declines probably were due to a combination of collecting, vandalism, vehicle kills, intensive predation by ravens, and natural causes of death. Unfortunately, the remains collected on this plot are less likely to be representative of the tortoises dying there than on many other tortoise plots, because of the high levels of human use. Some remains undoubtedly were carried away by people for souvenirs (Berry and Woodman 1984). Outside the fence, where vehicle use is intensive, tortoises killed by vehicles or carcasses shattered by vehicle contact are likely to be broken into small pieces and disappear much more readily than undisturbed remains. Therefore estimates of annualized mortality rates for adults and subadults are likely to be lower than actual.

Vandalism and vehicle kills occurred both inside and outside the fence at equivalent levels. The 20.4% figure for vandalism and vehicle kills is comparable to rates reported at other tortoise plots with moderate to high levels of human use but is substantially higher than sites with no or little human use, e.g., Ivanpah Valley and Goffs (Berry 1984c, 1986).

Changes in size-age class composition of the interpretive center population were possibly the result of (1) raven predation pressure, (2) release of captive and wild tortoises, and (3) immigration of subadult and adult tortoises, e.g., from higher density areas in the interior of the Natural Area. Ravens probably were responsible for reductions in juveniles and immatures. They appear to have been preying on juveniles (≤ 103 mm CL) at least since 1978-1979 and leaving the remains near the wooden fence posts (Campbell 1983). The proportion of juvenile carcasses with signs of raven predation were significantly higher than for any other tortoise study plot in California, with the exception of the Natural Area control plot (Berry 1985). One possible scenario is that raven predation increased about 1978-1979 in association with increased human use, fence construction, and development of interpretive structures. Juveniles up to five to seven years of age and ≤ 103 mm CL (hatched from about 1972 on) were at risk. By 1985, tortoises hatched in 1972 and later years had experienced higher mortality rates from ravens (and other sources) than previously, and thus were in lower proportions and under-represented in the juvenile and immature classes.

Adult and subadult numbers remained at approximately the same levels between 1979 and 1985 both inside and outside the fence, yet recapture rates indicate substantial losses of the individuals marked in 1979. Compared with recapture data from other study sites in California, the rates for adults and subadults inside the fence (50%) and outside the fence (30%) are low (Berry, unpub. data). The marked tortoises could have been removed by collecting or vehicle kills. Replacements may have come from tortoises released by visitors or tortoises immigrating from other areas, such as the interior of the Natural Area.

The control plot showed no statistically significant changes in total population but the decrease may be indicative of a downward trend in future years. Changes in size-age class composition were similar to those experienced on the interpretive center plot and were possibly due to raven predation also. Of the 77 remains of juveniles dying between 1974 and 1979, 70% showed signs of raven predation. For tortoises dying between early 1980 and June of 1982, the figure was 90%. The raven kills did not appear to be associated with the fence. Instead, the remains were concentrated in the quarter of the plot with the raven's nest (Berry 1985).

Deaths from vandalism on the control plot did not decline between the 1974 and 1982. For tortoises dying between 1974 and 1979 the figure was 14.6%, compared with 13.0% for tortoises dying between 1980 and mid-1982. Tortoises dying from signs of gunshots between 1980 and 1982 were not near the corner of the plot touching the fence edge, indicating that vandals must have walked or driven onto the Natural Area for a kilometer or more before shooting the tortoises. The estimated annualized mortality rate for adults and subadults dropped markedly between 1974-1979 and 1980-1982, however, from 4.7% to 1.3%. The latter figure is similar to mortality rates for adults at Goffs, an undisturbed study site in eastern California (Turner and Berry 1984b, 1985) and for some other remote tortoise plots (Berry et al. 1986).

The figures for deaths from vandalism may not represent the "worst case" situation at the Natural Area. In studies undertaken for the California Department of Fish and Game between 1980 and 1983, Campbell (1982) reported more extensive use of firearms on the southern and western boundaries than elsewhere, and Uptain (1983) showed most use on the western boundary. Both Campbell (1982) and Uptain (1983) reported acts of vandalism on the western and northern boundaries of the Natural Area.

MANAGEMENT IMPLICATIONS

Several issues need attention: (1) declines in tortoise populations inside the fence at the interpretive center plot; (2) the shift toward adults in size-age class composition on both plots; (3) deaths from vehicle kills inside the fence; (4) the high figures for vandalism on the boundary and the interior of the Natural Area; (5) the apparent intensive and successful predation by ravens on the juveniles; and (6) collection and release of other tortoises.

Declines in tortoise populations due to collecting, vandalism, and vehicle kills on the Natural Area might be reduced or eliminated by increasing the presence of law enforcement personnel at the Natural Area. How much patrolling and how much "presence" is needed to reduce or eliminate illegal activities? Obviously past and current efforts have been inadequate. We estimate that BLM personnel visited the Natural Area an average of once/week since 1980. Visits were usually to check the interpretive facilities and lasted for periods of less than an hour. (This estimate was taken from a summary of the BLM Ranger and recreation logs for 1985, prepared by George Moncsko). We have not sought records of patrols by California Department of Fish and Game wardens but will do so. We do not expect that frequent and regular patrols occurred.

The following patterns of patrols by law enforcement personnel should improve the situation considerably: (1) patrols 8-hours/day each weekend from late February through June and from late August through mid-October; (2) patrols 8-hours/day during the Easter vacation period, which may last two weeks because of differences in standard school vacation times; and (3) occasional patrols during the week at all times of year. The Ranger or Warden could also enforce the grazing closure.

A naturalist, resident at the interpretive facilities on weekends and during Easter vacation, would be helpful but probably would be unable to prevent vandalism and other illegal acts (see Campbell 1982). Closure of the Natural Area to shooting would facilitate law enforcement and, if posted at regular intervals on the fence, could reduce vandalism.

Reducing raven predation promises to be a challenge. Ravens are long-lived, extremely wary, and possibly the most intelligent of the raptors (see Berry 1985 for a summary of references). Several ravens may have developed a "juvenile" tortoise habit and are regularly and selectively seeking out juveniles (Dr. Hartmut Walter, pers. comm.). If they are the cause of changes in size-age composition at the two plots, then a plan should be developed to control their activities immediately. Simply obtaining a permit to shoot a few may not be an adequate solution.

The boundary fence at the Natural Area is functioning to protect habitat and populations significantly, particularly in the interior. The fence is likely to be more effective when completed, and if breaks are identified and repaired in a timely manner. The interpretive center facilities are receiving considerable visitor use by the public. New and rotating displays, particularly on vandalism, ravens, and study plot data, could enhance visitor enjoyment and through education, increase the protective attitude of the public.

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EXCAVATION OF WINTER BURROWS AND RELOCATION OF DESERT TORTOISES (*GOPHERUS AGASSIZII*) AT THE LUZ SOLAR GENERATION STATION KRAMER JUNCTION, CALIFORNIA.

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ABSTRACT - With the proposed construction of a solar generation plant at Kramer Junction, San Bernardino County, California, LUZ Engineering of Los Angeles contracted to remove desert tortoises from the construction area. Between December 9 and December 16, 1985, 490 acres of Mojave desert were systematically searched, and 280 tortoise burrows and kit fox dens excavated. Eight adult tortoises were found. The tortoises were temporarily relocated to a man-made hibernaculum at Edward's Air Force Base. Other animals were removed from the site, and released in a nearby section administered by the California Department of Fish and Game. These animals included 15 Merriam's kangaroo rats, 1 southern grasshopper mouse, and 1 Mojave rattlesnake.

INTRODUCTION

With the proposed construction of a solar electrical generation station (SEGS) at Kramer Junction, San Bernardino County, California, LUZ Engineering of Los Angeles contracted to remove hibernating desert tortoises from the construction area. The purpose of this report is to describe the results of the excavation and relocation of these tortoises.

The proposed site of SEGS 3 and SEGS 4 stations is approximately 2 kilometers north-northwest of Kramer Junction (Figure 1). The initial construction area encompasses about 490 acres which borders the west side of U.S. Highway 395 (T11N, R6W, S30 & S31; SBBM). The site represents the lower portion of a large bajada, and gently slopes down to the south. The vegetation of the site is extremely uniform, and is composed almost exclusively of spiny saltbush (*Atriplex spinifera*), with scattered individuals of cottonthorn (*Tetradymia axillaris*) and burro bush (*Ambrosia dumosa*). Creosote bush (*Larrea tridentata*) is conspicuously absent from the site.

METHODS

The site was divided into three sections (A1, A2, and A3). The first area, A1, is designated for the construction of evaporation ponds and support facilities. It is in the E 1/2 of Section 31, and lies adjacent to Highway 395. The second section, A2, lies in the W 1/2 of Section 31, and is designated to contain the solar mirrors of SEGS 3 and a portion of those for SEGS 4. The final area, A3, is in the S 1/2 of the SW 1/4 of Section 30, and will contain the remainder of the SEGS 4 mirrors.

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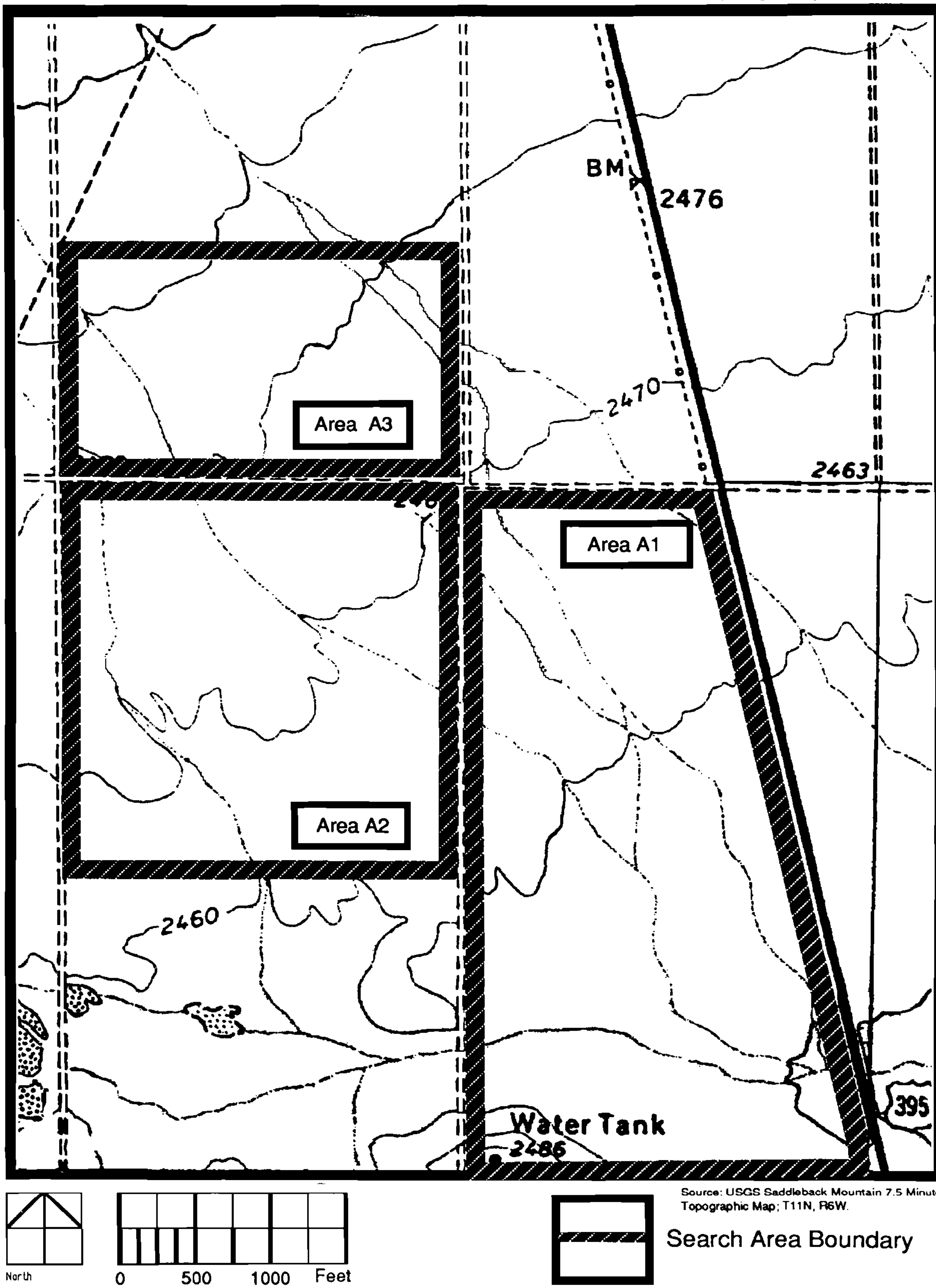

Figure 1. Search Areas for Kramer Junction Desert Tortoise Relocation, San Bernardino County, California. December 1985.

Field work was performed by the authors and volunteer helpers from California State Polytechnic University, Pomona. The areas were systematically searched in parallel belt transects until the entire site was covered. Each worker was responsible for a transect of approximately 30 feet in width. When a potential tortoise burrow was encountered, one of the two authors was called to investigate it. If it could not initially be determined that the burrow was empty, the burrow was flagged with surveyors tape, and its location mapped. Searching continued in this fashion until each area was completely searched. Upon the completion of the search and flagging, two-man teams hand excavated the flagged burrows. If a tortoise was encountered, one of the authors was called to handle the animal.

All captured tortoises were measured, weighed, photographed and marked according to procedures described by Berry (1984). Tortoises were assigned a unique number preceded by the letters "LUZ", and the LM11 scute (left marginal, No. 11) was filed to identify them as animals relocated during this project. The animals were placed in individual cardboard boxes, covered with newspaper, and placed inside a dry and abandoned water tower until the completion of the field work.

Searching and flagging of tortoise burrows and kit fox dens for the A1 section began on December 9, 1985. Although LUZ had informed the authors no construction was to take place on portions of A1, the entire section was searched. Searching and flagging of A2 and A3 proceeding in a similar fashion, and was completed by the afternoon of December 11.

Following the excavation of burrows located during the systematic searches, which was completed December 14, two-man teams randomly re-searched the three areas to excavate missed burrows, or to enlarge burrows whose terminus could not be determined during the initial digging. Field work was completed on the afternoon of December 15.

The captured animals were transported, in their boxes, to Baxter's home in Lake Mathews, California. There they were placed in a cool, dark storage shed until December 27, 1985, at which time they were transported to the northwest section of Edward's Air Force Base. There, they were placed inside a man-made hibernaculum constructed specifically for this purpose.

Attempts were also made to remove small mammals from the construction area. Sherman live-traps, lined with cotton and baited with peanut butter and oatmeal, were set on the nights of December 9, 13, and 14. There was a total of 197 trap-nights. Traps were not set the other nights due to below freezing temperatures.

RESULTS

A total of 282 burrows were excavated in the three areas. This yielded 8 adult desert tortoises and one Mojave Rattlesnake (*Crotalus scutulatus*). The sex ration of the tortoises was 50 percent male and 50 percent female. Males ranged in size (medial carapace length; [MCL]) from 230 mm to 265 mm, while females ranged from 238 mm to 265 mm MCL. Most tortoises exhibited some flaking of their scutes, and all were awakened by handling. One female urinated upon capture, while another urinated during marking procedures.

Thirteen sets of tortoise remains were found on the site. Three sets were relatively intact, including one which had been shot. However, most remains were scattered fragments of old bones. One dead female was discovered on the surface. It may have been flushed from its burrow by recent heavy rains, and later died from freezing. Eggshell fragments were found in two burrows.

Live-trapping resulted in the capture of 15 Merriam's kangaroo rats (*Dipodomys merriami*) and one southern grasshopper mouse (*Onychomys torridus*). These animals, and the captured Mojave rattlesnake, were relocated to a nearby section of property administered by the California Department of Fish and Game.

Other vertebrate species whose presence could be confirmed on the site included the: marsh hawk (*Circus cyaneus*), common raven (*Corvus corax*), cactus wren (*Campylorhynchus brunneicapillus*), water pipet (*Anthus spinoletta*), sage sparrow (*Amphispiza belli*), horned lark (*Eremophila alpestris*), white-tailed antelope squirrel (*Ammospermophilus leucerus*), and the black-tailed jackrabbit (*Lepus californicus*). Diagnostic evidence was found for the presence of the: burrowing owl (*Athene cunicularia*), Botta's pocket gopher (*Thomomys bottae*), domestic cat (*Felis domesticus*), domestic dog (*Canis familiaris*), and the coyote (*Canis latrans*).

SUMMARY

The SEGS 3 and SEGS 4 project site is in an area of Mojave desert that exhibits low perennial vegetative diversity. Dominated by spiny saltbush, it lacks most other perennial vegetation. Between December 9, and 15, 1985, 282 burrows were excavated. Eight desert tortoises were discovered, removed, and marked. These animals were temporarily relocated to a group hibernaculum at the Edward's Air Force Base. Fifteen Merriam's kangaroo rats, one southern grasshopper mouse, and one Mojave rattlesnake were also captured, and removed to a nearby Department of Fish and Game property.

ACKNOWLEDGMENTS

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LITERATURE CITED

Berry, K. H. 1984. A description and comparison of field methods used in studying and censusing desert tortoises. Appendix 2 *in*: K. H. Berry (ed.), The status of the desert tortoise (*Gopherus agassizii*) in the United States. Report to the Fish and Wildlife Service, Order No. 11310-0083-81.

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REPORT OF CONTINUING FIELD WORK ON THE DESERT TORTOISE (*GOPHERUS AGASSIZII*) AT THE TWENTYNINE PALMS MARINE CORPS AIR GROUND COMBAT CENTER, SPRING 1985

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ABSTRACT - Field work as part of a U.S. Navy contract for the study of the desert tortoise at the Twentynine Palms Marine Corps Air Ground Combat Center, was performed in the spring of 1985. Two phases of research were undertaken: (1) the establishment of a one-half square mile permanent study plot, and (2) monitoring of tortoises that were relocated to man-made burrows in December, 1984. Thirteen tortoises were captured, marked and released on the permanent plot. The distribution of tortoise burrows in the permanent plot possibly suggested their location may be associated with the ecotones of certain plant communities. The relocation effort was apparently successful; of the 11 animals relocated in December 1984, five were recaptured during searches of the relocation site. Little evidence was found that the relocated tortoises were attempting return to their original locations.

INTRODUCTION

With the proposed construction of a new VSTOL (vertical/short takeoff and landing) airstrip in 1984 at the Twentynine Palms Marine Corps Air Ground Combat Center (MCAGCC), the Department of the Navy contracted to study the tortoises in the construction zone and elsewhere on the base. The study had two thrusts: (1) to relocate tortoises which would be in danger during and after the construction of the VSTOL airstrip; and (2) to gather more information about tortoise numbers and ecology on the base. The general scope of the contract was to gather baseline habitat and population data for the tortoises in the Sand Hill and West Training Areas of the MCAGCC, and to formalize a management plan for the desert tortoise within these two areas.

Relocation of tortoises in the construction zone was accomplished in December 1984. Tortoise (and other) burrows were first marked and then excavated, and tortoises found were removed. These animals were placed in man-made burrows located approximately 300 m from the construction site (Burge et al. 1985).

To investigate the population structure and density of tortoises in the Sand Hill Training Area, a one-half square mile permanent study plot (Permanent Plot No. 1) was established. Systematic search and capture/recapture techniques were carried out on Permanent Plot No. 1 from April 22, 1985, until June 6, 1985. All field work was performed by the authors, with assistance from a Marine radio-operator.

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This report summarizes the field work on Permanent Plot No. 1, and evaluates the relocation effort of December 1984.

METHODS

The Twentynine Palms MCAGCC is located approximately eight kilometers (km) north of Twentynine Palms, California. Permanent Plot No. 1 is located in the Sand Hill Training Area of the MCAGCC at T2N, R7E, S6 (SBBM; Figure 1), at an elevation of approximately 762 meters (m) above sea level.

Permanent Plot No. 1 encompassed 1.3 square km (one-half mile square). The plot was divided into 64 equal sized squares (grids) of 142 m on a side. All corners were marked by steel reinforcing bar ("rebar") and a 2.4 m section of PVC pipe. The entire plot was layed-out with grid lines oriented to true north. Except for the location of the northeast corner, accomplished by Betty Burge in the spring of 1985, all survey work was performed by Marine Corps survey crews.

Field procedures were carried out per the instructions of Betty Burge, Project Field Supervisor, between April 22 and June 6, 1985. Grids were systematically searched on foot in parallel belts. All grids were systematically searched once during the field work. All 64 grids were searched in a north-south belt alignment. Thirty-two grids were searched a second time in an east-west belt alignment. Secondary searches concentrated on grids where relatively abundant tortoise sign had been found, or grids where animals were captured. Random searching of the permanent plot was also performed. All searches concentrated on looking for tortoises less than 140 mm medial carapace length (MCL), the assumption being that larger tortoises would be spotted in the process.

Seven times during the field season, the Relocation Site (RS) was systematically searched. Searches included the RS, the area between the RS and the VSTOL construction zone, and the area immediately south of the RS. Searching of the RS alternated between cross-slope searches (parallel to the Relocation Road) and up/down-slope searches.

When tortoises, tortoise remains, tortoise burrows, scats, predator sign or dens, or eggshell fragments were found, these items were "processed". Processing refers to the marking, sexing, and collection of data on live tortoises, the collection and examination of scats, remains and eggshells, and the mapping and examination of burrows and sites. All data was entered onto forms supplied by Burge.

Other data and samples were obtained to provide information on microhabitat. This information included the daily temperature and humidity, vegetation data, soil samples, and information on other vertebrate species found on the plot or nearby.

RESULTS

Permanent Plot No. 1

Weather

Daily high temperatures during the field season were in the mid-30s centigrade. Maximum temperatures occurred typically around 1300 hours (PST). Daily low temperatures were in the low-teens centigrade, and normally occurred just before sunrise. Relative humidity varied from lows of about 15 percent during the hottest part of the day, to highs of about 60 percent just before sunrise.

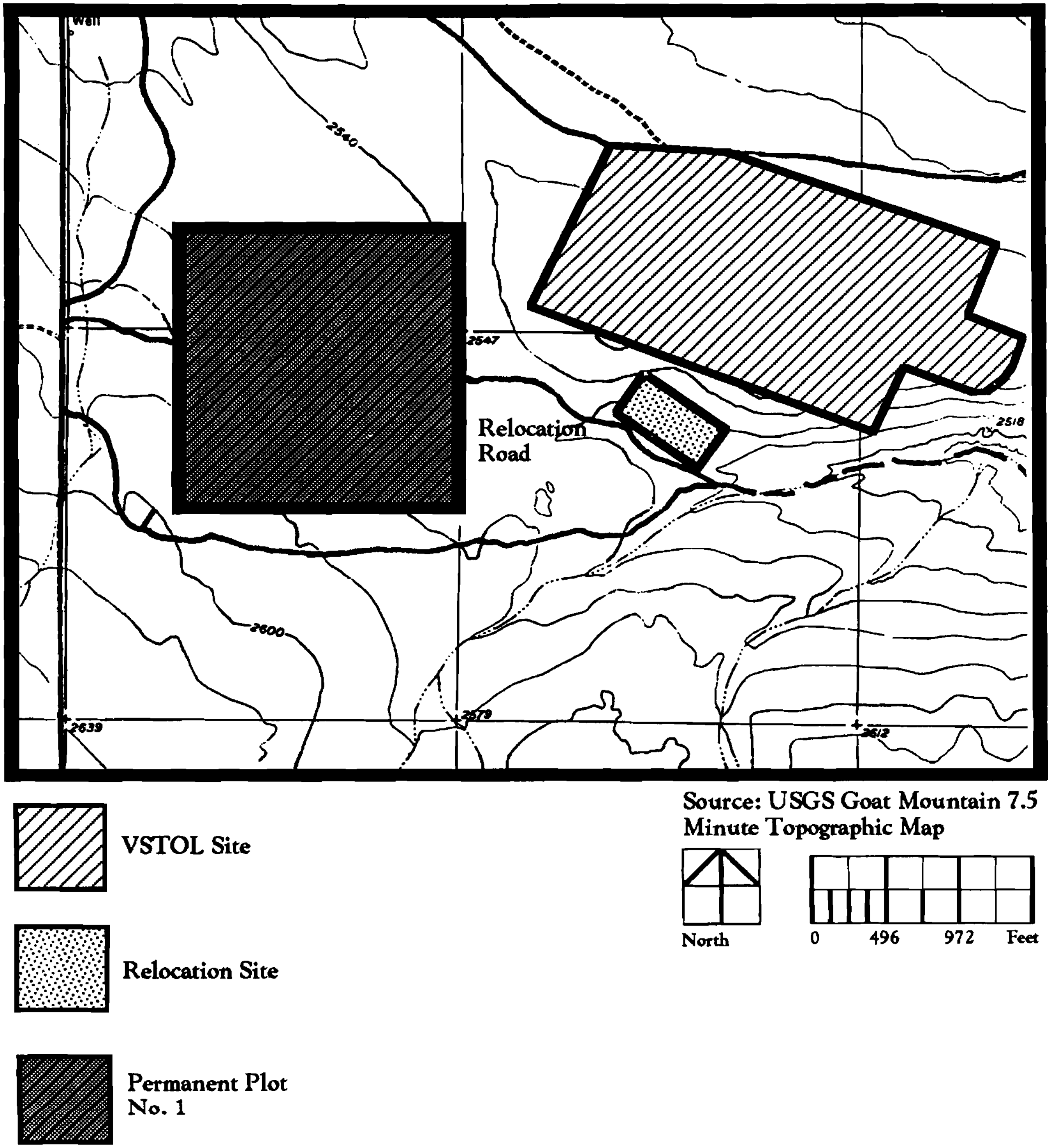

Figure 1. Vicinity map of Permanent Plot No. 1, the VSTOL airstrip and the Relocation Site.

Every afternoon, winds of about 37 km per hour would blow from the south. These winds would often pick-up sand, dust, and litter. Much of the litter in the permanent plot is blown in from the area around (and northwest of) Sand Hill. The wind would typically shift to the northwest in the evenings and at night. These northwest winds were significantly cooler than the southern winds of the day.

Vegetation

Vegetation patterns were mapped (Figure 2) and photographed. A 2 m by 100 m belt transect for plant community structure was permanently established. Originally designed to sample both perennial and annual vegetation, annuals could not be satisfactorily sampled because they had already died. Vegetation in the permanent plot was sparse everywhere, and dominated by burrobush (*Ambrosia dumosa;* AMDU). Four plant communities were recognized: (1) galleta grass (*Hilaria rigida;* HIRI) and AMDU; (2) creosote bush (*Larrea tridentata;* LATR) and AMDU; (3) areas of mixed HIRI/AMDU/LATR; and (4) extremely sparse areas of LATR/AMDU.

In addition to these species, other common plants included: desert mallow (*Sphaeralcea ambigua*); desert trumpet (*Eriogonum inflatum*); desert dandelion (*Malacothrix* sp.); and desert marigold (*Baileya pleniradiata*). The general vegetation pattern reflected the drainage pattern of the plot, the edaphic environment, topographic exposure to winds, or a combination of these factors. Generally speaking, the permanent plot relief was nowhere particularly pronounced.

HIRI/AMDU vegetation appeared in areas of lesser slope and sandy soils. Although areas of mixed HIRI/AMDU/LATR occurred, the ecotones, or edges, of the HIRI/AMDU were often abrupt. The majority of the plot supported LATR/AMDU. Extremely sparse areas of LATR/AMDU were found in places, most notably in higher, exposed places. Winds as well as soils may be responsible for these depauperate areas, where sometimes hundreds of square meters had essentially no perennial vegetation. A small dry lake bed was found in the northern portion of the site. It was dominated by desert mallow. Although only one tortoise was found in the vicinity of the dry lake bed, abundant tortoise sign was found there.

In summary, winds, relief, and possible soil differences combine to produce a sparse, open vegetation mosaic of seemingly low productivity. Many ecotones exist on the permanent plot.

Tortoise Burrows

All tortoise burrows were examined and their approximate positions plotted (Figure 2). Other burrows were examined but their positions not plotted. Of 91 burrows mapped, about half (48) could roughly be considered near the edge of a plant community. This distribution was particularly striking in the northeastern and southeastern sections of the plot. Generally speaking, burrows were not found deep within HIRI/AMDU zones or areas of sparse LATR/AMDU, but instead tended to encircle their edges. This may be the result of such diverse environmental characteristics as higher diversity of edge vegetative resources, edaphic conditions dictating successful burrow construction, or enhanced cover. This distribution pattern deserves further research. Burrow location, as depicted in Figure 2 is an approximation. To confirm that tortoise burrows are associated with ecotonal areas, more precise data on location and burrow characteristics are required.

Burrows were often found beneath LATR. Roots supplying support and protection for the burrow roof is a probable cause. The presence of a caliche soil horizon of extremely tough, cemented soil beneath the surface, could also be a factor in determining burrow location.

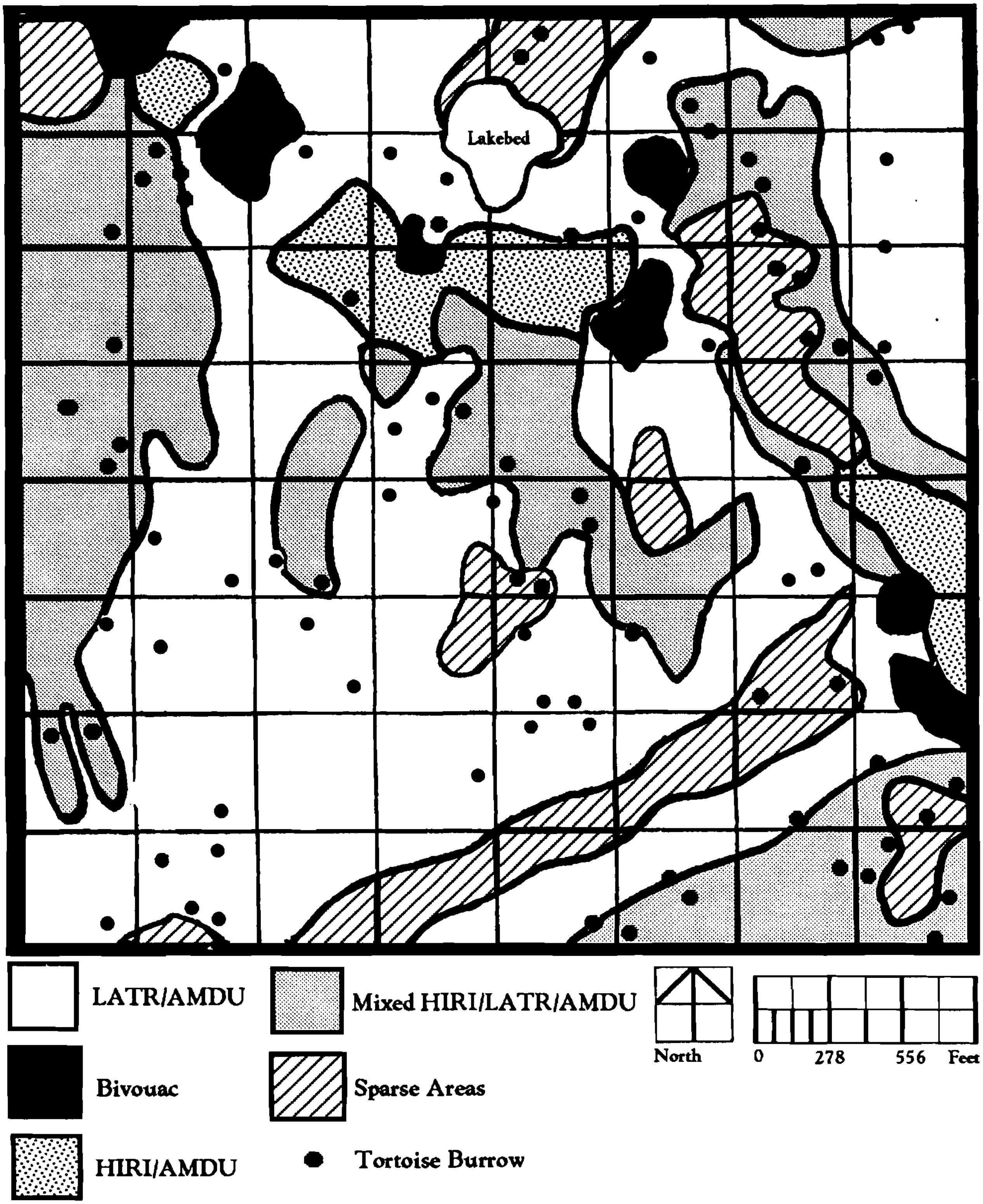

Figure 2. Plant communities of Permanent Plot No. 1. (see text for explanation of abbreviations).

The roots of creosote bushes may inexorably break apart the hardpan to facilitate burrow construction. In other areas where the hardpan had been breached (i.e. artillery mounds), burrows were always present, both in the mounds and in the accompanying trenches.

Tortoises

Thirteen tortoises were captured and marked in the permanent plot during the field work. Another tortoise was observed in the permanent plot, but could not be captured without destroying its burrow. Details of individual animals and captures may be seen on the Permanent Plot Tortoise Roster (Table 1). One tortoise (No. 43 - the only animal too young to be sexed) was initially captured by the Marines off the plot on May 20, but was recaptured on May 23 on Relocation Road on the permanent plot. The possibility exists that it was released into the permanent plot by the soldiers.

The 13 tortoises of Permanent Plot No. 1 were assigned to age/size classes based on their MCL (Table 2). Eleven of the animals had an MCL of greater than 214 mm, with only two others of smaller classes. These 11 animals represent 84.6 percent of the captured tortoises. If these low numbers are a significant sample of the population, it appears highly skewed toward adults.

The sex ratio (Table 3) of all animals was 50 percent male and 50 percent female. Among adults the ratio is 1.51 to 1. These ratios were tentative because the low numbers of animals captured may not be a representative sample of the general population. The average MCL of adult-2 males was 279.3 mm ($n = 6$, $s = 28.1$), while for adult-2 females the average MCL was 246.0 mm ($n = 5$, $s = 20.4$).

Predators and predation

Three major terrestrial predators were found on the permanent plot. All were canids: the kit fox (*Vulpes macrotis*); the coyote (*Canis latrans*); and the feral dog (*Canis familiaris*).

Fifteen kit fox dens were located on the permanent plot. Most (8) appeared old and unused. No evidence of tortoise predation was found at any of these sites. Interestingly, at one large kit fox den, tortoise No. 10 was recaptured while resting in a kit fox burrow entrance. The foxes at this den consisted of one adult female, and two juveniles. Remains found around the various dens indicated rodents and lagomorphs to be their principal prey. Reptile and avian remains were only occasionally found.

One coyote was observed during the field work. However, coyote scats were common. Examination of their scats revealed that rodents and lagomorphs were common prey. No tortoise remains were found in coyote scats.

Feral dogs were reported to be in the area by many of the Marines. Large canid tracks were commonly found in all areas, and dogs were frequently heard barking at night.

Birds of prey and bird scavengers were frequently observed at the permanent plot. These included the red-tailed hawk (*Buteo jamaicensis*) and many ravens (*Corvus corax*). The nest of a burrowing owl (*Athene cunicularia*) was found in the permanent plot, but no individuals were observed. Vertebrates found on or near the permanent plot are listed in Table 4.

Table 1. Summary of Tortoise Roster Data for Permanent Plot No. 1 - Spring 1985. Twentynine Palms MCAGCC.

Tortoise number	Sex	MCL[2]	Shell type[3]	Number applied on[4]	Capture Dates[1] Initial	Recapture
10	M	273	H	V4	APR 30	MAY 02
24	F	214	H	V4	APR 30	
25	F	254	H	V5	MAY 01	
26	M	334	H	V4	MAY 01	MAY 08 MAY 16
27	M	267	H	V5	MAY 02	MAY 20 MAY 22
41	F	248	H	LC3	MAY 15	MAY 16
43	JUV	157	H	V5	MAY 20	MAY 23
48	M	262	H	V5	MAY 29	JUN 03
49	M	258	H	V5	MAY 30	
67	F	165	H	V5	MAY 02	
68	F	270	H	V4	MAY 02	MAY 07 MAY 22 MAY 28
69	F	244	H	V4	MAY 02	
70	M	282	H	V4	MAY 07	

[1] All dates in 1985
[2] MCL = Medial Carapace Length in mm
[3] H = Hard Shell; 11 or more marginal scutes per side
[4] V = Vertebral scutes; LC = Left costal scutes

Table 2. Distribution of Desert Tortoises of Permanent Plot No. 1 Among Seven Age/Size Classes - Spring 1985. Twentynine Palms MCAGCC.

Age Class	Size (mm - MCL)	No. of Individuals	Percent
Adult-2	> 240	10	76.92
Adult-1	208 - 240	1	7.70
Subadult	181 - 207	0	0.00
Immature-2	141 - 180	2	15.38
Immature-1	101 - 140	0	0.00
Juvenile-2	60 - 100	0	0.00
Juvenile-1	< 60	0	0.00
Total		13	100.00

Table 3. Sex Ratios of Adult and Subadult Tortoises on Permanent Plot No. 1 - Spring 1985. Twentynine Palms MCAGCC.

Age Class	No.	Males		Females		Sex Ratio
		No.	%	No.	%	
Adult-2	10	6	60.0	4	40.0	1.50
Adult-1	1	0	0.0	1	100.0	–
Subadult	1	0	0.0	1	100.0	–

Predation on the tortoises in the Sand Hill area may be significant. Roughly half (6 of 13) the animals captured in the permanent plot had nicks and chew marks on their shells. Tortoises found outside the permanent plot also often exhibited extensive carapace and plastron damage. Coyotes and dogs account for most predation of adult tortoises, while kit foxes and ravens may take younger tortoises.

Ten sets of tortoise remains were found in the permanent plot. Most were old remains of adult animals. Due to their advanced state of decay, ages were unable to be determined from these remains. Two sites were found where eggshells were present. Both sites consisted of scattered small fragments outside burrows. One juvenile carapace was found just off the southwest corner of the plot (MCL = 57 mm). This small individual had been the prey of a bird; the top of its carapace had been peeled off and the viscera inside removed.

Human impacts

Human impacts have been considerable. Use as a military training area for desert warfare has led to a general degradation of habitat. Tracks of tanks, 2 1/2 ton trucks, jeeps, and light armored vehicles (LAV) were found everywhere on the permanent plot. The tracks were mostly old, but vegetation affected by the passing of the vehicles was just beginning to recover. Some shrubs were killed outright.

Few recent tracks appear on the plot. There were two important exceptions. A group of LAVs traversed the permanent plot and RS sometime in February 1985. Tracks were also left by the survey crews who layed out the grids. The survey crew tracks paralleled the south plot boundary, just outside the plot, and in one location proceeded north through the plot to Relocation Road. Their impact was relatively minor. However, the LAV tracks were very deep (approximately 25 cm) and their impact upon the vegetation was, in places, considerable. Probably due to the overall lack of slope, and the freshness of the tracks, no erosion problems could be ascertained. One tortoise burrow was collapsed by a vehicle, but no obvious connection between any remains found and vehicles could be ascertained.

Two dirt roads cross the permanent plot. The impacts from these roads are two-fold. Tortoises may prefer to travel on the roads, thus exposing themselves to the possibility of being crushed. Further, these roads allow vehicle access directly into the permanent plot. These roads were easily accessed by civilians from Border Road, and constitute a route of entrance by poachers and off-road vehicles. Civilians were frequently observed illegally entering the base via this route. Many places were found where trespassers had shot targets (bottles, cans, paint cans). Dirt bike tracks were found in the southwest grids of the plot, and were occasionally heard nearby.

A second form of human impact is the artillery mounds (AMs or tank pits). Forty-two AMs were found in the permanent plot, but these may be a blessing in disguise. Varying from about 1 m to 4 m in height, these mounds (and their trenches) provide excellent sites for burrow construction. Being a direct route through (or above) the tough caliche hardpan, every mound or trench had at least one burrow. Artillery mounds may actually be a form of habitat enhancement.

Another human impact was the the bivouacs. Seven bivouacs were found on the plot (Figure 2). They represent areas of past military encampments. They are completely devoid of vegetation. Their total area represents approximately 5% of the permanent plot. Old trash (bottles, shell casings) are found around the edges of such areas, and a web of tracks usually radiate from them.

Summary and discussion

Permanent Plot No. 1 is a sparse, wind-blown section of Mojave Desert which supports a relatively low density of desert tortoises. Density is probably about 30 animals per square mile. This agrees with the estimate reported by Kirtland (1984) for tortoise density on the VSTOL site. The population appears skewed towards large/old tortoises with very low recruitment of young animals. However, because of their small size and cryptic coloration, juvenile tortoises are often missed during surveys, and are frequently under-represented.

The large number of burrows found compared to the number of observed animals, and the lack of sightings in areas of seemingly high sign density (i.e. the lake bed), are interesting observations. Why would only 13 or so animals require close to 90 burrows? There are four possible explanations. First, field personnel may have failed to spot tortoises. Although possible, the trend of increasing recaptures over the field season, and the number of off-site captures (including a juvenile) tend not to support this conclusion. Second, one tortoise may have several burrows, some currently unused. This is probably true, but not to the extent the data might

Table 4. Confirmed Vertebrate Fauna of Permanent Plot No. 1 - Spring 1985. Twentynine Palms MCAGCC.

Common Name	Scientific Name
Herps	
desert tortoise	*Gopherus agassizii*
desert horned lizard	*Phrynosoma platyrhinos*
zebra-tailed lizard	*Callisaurus draconoides*
leopard lizard	*Gambelia wislizenii*
western whiptail lizard	*Cnemidophorous tigris*
side-blotched lizard	*Uta stansburiana*
long-nosed snake	*Rhinochelius lecontei*
gopher snake	*Pituophis melanoleucus*
coachwhip	*Masticophis flagellum*
western patch-nosed snake	*Salvadora hexalepis*
glossy snake	*Arizona elegans*
sidewinder	*Crotalus cerastes*
mojave rattlesnake	*Crotalus scutulatus*
Birds	
red-tailed hawk	*Buteo jamaicensis*
turkey vulture	*Cathartes aura*
screech owl	*Otus asio*
logerhead shrike	*Lanius ludovicianus*
common nighthawk	*Chordeiles minor*
common raven	*Corvus corax*
mourning dove	*Zanaida macroura*
horned lark	*Eremophila alpestris*
black-tailed gnatcatcher	*Polioptila melanura*
western kingbird	*Tyrannus verticalis*
black-throated sparrow	*Amphispiza bilineata*
roadrunner	*Geococcyx californianus*
Mammals	
pocket gopher	*Tomomys bottae*
deer mouse	*Peromyscus maniculatus*
merriam's kangaroo rat	*Dipodomys merriami*
desert kangaroo rat	*Dipodomys deserti*
whitetail antelope squirrel	*Ammospermophilus leucurus*
desert woodrat	*Neotoma lepida*
black-tailed jackrabbit	*Lepus californicus*
desert kit fox	*Vulpes macrotis*
coyote	*Canis latrans*
feral dog	*Canis familiaris*

suggest. Still, these may not be unusual numbers. Burge et al. (1985) found only eleven tortoises for approximately 300 burrows excavated. The authors, in December 1985 (report, these proceedings) found eight tortoises for approximately 280 burrows excavated near Kramer Junction, San Bernardino County. Third, some burrows may have been constructed by deceased animals. That is, the population has declined from previously higher levels. This possibility may be supported by the lack of young tortoises found (a population in decline might be expected to have fewer young), the small number of eggshells found, and the 10 sets of remains. Finally, some burrows may be from animals whose home range is mostly adjacent to the plot. These reasons, or a combination of these reasons, may help explain the high number of burrows found relative to the number of animals captured. Regardless, the number of burrows found on a site may not be a good indicator of the population there.

Burrow distribution may reflect the general inability of the animals to locally breach the caliche hardpan. It may also be related to some ecotonal quality such as plant diversity or edaphic conditions. This latter possibility may have important effects for tortoise relocation and habitat management should more precise data support this hypothesis.

Man's impacts are visible everywhere on the permanent plot, but are beginning to recover. Some of these impacts actually allow new colonization by providing new sites for burrow construction. If off-road travel and civilian access are reduced, the area may see further recovery of the tortoise population.

Relocation Site

Of the eleven animals that were relocated to man-made burrows in December 1984, five were recaptured during field work. Details of individual animals and captures may be found on the Relocation Site Tortoise Roster (Table 5). This represents 45.5 percent of the relocated animals. One 76 mm juvenile was also captured on the RS. Of the six animals that emerged from artificial burrows within hours of their relocation (Burge et al. 1985) four were recaptured during the field work.

Many of the man-made burrows exhibited no sign of use. This was particularly true of small burrows which had not received relocated tortoises. Burrows which showed use by tortoises were in the eastern sections of the RS. Other burrows exhibited rodent use, reptile use, or no use at all. A number of natural burrows were found in the RS and adjacent search areas. One area of five closely spaced burrows, just north of the RS boundary, supported a great deal of activity. With a few exceptions, most sightings occurred there. One juvenile tortoise was found recently emerged from the burrow it was initially relocated to. An adult relocated male was found within an artificial burrow. It appears that the RS is being utilized by at least some of the relocated animals.

It may be that the RS is within the home range of every tortoise relocated from the VSTOL site. It was thought that the relocated tortoises might attempt to return to the VSTOL site. Although tracks of an adult tortoise were found paralleling the VSTOL fence line, at no point did the tracks attempt to pass through the fence. No tortoise tracks were observed within the fenced VSTOL site. Several natural burrows and scats were found in the area between the RS and the VSTOL site. However, only one animal was captured near the VSTOL site. Since this same animal was spotted earlier in the season by Betty Burge on the VSTOL road, it may have been the individual responsible for the tracks seen along the fence line. Another animal was captured near the airfield earlier in the season by Roger Twitchell, MCAGCC naturalist. At least two of the animals then, have been seen near the area from which they were originally relocated.

Table 5. Summary of Tortoise Roster Data for the VSTOL Relocation Plot - Spring 1985. Twentynine Palms MCAGCC.

Tortoise number	Sex	MCL[6]	Shell type[7]	Number applied on[8]	Capture dates[5] Initial	Recapture
R25	M	306	H	V5	MAR 21	APR 30 MAY 30
R60	F	274	H	V5	APR 23	MAY 03 MAY 16
R62	JUV	209	H	LC4	MAY 13	
R65	M	274	H	LC4	MAY 03	JUN 03
R66	JUV	166	H	V5	APR 23	
R70	JUV	76	S	V4	MAY 23	

[5] All dates in 1985
[6] MCL = Medial Carapace Length in mm
[7] H = Hard Shell; 11 or more marginal scutes per side
S = Soft Shell; 11 or more marginal scutes per side
[8] V = Vertebral scutes; LC = Left costal scutes

Summary and discussion

About half the animals relocated from their natural burrows in December 1984, were recaptured at or near the RS during the spring of 1985. In this respect, the relocation may be considered 50 percent successful. This does not imply that the other 50 percent died as a result of the relocation, but only that about half the animals remained near the RS. All relocated animals were placed in burrows in the eastern and northern sections of the RS. This overcrowding may have forced some individuals from the area, but apparently not to the other man-made burrows. Indirectly, the low density of tortoises found in the permanent plot, and directly, the lack of tortoises found within the VSTOL site by construction crews, support the assumption that the tortoises removed during the December effort, represented most or all of the animals potentially affected by the airfield construction.

Not all the relocated tortoises moved back towards their former homes in the VSTOL site. Although they may still have been within their home ranges, it appears that individuals vary in their tendency to exhibit homing behavior.

The fence line around the VSTOL site was successful at keeping tortoises out. Tracks were seen paralleling the fence, but nowhere were they observed to breach the fence.

It is felt that the relocation of tortoises from the VSTOL site was successful. About half the animals stayed in the area, and a few were using the man-made burrows. Where ever the final destination of the other 50 percent, it is a better fate than that of remaining in the construction area.

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ASSESSMENT OF PRODUCTION OF ANNUAL PLANT SPECIES IN THE WESTERN MOJAVE DESERT, CALIFORNIA

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ABSTRACT - The magnitude and spatial distribution of annual plant productivity was measured in the vicinity of Teagle Wash, 18 km (11.3 mi) S.E. of Ridgecrest, California. The study site was located in a Creosotebush Scrub plant assemblage. Total cover of shrub species was 15.8 percent. Annual production was measured by seven, 0.1 square-meter quadrants in each of three production categories: (1) inter-shrub spaces or "low" production areas, (2) the drip-line areas of shrubs of "intermediate" production areas, and (3) directly under the shrub canopy or "high" production areas. Productivity estimates varied from a low of 100 kg/ha (89 lb/ac) in an inter-shrub sample to a high of 954 kg/ha (850 lb/ac) under a shrub canopy. Average production in the three production area categories was 237 kg/ha (211 lb/ac), 488 kg/ha (435 lb/ac), and 746 kg/ha (665 lb/ac), respectively. However, only about 12% of the study site was determined to be in the high production area category. A weighted average production for the study site was calculated to be 289 kg/ha (257 lb/ac). The drip line or intermediate production areas were melded into the high production areas for this purpose and no doubt resulted in an overestimation of the total production under shrub canopies; this was necessary because of the difficulty in defining the area of transition between the inter-shrub spaces and areas under shrub canopies. The weighted average production is far closer to that estimated from inter-shrub spaces than from either under the canopy of shrubs or from under the drip line. Because of the relative ease of data collecting and interpretation, and because of reduction of the chance of overgrazing due to accidental over allocation by managers of forage, it seems prudent to use production estimates gleaned from inter-shrub spaces as livestock "turn-out" determinants rather than estimates taken from under shrub canopies or drip lines. Production estimated from plots under drip lines do not necessarily represent an "average" production and should not be relied upon unless they are part of a weighted averaging analysis of the annual plant production of a desert ephemeral pasture; one which takes into account the different aspects of spatial distribution of the component annual plant species.

INTRODUCTION

With the advent of the International Biological Program (IBP) in the later 1960's and 1970's, much attention was given to the determination of net primary production in the world's ecosystem; the desert biome was no exception. Although true deserts are considered unproductive

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(Grime 1979), there is often a broad range of mean potential yearly productivity which depends upon the physiographic and climatic nature of the region in question. Within one desert, potential productivity of the various vegetation types (i.e. plant assemblages) follows principally a temperature/precipitation gradient which is influenced and modified by topographic relief (Whittaker and Niering 1975). Secondary factors influencing potential, primary, plant productivity may include edaphic conditions such as soil-compaction (Lathrop and Rowlands 1983), salinity, nutrient availability, high concentrations of toxic chemicals, substrate stability, and environmental stresses such as herbivore grazing as well as other natural and artificial perturbations of the environment (Walter 1973, Whittaker 1975, Stoddard et al. 1975, Grime 1979, Szarek 1979). In general, the potential primary productivity of a plant community is inversely proportional to the relative degree of environmental stress. In deserts where such stresses are common, production is generally much less than in more mesic ecosystems of similar land area (Grime 1979). Walter (1973) reports that phytomass production is subject to certain variation in one and the same region. It is higher in a year with good rainfall, lower in a bad year.

According to Beatley (1976) winter annuals are widely fluctuating components of the Mojave Desert and transitional communities and are a distinctive feature of warm desert vegetation. The extent of production of winter annuals is highly dependent upon the frequency, amount, and time between precipitation events. Seasonal productivity and reproductive success of desert annual plants is highly variable from plant to plant, site to site, and season to season. Measurements of total productivity with the objective of defining either the mean or extreme productivities in any given kind of desert vegetation are confronted in all of the vegetational components with spatial and temporal variations which require recognition, measurement, and definition (Beatley 1969). Norton (1974) recognized that in good years annual plant production in the Mojave Desert can be as high as 1,000 kg/ha (890 lb/ac) and may exceed that of perennial plants. In other years, when rainfall is scarce, annual plant productivity may be entirely nil in these same areas (Lathrop and Rowlands 1983). Walter (1973), writing with great insight, noted that Ephemeral plants fulfill a buffer role in that they exploit the excess water which the perennials are unable to utilize in a year of good rain. The phytomass of the perennials is determined by the rainfall in dry years, since these times somehow have to be survived.

The spatial distribution of annual plants in the California desert is interesting. There is a very close relationship between both the occurrence and production of annuals and proximity to shrubs or even old shrub mounds where the original plant which occupied the mound has died and disappeared (Went 1942, Muller 1953, Norton 1974). However, the pattern is not always consistent from one place to another even when the areas being compared are very similar in their physical characteristics (Johnson et al. 1978). As a generalization, the inter-shrub spaces are far less productive of desert winter annuals than under the canopies of desert shrubs. This is no doubt in part a reflection of increased nutrient availability produced by accumulation of litter under these shrubs and possibly a concentration of runoff around the base of shrubs (especially *Larrea tridentata*) due to water repellency of the soil immediately beneath them (Adams et al. 1970). A long-lasting water repellent layer would also explain why annual plants continue to form "halos" around old mounds where the former shrub occupant is defunct.

Obviously any allocation or use of annual vegetation in the form of ephemeral forage for herbivores is going to be affected and in part constrained by the phenomena discussed above. Furthermore, the reliable estimation of levels of productivity of annual plants and rates of depletion through the growing season is crucial to the proper management of ephemeral rangelands and, in turn, the native and domestic herbivores that exploit these rangelands. Any determination and allocation of Animal Unit Months (AUMs) within a specified area demands some knowledge of the potential productivity and phenology of the annual vegetation, temporal variability, spatial variability (vis a vis shrub mounds vs. inter-shrub spaces) and a reliable system for assessing productivity as it relates to these sources of variation. The purpose of this report will be to assess spatial variability of annual plant production on a site in the western Mojave

Desert and investigate the implication of this variability to allocation of forage. In addition, a method of integrating different estimates of ephemeral plant productivity within a stand of desert scrub by means of one measurement will be discussed.

STUDY SITE

Location

The study site was located about 18 km (11.3 mi) S.E. of Ridgecrest, California near Teagle Wash, San Bernardino County in T28S, R41E, NW 1/4 Sec. 8, SW 1/4 Sec. 5. The elevation of the study site is approximately 869 m (2850 ft). The slope aspect is east-southeast facing at about 3 percent. The dominant regional landforms are gently rolling hills, interrupted by low, yet rugged desert mountains.

Climate

The climate of the site is typical of the west central Mojave Desert of California with hot, relatively dry summers and cool moist winters. Growth of both perennial and annual vegetation occurs for the most part during the spring months. Except for a few species, most plants are dormant or survive as seed during the hot, dry summer. Historical (1938 - Present) meteorological data are available from Randsburg (35^{o} 22′, 117^{o} 39′, elev. 1076 m [3530 ft]), site of a N.O.A.A. weather station. The normal annual precipitation is 143.5 mm/year (5.7 in) some falling as snow, with only 10 percent occurring during the summer months (July - September, inclusive) in the form of convectional (i.e., thunder) storms. Precipitation as measured at the nearby U.S. Naval Weapons Center (elev. 679 m [2229 ft.]) averaged 75.7 mm/yr (3.0 in) between 1946 and 1976; actual average annual rainfall at the study site is somewhere between those extremes. In the winter and spring (January - May) of 1981 when the study took place, total precipitation as measured at Randsburg was 131 mm (5.2 in); 50.8 mm (2 in) above normal for those months, however, precipitation was 45.7 mm (1.8 in) below normal between October 1 and December 31, 1980. Summer temperatures in the general area often exceed 43°C (110°F) and below freezing temperatures are not uncommon during winter nights.

Regional Vegetation

The dominant regional vegetation of the area surrounding the site is Creosotebush Scrub whose primary plant species include *Larrea tridentata, Ambrosia dumosa* and *Cassia armata*. This plant assemblage generally occupies the rolling upland areas of the region. Secondary plant species include: *Opuntia echinocarpa, Acamptopappus sphaerocephalus, Lycium andersonii, Hymenoclea salsola, Grayia spinosa, Atriplex* spp., and *Yucca brevifolia*. Other important types of vegetation include Mojave Saltbush - Allscale Scrub and Cheesebush Scrub. The former occupies the bottoms and lower slopes of basins. Primary plant species include *Larrea tridentata, Ambrosia dumosa, Lycium andersonii*, and *Grayia spinosa*. This vegetation type is better suited to more saline and slightly colder conditions than Creosotebush Scrub. Cheesebush Scrub occurs for the most part in the bottoms of desert washes and generally in almost any disturbed area. Its primary species constituent is *Hymenoclea salsola* which usually occurs within the Creosotebush Scrub but is known to be a vigorous invader/increaser species following disturbance (Vasek et al. 1975).

Disturbance is not uncommon in the area and for the most part can be attributed to three primary agents: (1) sheep grazing, (2) ORV (off-road vehicle) operations, especially motorcycles and (3) mining. Of these, ORV driving and mining are the most site intensive; ORV driving and sheep grazing affect the greatest area. All these activities result in site destruction by denudation of vegetation, soil surface disruption, and soil compaction. Off-road vehicle operation is probably the most destructive because of its ubiquitous nature and capacity for affecting soils and vegetation (Rowlands 1980). Mining covers too small an area to be considered as highly significant, although some areas of concentrated activity (Red Mountain, Atolia, Fiddler Gulch, etc.) are heavily impacted. The grazing of sheep results in heaviest damage at watering and bedding sites. Effects on vegetation of open ranges are difficult to assess but probably result in increases in weedy annuals such as *Schismus arabicus, S. barbatus, Erodium circutarium* and perhaps certain perennial grasses, such as *Stipa speciosa*, over perennial shrubs.

Disturbance assemblages consist for the most part of such short-lived pioneer species as *Hymenoclea salsola, Acamptopappus sphaerocephalus, Gutierrezia microcephala, Haplopappus cooperi* and *Eriogonum fasciculatum*, and introduced grasses and herbs such as *Schismus spp., Erodium circutarium* and *Salsola spp.* However, on occasion, a disturbed area will revert to the original vegetation type without going through an "intermediate" phase if there is no "pool" of invader species nearby to take advantage of the disturbance (Rowlands 1980).

Soils

The dominant soil type within the area of the study site is an entisol, a typic torrifluvent of the Anthony series. It covers 60 - 80 percent of the area in question, including the study site, and is coarse-loamy mixed (calcareous) and thermic. The parent material is mixed alluvium. This type generally occupies alluvial plains and low terraces. There is little or no profile development, depth to bedrock is greater than 1.5 m (60 inches). Susceptibility to erosion is moderate, generally due to wind, whereas compaction potential is slight to moderate; pH is 7.4 - 8.4 or slightly alkaline. The shrink swell potential is low. The composition at 0-7.5 cm (0-3 inches) is that of a gravelly, loamy sand; at 7.5-100 cm (3-40 inches) the composition is that of a gravelly, sandy loam. Surface gravel constitutes from 20-70 percent of the cover. Surface color is pale brown or light yellowish brown.

Other soils in the region are types belonging to the Mojave, Calvista and Tujunga series. The first two are aridisols whereas the latter are entisol types. Further documentation on soils can be found in the Red Mountain Unit Resource Analysis (BLM 1976).

MATERIALS AND METHODS

The study was initiated on March 4, 1981 and ended April 28, 1981, while the author was employed by the Ridgecrest Area Office of the Bureau of Land Management. A linear transect running approximately due west was initiated from a "random" point (the impact site of a stone thrown backwards over a shoulder). Every ten paces (a pace being two long steps, or about 2 m), a 0.1 m^2 sampling frame was dropped in an intershrub space (low production area) and all the annual vegetation within the frame was harvested, weighed, air dried and weighed again to the nearest 0.5 gram. A pesola spring balance, graduated in 1 gram increments to 300 grams was employed. Two other 0.1 m^2 samples were taken under the crown (highest production area) and drip line (intermediate production area) of the nearest large shrub with a well-formed ring of annual plants growing beneath. This was always a creosotebush (*Larrea tridentata*). Although armed senna (*Cassia armata*) and white bursage (*Ambrosia dumosa*) were also present, neither of these species had well developed rings of annual plants growing beneath. The annual vegetation within the sample frame was treated in the same manner as that taken from the intershrub area. Seven samples were taken in each category for a total of twenty-one samples.

Because of the heterogeneous distribution of annual plants in creosote bush scrub vegetation as mentioned above, an attempt was made to achieve a weighted estimate of annual plant production by determining the percent of the area under the shrub canopy. A 75 foot permanent quadrant (23 m x 23 m) was made on the test site using a surveyor's transit. All perennial shrubs were counted within this plot according to species. Their individual covers were calculated according to the formula:

$$C_1 = \left[\frac{D_1 + D_2}{4}\right]^2 \pi$$

where C_1 is cover in square feet or meters and D_1 and D_2 are the major and minor shrub diameters out to the drip line. From this value was subtracted the area of the shrub base calculated as:

$$C_2 = \left[\frac{D_{B1} + D_{B2}}{4}\right]^2 \pi$$

where C_2 is the cover of the base of the shrub and D_{B1} and D_{B2} are the major and minor diameters of the base (taken here to mean the cluster of stems at the center of the shrub or bare area at the shrub center). So that the area of high production (A) was calculated as the area between two concentric circles or:

$$A = C_1 - C_2$$

No attempt was made to evaluate an area of intermediate production as the drop off in production from under the shrub canopy space to the intershrub space seemed to follow a gradient (at least visually) and lines of demarcation could not be drawn. It is hoped that extending the area defined as that of high productivity out to the edge of the shrub drip line will integrate this gradient. Some error is unfortunately unavoidable.

RESULTS

Since forage allocation on rangelands has been and in most cases continues to be done using English measurements, this tradition is continued below in the interests of consistency and ease of comparison. Metric equivalents are provided both in the results and in the referenced tables.

Three species of perennial shrubs were sampled on the site (Table 1). Total cover of perennial plants was 15.8 percent. The absolute value for C_1 as defined above for three perennial shrub species was 905.4 ft^2 (84.1 m^2); C_2 summed for all species was 220.5 ft^2 (20.5 m^2) leaving A, the area of the high production zone as 685.4 ft^2 (63.6 m^2) out of a total sample area of 5625 $ft.^2$ (522.6 m^2) or about 12 percent of the area.

Fourteen species of annuals (Table 2) were encountered on the study site, of which *Erodium circutarium, Schismus arabicus* and *Bromus rubens* were visually judged to be the most important. Results of harvesting from the three production categories defined in the methods section are presented in Table 3 along with an ANOVA summary of differences among treatments of biomass and percent moisture. Biomass was significantly different among the three treatments ($P < .01$) and increased in the order: Shrub canopy > shrub drip line > intershrub spaces. Moisture levels of the harvested plants also proved to be significantly different among treatments

Table 1. Summary of density and cover of the three primary shrub species sampled within the study area in a 5,625 Ft^2 ($529M^2$) quadrant.

Species[1]	Density		Cover (%)	
	Per Acre	Per Ha	Absolute	Relative
Ambrosia dumosa	62	155	0.4	2.2
Cassia armata	31	78	0.5	3.3
Larrea tridentata	116	290	14.9	94.5
Total	209	523	15.8	100.0

[1] Other perennial species present but not within sample area:

Acamptopappus sphaerocephalus *Lycium andersonii*
Hymenoclea salsola *Opuntia echinocarpa*

Table 2. List of annual plant species found within the Teagle Wash study site[2].

NATIVE	INTRODUCED
Amsinckia tesselata	*Bromus rubens*
Coreopsis calliopsidea	*Erodium circutarium*
Eriogonum inflatum	*Schismus arabicus*
Eriogonum thomasii	*Sisymbrium altissimum*
Eschscholzia minutiflora	
Gilia latiflora ssp. *davii*	
Lotus humistratus	
Lupinus sparsifolius	
Pectocarya ssp.	
Phacelia tanacetifolia	

[2] Nomenclature follows Munz (1974).

($P < .01$), however, after examining Table 3 it is apparent that the major difference was between those plants growing under the canopy and both those at the edge of the drip line and intershrub spaces whose moisture contents were virtually identical.

Overall, production varied from a low of about 89 lb/ac (100 kg/ha) in an intershrub sample to 850 lb/ac (954 kg/ha) under a shrub canopy. With the data presented above, we can calculate a weighted estimate of annual forage production based on the relative amounts of each production category in the area. For example: In a 100 ac (40.5 ha) plot, about 12 percent of the area (i.e. 12 ac) would fall under the high production category and at an average annual plant production level

Table 3. Summary of moisture and biomass differences among three treatments of annual plant harvesting.

Plot	Inter-Shrub Spaces			Shrub Drip Line			Under Shrub Canopy		
	Percent	Biomass		Percent	Biomass		Percent	Biomass	
	Moisture	lb/ac	kg/ha	Moisture	lb/ac	kg/ha	Moisture	lb/ac	kg/ha
1	0.62	224	251	0.70	403	452	0.77	448	503
2	0.73	313	351	0.72	492	552	0.78	850	954
3	0.67	89	100	0.69	582	653	0.73	537	603
4	0.65	268	301	0.67	268	301	0.77	761	854
5	0.67	179	201	0.62	582	653	0.84	716	804
6	0.70	134	150	0.64	448	503	0.75	806	905
7	0.73	269	301	0.70	268	301	0.75	537	603
Mean	0.68	211	237	0.68	435	488	0.77	665	746
Variance	0.00144	5556.0	---	0.00111	14776.8	---	0.00106	20825.7	---

ANOVA Table for Biomass

Source of Variation	dF	SS	MS	F	
Treatments	2	721998.8	360999.4	22.6**	F[0.01] (2,18) = 6.01
Error	18	288109.4	16006.1		
Total	20	1010198.2			

ANOVA Table for Plant Moisture Content

Source of Variation	dF	SS	MS	F	
Treatments	2	0.03847	0.01923	13.7**	F[0.01] (2,18) = 6.01
Error	18	0.02523	0.00140		
Total	20	0.06370			

of 665 lb/ac (746 kg/ha) (Table 3), about 7980 lb (3627 kg) of forage would be produced. About 4 percent of the test area was found to be occupied by the bases of shrubs and had little or no annual production. Therefore, as far as annual plants are concerned, four acres would be nonproductive. The remaining 84 acres would be inter-shrub space producing at an average rate of 211 lb/ac (237.1 kg/ha) (Table 3), resulting in a production of about 17,724 lb (8056.4 kg) of forage for a grand total of 25704 lb (11,683.6 kg) over 1000 acres. About 31 percent of the total production of forage came from underneath shrub canopies. What is interesting is that the average total production per acre is 257 lb/ac (288.4 kg/ha); only about 46 lb/ac (52 kg/ha) more than the average for intershrub spaces. To reiterate, the shrub drip line production category has been melded into the shrub canopy category because of difficulty in precisely defining the drip line area on the ground; the drip line zone takes the form of a continuum. As a result, the amount of area considered to be in high production may be slightly exaggerated as would be the amount of forage coming from this area.

DISCUSSION

The overall average production of about 257 lb/ac (288.4 kg/ha) for this site agrees well with production figures for winter annuals presented in other studies. Production data presented by Beatley (1969) for dry biomass of winter annuals on the Nevada Test Site varied from less than 1 to over 753 kg/ha with mean values for three different sites in each of three years varying from 10 to 180 kg/ha. Similar data collected in the south central and southwestern Mojave by Johnson and Rice and presented in Lathrop and Rowlands (1981) varied from 446 kg/ha to over 1100 kg/ha. In the Sonoran Desert, Halvorsen and Patten (1975) measured 950 kg/ha of winter annual production in 1973 (a wet year) but less than 100 kg/ha in 1974 (a dry year). According to Norton (1974) annual production on a Mojave Desert site was 3.2 kg/ha in 1972, a dry year, and 430 kg/ha in 1973, a wet year. It is obvious that productivity varies from year to year, site to site, and even from place to place within the same site. The winter and spring of 1981 were wetter than normal in the western Mojave Desert near the study site, but the fall and winter of 1980 were drier than normal. Between October 1 and December 31, the Naval Weapons Center at Chino lake received only 0.8 mm (0.03 in) of precipitation and Randsburg only 1.8 mm (0.07 in; 1.8 in below normal). Even though the following spring was above average, and almost canceled out earlier deficiencies, annual plant growth was considerably retarded. In previous years, (1978, 1979) production in Teagle Wash was well over 1000 kg/ha. (BLM unpublished data), so that the data presented in this study represent those of a "dry" year in spite of the ample moisture late in the growing season.

Forage quality was not considered in this study. Plants growing under shrubs tended to retain moisture longer into the season and as a consequence would be more palatable to livestock and presumably native herbivores such as the desert tortoise (*Gopherus agassizii*).

Additionally, native annual species appear to be relatively less preponderant in intershrub spaces and relatively more numerous and well developed under shrub canopies. Introduced annuals are common throughout. Other authors do not seem to have broken down their data into native vs. nonnative and into different production categories. As a result, there is difficulty in comparing situations. Inouye et al. (1980) reported that *Erodium circutarium*, an alien, and *E. texanum*, a native, comprised over 40% of the total annual biomass near Silverbell, Arizona. A subdivision by species was not made, however, the biomass was distributed almost equally between the two. Johnson and rice (as presented in Lathrop and Rowlands 1981), however, showed that, depending on the area, less than 0.5 percent to 100 percent of the winter annual biomass was composed of native species; nonnatives predominated at every site in the western Mojave near Ridgecrest, but only at one out of three sites in the central Mojave hear Ludlow, California, and south through Johnson Valley. In southern Arizona, Waser and Price (1981) found that the relationship between grazing and annual plant cover was not consistent between years and that diversity of annuals decreases uniformly with grazing. These factors could be important in any forage allocation to native herbivores which may be more dependent on native plant species for forage than sheep or other domestic livestock.

As a general condition, it seems that even though production under shrub canopies may be an important constituent of the total production of annual plants, at the site studies, here 31 percent, it is nonetheless the smaller proportion of total productivity. The production under the shrub canopies will always be a function of the shrub distribution and cover; according to Walter (1973) the latter is probably constrained by dry years. Shrub cover at the Teagle Wash site was high (16 percent) in comparison to other areas. Rowlands (1978) showed that cover of perennial plant species in Joshua Tree Woodlands was generally less than 10 percent: If annual plant production under shrub canopies is proportional to shrub cover (and we have no reason to believe it is not), it could be less in most other areas.

It seems prudent, therefore, to determine beforehand exactly what forage measurements will be most important to determine AUM allocations. If behavior of animals is such that the moister, more palatable forage under shrub canopies is to be used by livestock and herbivores to the exclusion of that in the intershrub spaces, then allocations based only on that available from under shrubs should be used, keeping in mind that this amounts to the smaller proportion of available forage.

In systems where livestock turnout is determined by a certain level of forage production, basing turnout on production under shrub canopies could lead to overgrazing in inter-shrub spaces. It seems more reasonable to base turnout dates on production levels in inter-shrub spaces rather than on a simple (as opposed to a weighted) average based on production plots located under shrub canopies and in inter-shrub spaces or from plots located under the drip line. Production values taken in inter-shrub spaces will always be minimum values, but will result in fewer problems. Overgrazing in intershrub spaces would be minimized; the data is easier to collect; less interpretation is required; and there would be far less chance to premature turnout. The estimated productivity based on weighted estimates of the site studies in this report was 288.7 kg/ha (257 lb/ac) which is far closer to the amounts measured in inter-shrub spaces than at the drip line or under the shrub canopy. Naturally, the most accurate, but also the most time consuming, estimates are the result of proper analysis of spatial distribution of production by means of entitation, stratified sampling, and weighted averaging.

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MOJAVE DESERT RANGE PROJECT

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The Mojave Desert Range Project (MDRP) was organized in 1982 in an effort to serve the various user groups of the Mojave desert. The four states of California, Arizona, Nevada, and Utah are actively participating in the project, providing a focus for identification of problems and issues on the Mojave that can be solved through education and research. The mainstay of the project has been the Cooperative Extension Service of each state, while other active participants include state and federal land management agencies, user groups and concerned organizations.

The first objective for the project was to identify and prioritize the issues and problems the MDRP could effectively address and to design educational programs or sponsor research for their resolution. The second objective was to compile a database of available resources to be used by project members in resolving these problems and issues.

The first objective resulted in a list of problems and issues that user groups prioritized:

(1) The desert tortoise and livestock grazing relationship;

(2) Urbanization and the pressures it puts on the desert, the wildlife, and the livestock producers through vandalism, theft, ORVs, camping and other range etiquette problems;

(3) Livestock production economics;

(4) Desert bighorn sheep and its relationship to livestock grazing;

(5) Grazing systems that should be analyzed for the Mojave.

The second objective resulted in a bibliography of Mojave desert resource publications. This bibliography will be published using grant funds from the Renewable Resources Act.

The MDRP has been very involved in the desert tortoise issue; the project has sponsored a Desert Tortoise Workshop where the latest research was presented for the education of the members. Members of the project will be participating in future research projects to insure the resulting data can be used to make sound management decisions pertaining to livestock grazing and the desert tortoise.

Economics of livestock production on the Mojave desert is the next issue being addressed. Funding has been requested for research in this direction. The MDRP would like to identify successful economic tools that can be used by the desert livestock producer to improve his economic situation. These tools may involve marketing, enterprise accounting, resource identification and use or others.

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MINUTES OF THE DESERT TORTOISE SUBCOMMITTEE OF THE MOJAVE DESERT RANGE PROJECT

The Mojave Desert Range Project problem statement on the desert tortoise was handed out. This was followed by considerable discussion of ongoing research, information needs and research needs.

The Nevada Department of Wildlife is currently doing census work to delineate tortoise distribution, population density and trends. The Bureau of Land Management is planning intensive soils and vegetation mapping in tortoise areas. They hope to develop ecological site and condition descriptions so they can better understand the vegetation implications of livestock, grazing. Betty Burge has been studying fecundity and hatching survival.

Jim Sullins reported on proposed research by UCLA scientists on nutritional physiology of desert tortoise.

The committee settled on the following as priority research needs:

I. Concerning Desert Tortoise Nutrition

(A) What are the nutritional forage quantity and quality needs for:
  (1) maintenance of adults?
  (2) growth of subadults?
  (3) reproduction?

(B) How do desert tortoises actually obtain these nutrients from their diet in various plant communities?

(C) Does livestock grazing decrease the forage available to desert tortoises in such a manner so as to impair maintenance, growth, or reproduction?

II. Concerning Desert Tortoise Habitat:

(A) Does livestock grazing impair the physical habitat, burrows, shrub cover, etc. in such a way that desert tortoises are placed at increased risk?

With this in mind, discussion centered on contributions we could each make from our agencies. Karl Weikle suggested contacting the National Outdoor Coalition in Fontana, California, for research funding. Defenders of Wildlife could be approached for funds. The BLM may have some money for research. If it is done in their district, they will have more local control. The local Grazing Advisory Boards could possible contribute some money if it was used locally. The Nevada Department of Wildlife could administer a research proposal if some funding were available. University research money may be available if a scientist takes the initiative to get a proposal funded. UCLA is doing research currently at Goffs. An additional student wants to do research on hatching and egg survival. The U.S. Fish and Wildlife Service may conduct or fund some research through three of their regions. Their biologists familiar with the desert tortoise are interested.

We established our role and goal. It was suggested to this committee that it should function as a subcommittee of the Mojave Desert Range Project.

Our Role is to promote research on the relationship of multiple use to the desert tortoise. Our Goal is to facilitate support, coordination and communication between agencies, interest groups and researchers. Jim Sullins was elected as committee chair and Ross Haley was elected as secretary.

An early task for the committee will be to review and comment on the research proposal of Brian Henen. It will be sent out with the minutes of this meeting. Comments on the research proposal should be sent to Jim Sullins. The project meets our priorities for research and we therefore support it. Various agencies represented on the committee will do whatever they can to help the researchers. Betty Burge will draft a letter telling potential researchers about our committee. This will be sent out by Jim Sullins.

Future meetings will be called by the chair. We adjourned at 12:50. Respectfully submitted by Sherman Swanson, Acting Secretary.

RANGE AND WILDLANDS ETIQUETTE

Many of the problems associated with growing urban pressure on the Mojave desert could be corrected with a better knowledge of range and wildlands etiquette. A large number of those individuals involved in acts of vandalism, livestock damage, and wildlands misuse are not aware of the consequences of their actions or the possible penalties for their misdeeds.

This urbanization-driven problem was identified by the MDRP as a priority issue and a means of helping resolve this problem was developed in Arizona. The tape and slide set shown has been made available to be used in schools and other organizations in an attempt to increase the public knowledge of range etiquette. The MDRP has obtained $500 to make a similar but localized tape available for the California desert, however matching funds will be necessary to produce enough sets to have an effective program. Your comments on the effectiveness of this effort would be appreciated.

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PATTERNS OF MATE-SEEKING AND AGGRESSION IN A SOUTHERN FLORIDA POPULATION OF THE GOPHER TORTOISE, *GOPHERUS POLYPHEMUS*

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ABSTRACT - Observations on courtship and combat were made as part of a long-term study of a population of *Gopherus polyphemus* at Archbold Biological Station, Highlands County, Florida.

Dominant males maintained burrows of their own and visited as many as four different females at separate burrows during spring, summer, and fall. Courtship occurred at these burrows, where males head-bobbed into the entrances and awaited the emergence of the respective female occupants. The largest male was dominant to smaller males in each of two areas studied intensively, and the two largest females in each area were those most frequently visited. As many as three different males visited the same female in a single season, and males visited the same females from year to year despite changes in the locations of preferred burrows.

Defense of burrows by both males and females was observed, and fighting between males occurred over access to females and their burrows. Large males, by assertion of their dominance when other males were encountered, maintained spatiotemporal territories within which there were opportunities to breed with particular females. Patrolling and maintenance of harems by males was impeded by their slowness of movement relative to the dispersion of the females they visited, and subordinate males probably mated with preferred females in the absence of dominant males.

INTRODUCTION

Land tortoises of the genus *Gopherus* are common and conspicuous in parts of southern North America, but patterns of sexual behavior in the wild remain almost completely unknown in all four living species. Courtship sequences, involving head-bobbing, circling and ramming, biting, and mounting, have been described in *G. agassizii* (Camp 1916; Miller 1932; Grant 1936; Woodbury and Hardy 1948; Housholder 1950; Nichols 1953, 1957; Miller and Stebbins 1964; additional references in Douglass 1975, 1977), *G. berlandieri* (Hamilton 1944, Housholder 1950, Schlögl 1969, Weaver 1970), *G. flavomarginatus* (Legler and Webb 1961), and *G. polyphemus* (Auffenberg 1966, 1969). Very little information is available, however, on the spatial and temporal contexts of mate selection in these species.

1 Manuscript completed September 1977; references cited in this paper are complete only through that date. The present paper consists of a revised and expanded draft of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Arts in the Department of Biology, University of South Florida, 1976.

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The paucity of information on the breeding habits of G. *polyphemus* was emphasized by True (1882), Carr (1952), and Auffenberg (1966). Actual patterns of mate-seeking in the wild have not been reported, and the role of fighting and patterns of burrow use are poorly understood. Patterns of mate-seeking in a southern Florida population of G. *polyphemus* are described in this paper.

MATERIALS AND METHODS

Observations were made at Archbold Biological Station, 12 km south of Lake Placid, Highlands County Florida, during the summers of 1970, 1971, 1973, and 1974, from January 1975 through May 1976, and during May 1977. The study locality (27°11'N, 81°21'W) is near the southern end of the Lake Wales Ridge of central Florida, and is near the southern limit of the natural range of G. *polyphemus*. Major habitats occupied by gopher tortoises at the Station (Figure 3, p. 186 [Appendix]) are:

(1) low flatwoods - dense stands of slash pine (*Pinus elliottii*), with dense to open understory of saw palmetto (*Serenoa repens*), gallberry (*Ilex glabra*), and fetterbush (*Lyonia lucida*);

(2) scrubby flatwoods - scattered slash pines and sand pines (*Pinus clausa*), with dense shrub layer of scrub oak (*Quercus inopina*), live oak (*Q. virginiana*), Chapman's oak (*Q. chapmanii*), rusty lyonia (*Lyonia ferruginea*), saw palmetto, and scrub palmetto (Sabal *etonia*); ground cover sparse;

(3) sand pine scrub - dense to open stands of sand pine, with well-developed shrub layer similar in composition to that in scrubby flatwoods;

(4) slash pine-turkey oak woodlands - scattered slash pines, with open understory of turkey oak (*Quercus laevis*), myrtle oak (*Q. myrtifolia*), live oak, Chapman's oak, rusty lyonia, and scrub hickory (*Carya floridana*); ground cover sparse, with wiregrass (*Aristida* sp.) and forbs; this habitat occupies highest elevations (54-68 m);

(5) cultivated areas - old fields with grasses and forbs (mowed periodically), scattered trees and thickets, and pineapple patches; mowed lawns; grassy road-shoulders.

Open sand fire lanes about 15 m in width extend through most of these habitats and are used extensively by gopher tortoises for feeding and travel.

During and 8-yr period (September 1967-August 1975), 366 tortoises were marked by Station personnel on a 429-ha tract. Tortoises with marked concavity of the plastron, thickened anal scutes, and elongated gular projections were classified as males. In some cases, sex identifications based on these criteria were verified when animals extruded their penises during handling.

Behavioral observations were made in the laboratory and while following marked animals upon their release. Day-long observations of the activities of certain large males were made from blinds and observation towers overlooking their burrows. Active burrows were located by following marked animals and by searching certain areas of suitable habitat; burrows were marked with numbered stakes (B-1, etc.) and their inhabitants noted. Some animals were captured in Tomahawk Live Traps set at burrow entrances. The mounds of sand outside numerous burrow entrances were checked for disturbance and the sand swept smooth in order that tracks made could later be detected; this procedure allowed discernment not only of exact distances to which tortoises emerged from burrows in particular intervals, but, in some cases, directions of movement and the presence of other animals. It was found that "hand-bobbing" or hitting the sand at burrow entrances elicited responses in certain individuals, and this procedure was used at several burrows. In some cases, encounters were staged between males in order to determine dominance-subordinance relationships.

Tortoises were marked for individual recognition by filing notches or drilling small holes in the marginal scutes according to a numbering scheme. In the following accounts, plastron lengths are indicated in parentheses following tortoise numbers. All times reported are in hours Eastern Standard Time (EST).

RESULTS AND DISCUSSION

Adult *G. polyphemus* in the Archbold population rarely exceeded 300 mm in plastron length or 6 kg in weight. Of 174 marked individuals for which sex was determined, 94 (54%) were males; this ratio did not differ significantly from 50:50 ($X^2 = 1.13$, df = 1, $p > 0.05$). Animals in the population studied were strictly diurnal in their outside activity (Douglass and Layne 1978) and were fairly sedentary over the years. Each adult made regular use of one to several deep, well-constructed burrows (Douglass and Layne 1977); just outside the entrance of each burrow was a mound of sand 1-2 m in diameter.

Because they are the first accounts of courtship and combat to be reported in wild *G. polyphemus*, detailed descriptions of courtship behavior, individual movements, and patterns of burrow use of three adult males are included in the APPENDIX (Cases 1 through 3) in order that component behaviors may be viewed in proper context. The overall study area and locations of certain burrows in the areas inhabited by each of these males are also indicated (Figure 3, p. 186; Figure 4, p. 187; Figure 5, p. 193; Figure 6, p. 199 [APPENDIX]). Reference will be made to the case histories in describing various elements of the mating system.

SEXUAL BEHAVIOR

Mate-seeking

Published information on mate-seeking in tortoises of the genus *Gopherus* is meager, and is here reviewed in its entirety. Carr (1952) reported having found no mated pairs among the "thousands" of wild *G. polyphemus* he observed. The pair found copulating by Kenefick (1954) was about 0.3 m inside a burrow facing in. Weaver (1970) reported that *G. polyphemus* individuals have restricted (mutually exclusive) activity ranges and that animals of both sexes must leave their own activity areas to search for mates during the breeding season. Although Woodbury (1948) reported that mating in *G. agassizii* is usually promiscuous, Nichols (1953, 1957) observed that a captive male chose a mate each spring and, with one exception, was attentive to no other females during that season. With one exception, this captive chose a female each spring different from that of the previous year. Berry (1974a) reported that adult male *G. agassizii* emerge from summer dormancy and travel from burrow to burrow courting females. Males have been found within a few meters of the burrows of females courting the occupants (Anonymous 1973). Woodbury and Hardy (1948) reported having found a pair of *G. agassizii* which had apparently just copulated; the female ran to a nearby summer hole when approached. Weaver (1970) noted that male *G. berlandieri* often head-bobbed at females in "pallets" (shallow excavations).

In the present study, large male *G. polyphemus* maintained burrows of their own and visited as many as four different females at separate burrows during spring, summer, and fall. Courtship occurred at these burrows, where males head-bobbed into the entrances and awaited the emergence of the respective female occupants. Slight movements of the female inside the tunnel elicited vigorous head-bobbing and backing up to the far edge of the mound by the male. On some occasions (Cases 1 and 2), males spent several consecutive hours in this manner, head-bobbing occasionally and maneuvering slightly while remaining on the burrow mound. Males sometimes moved from the burrow of one female to that of another (to as many as three in a single day), courting at each entrance (Cases 1 and 2).

Movements to the burrows of females were fairly direct, and little feeding was done along the way. Courtship forays were generally longer both in duration and in distances moved then were feeding forays: four of the latter averaged 29 min in duration (range, 11-55 min), while courtship visits, as indicated, sometimes lasted several hours.

Examples of behaviors characteristic of male courtship visits are to be found in the following excerpt from Case 2:

> A day-long watch of B-158 was begun at 0920 h on July 24, 1975. Male 201 was inside the tunnel at this time and had basked that morning on the burrow mound. He emerged at 0930 h and basked on the mound in partial sunlight for 48 min, then re-entered the burrow. At 1116 h he emerged again and basked briefly, then (at 1120 h) left the mound and moved steadily east through underbrush and across the newly-mowed east field to B-168 (Figure 5), inhabited at this time by female 332. Number 201 moved directly between B-142 and B-159 without investigating either burrow, and took only two or three bites of vegetation along the way. He arrived at B-168 at 1138 h and paused on the mound, then entered the burrow slowly, tossing a few scoops of sand with his forefeet but with no head-bobbing. At 1150 h he emerged to about 1 m outside the entrance, turned 180°, and head-bobbed weakly (in bursts of two or three bobs) into the entrance. He then advanced slowly toward the entrance, head-bobbing and occasionally tossing sand, and at 1158 h stopped with his head in the entrance. He remained in this position with only slight movements (including one series of vigorous head-bobs directed at a nearby knob of wood) until 1218 h, when he backed up several centimeters head-bobbing. He quickly backed up another 0.3 m 5 min later; these movements were apparently elicited by advances or other movements of the female (332) inside the tunnel. When the female emerged to about 0.3 m outside the entrance at 1232 h, male 201 backed up rapidly, head-bobbing vigorously and keeping about 1 m between them. The female advanced another 0.3 m 4 min later, and 201 backed up to the far edge of the mound, head-bobbing vigorously and maintaining their 1 m separation. At 1238 h the female turned 180° and walked back into the burrow. Number 201 ran after her, head-bobbing just behind her shell, and mounted her momentarily as she entered the burrow; he was scraped off by the overhang as she entered. The female emerged to about 0.6 m outside the burrow 4 min later, and 201 backed up quickly to his former position at the far edge of the mound, head-bobbing vigorously. The slightest movements of female 332 elicited immediate, intense head-bobbing by the male. She suddenly re-entered B-168 at 1255 h, but 201 remained in his position in direct sunlight with his head elevated and forelimbs extended laterally, motionless except for occasional closing and opening of his eyelids. He advanced to within 0.3 m of the entrance at 1322 h and head-bobbed occasionally into the tunnel. Female 332 emerged again to about 0.3 m outside the burrow at 1348 h, and again 201 backed up head-bobbing to the top of the mound. When she emerged another 0.3 m 2 min later he backed up to the far edge of the mound as before, head-bobbing at her. He head-bobbed wildly at 1412 h as the female emerged several more centimeters to rest with her limbs extended. She ran frightened into the burrow at 1430 h; male 201 head-bobbed as she left but held his position as before. At 1500 h a light rain began, and 201 remained motionless at the far edge of the mound with his head elevated and

forelegs extended laterally. When startled by my movements, he hurried to the burrow entrance and stopped; he remained in this position for the remainder of the afternoon.

All of the evidences of actual mating obtained in this study (tracks, Case 1; mounting attempts, Case 2; mated pair, Case 3) were found within a few meters of burrow entrances. Mating may occur when individuals encounter one another during activity outside of burrows, but male visitation and courtship at the burrows of females is clearly the usual pattern in the population studied. The roofs of tunnels are usually not sufficiently high to allow mounting by the male, and the mate-seeking behavior of males, involving head-bobbing and extended periods of waiting on burrow mounds, appears to be adjusted to dependence on the emergence of females for mating. If mating could occur inside burrows, it would seem more efficient for males to enter tunnels directly and mount the occupant females or even force them against the tunnel walls to mate. The female's reluctance to emerge completely is what prevented consummation of courtship in each of the cases observed. Waiting at or near the burrow of a female for extended periods of time ensures that the male is present when she does emerge and probably allows for expulsion of rival males who may approach.

In a study of activity and thermoregulation in *G. polyphemus* at this locality, Douglass and Layne (1978) reported that males were captured more frequently than females during most of the year and were active both earlier and later in the day. The significantly greater frequency of male captures seems attributable to both the wider ranges of movement of males and their greater frequency and duration of outside excursions. The tendency of males to be active both earlier and later in the day probably reflects, in part, the advantages of early arrival and prolonged waiting at the burrows of females.

The largest male (i.e. 96 and 201, respectively) was dominant to smaller males in each of two areas studied intensively (Agonistic Behavior), and the two largest females in each area (185 and 214, 374 and 332) were those most frequently visited (Tables 1 and 2, in APPENDIX). A given male visited as many as four different females in a single season, and as many as three different males are known to have visited a single female in a season. In addition, males visited some of the same females from year to year despite changes in the locations of their preferred burrows.

The case of male 96 is outlined in Figure 1 as an example of the constancy of association of certain males with particular females. Male 96 courted female 185 in 1971, 1973, and 1975 despite changes in the location of her preferred burrow. In 1975, competition existed between males 96, 299, and 161 for opportunities to breed with this female; male 96 was clearly dominant at her burrow.

The tendency of a male to prefer the use of different burrows while courting females in different parts of his home range is illustrated in Figure 2. In 1975, the burrows of the two largest females in the home range of male 201 (i.e., 374 and 332) were 260 m apart. The male made alternate use of four different burrows as bases from which to court these females. (He courted female 332 at another burrow nearby in September 1975, and, although he apparently neglected female 35, courted female 66 at a burrow far to the west in 1974 and female 256 at each of three different burrows (not shown) in 1974, 1976, and 1977, respectively.)

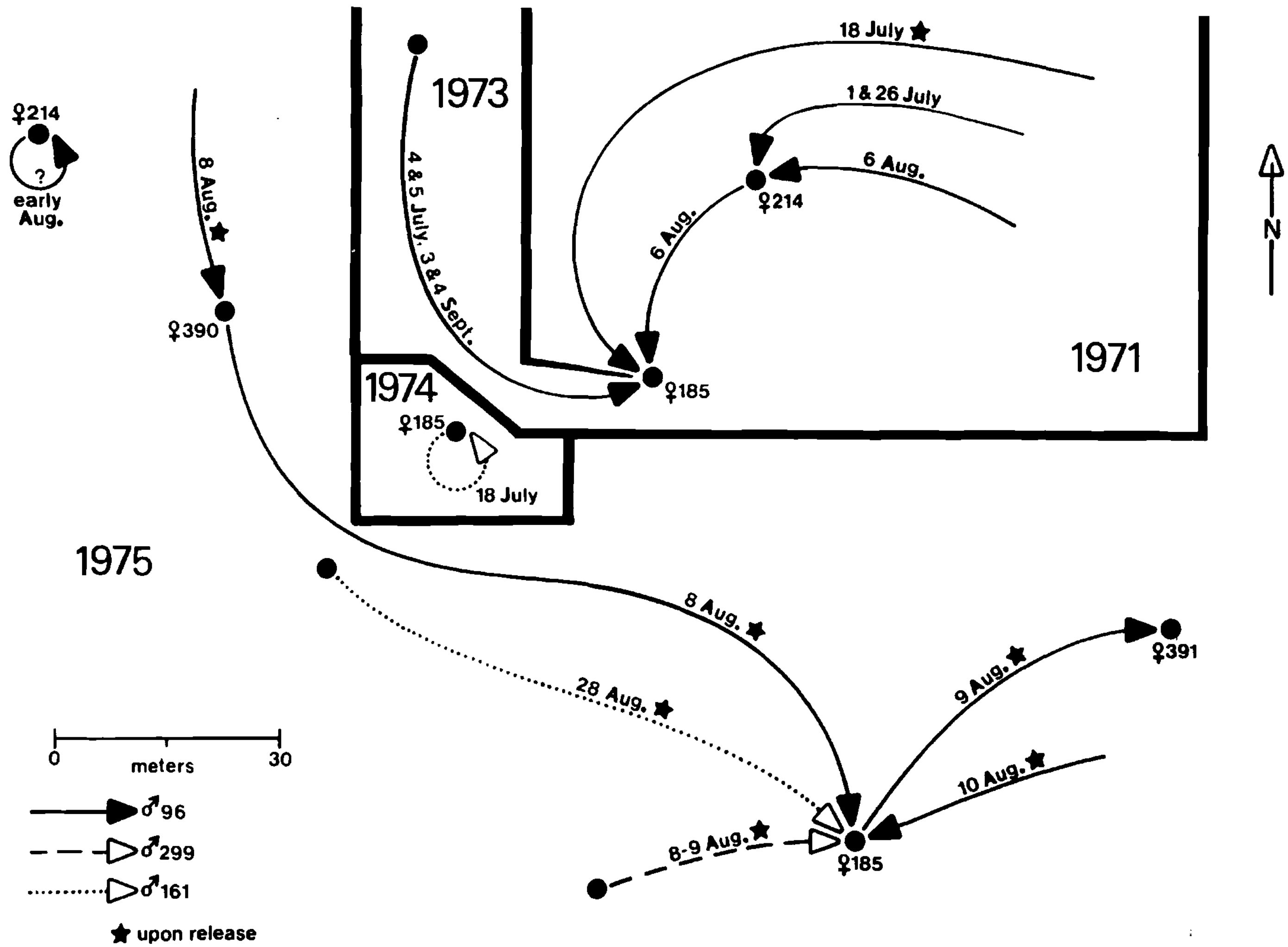

Figure 1. Arrows indicate courtship visits (slightly schematized) made by three *Gopherus polyphemus* males, based on evidence from tracks, trapping, direct observation, and following of marked animals upon their release. Solid dots represent tortoise burrows, and heavy black lines separate observations made in four different years. Despite changes in the location of her preferred burrow, female 185 was visited and courted by male 96 in 1971, 1973, and 1975, by male 161 in 1974 and 1975, and by male 299 in 1975. Male 96 was dominant to each of the two smaller males at the burrow of this female in 1975. He also courted female 214 in 1971 and sibling females 390 and 391 at their burrows in 1975. See text and Case 1.

Although it is not known how female receptiveness may vary seasonally or individually, it may be that variations in this or in general activity affect the preferences shown by courting males. Long-term associations of males with particular females are not simply consequences of burrow proximity: burrows of frequently-visited females were farther from the burrow of the courting male than were those of certain neglected females in each case (e.g., the burrow of 35 and of 256 in the home range of male 201 during 1975).

It seems probable that gopher tortoises recognize one another individually in some areas; certain individuals are associated fairly constantly from year to year, and it is likely that olfactory and possibly visual recognition play an important role in their societies.

Use of old burrows as landmarks by males

When released on fire lanes after handling, tortoises generally moved directly along well-worn paths to preferred burrows and entered, bypassing ones not their own. Burrows in some areas were interconnected by well-worn trails, and males 96 and 201 often crossed the mounds of active and abandoned burrows in the course of their movements (examples in Cases 1 and 2). Number 96 used old burrows as landmarks in dense woods, and sometimes paused to investigate burrow mounds before moving on. In addition, six other males, upon release, crossed the mounds of old or active burrows before entering their own. These males were: 24 (262 mm) on July 13, 1973, April 20, 1975, and August 29, 1975; 161 (224 mm) on August 28, 1975; 209 (205 mm) on June 20, 1971; 221 (229 mm) on August 10, 1971; 273 (233 mm) on November 29, 1975; and 426 (232 mm) on April 1, 1976. Some of the burrows whose mounds these males crossed had been occupied formerly by females. Tortoise tracks were occasionally found crossing burrow mounds without entering the tunnels. Females returning to their own burrows were not seen to cross the mounds of old burrows in this manner.

Males somehow learn the locations of new burrows of particular females as the latter relocate from year to year. Males sometimes use as landmarks burrows occupied formerly by females or by themselves, and in this way might effectively "track" preferred females from season to season and learn of intrusions by other individuals in their home ranges. The fact that in some cases burrows of females represent extreme points of capture of males further suggests the importance of the former in determining the home range limits of males (e.g. Figure 5).

Scent-marking and olfaction

The possible role of olfaction in the orientation of *Gopherus* was mentioned by Auffenberg (1969). Gourley (1969) believed that the trails surrounding *G. polyphemus* burrows, by their provision of visual and olfactory cues, are the primary source of short-range orientation information for these animals, and Camp (1916) reported that *G. agassizii* occasionally test the ground with the tips of their snouts while moving about.

In the present study, courtship forays of *G. polyphemus* males were often surprisingly direct even in dense scrub, and sometimes involved movements of hundreds of meters. Males "knew" the locations of burrows of certain females and seemed to locate them primarily by recognition of subtle visual landmarks. The existence of trampled paths between some burrows and the tendency of males to move past old burrows on their forays has been mentioned. In most forays observed, males were not seen to press their nostrils to the ground or to other objects along the way. The possible role of olfaction in trailing or in recognition of other individuals is considered here.

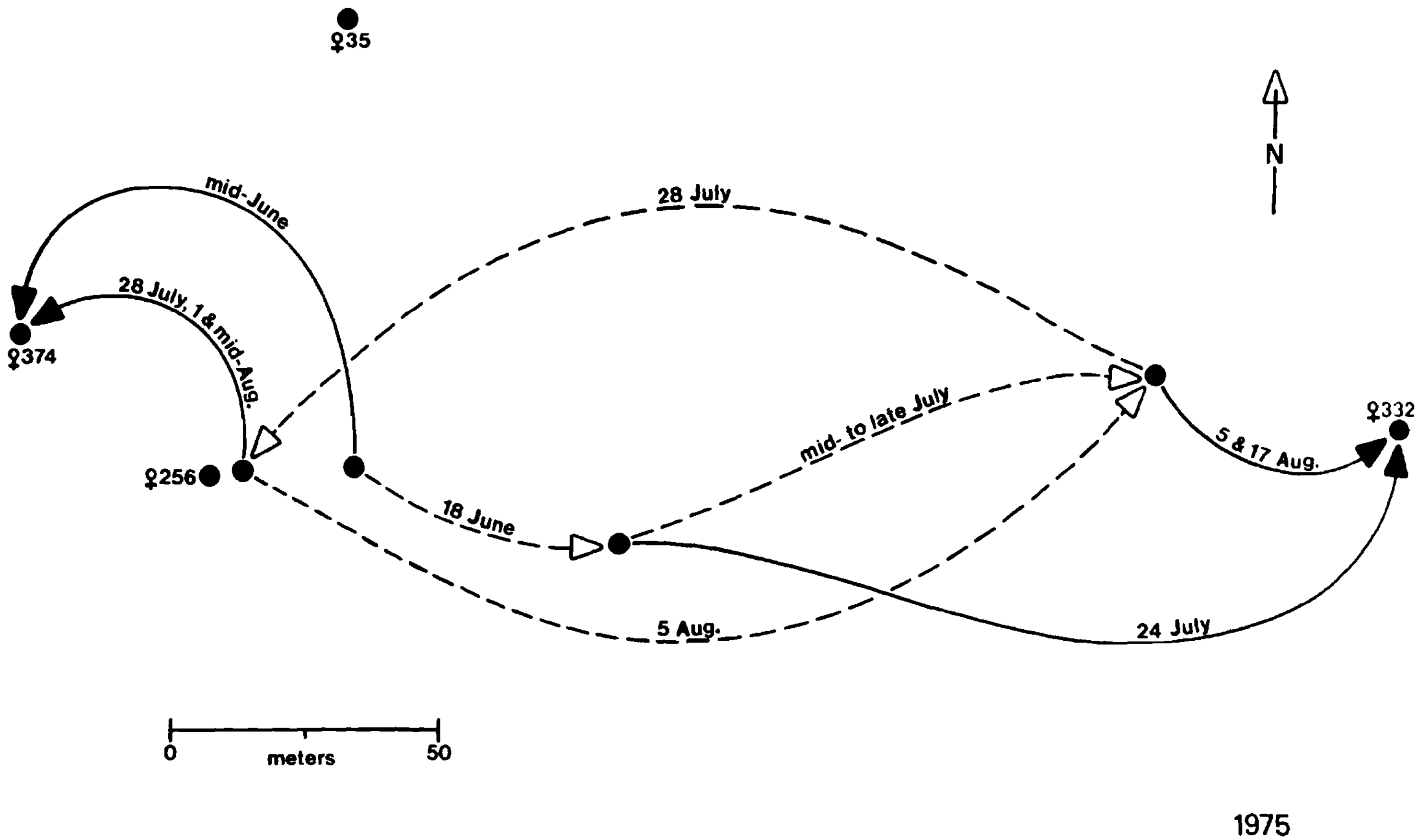

Figure 2. Solid arrows indicate known courtship forays (slightly schematized) of *Gopherus polyphemus* male 201 during 1975. Dashed arrows show shifts in his burrow preference; solid dots represent tortoise burrows. Male 201 made alternate use of each of two burrows in the west field as bases from which to court female 374 and of two burrows farther east as bases from which to court female 332. See text and <u>Case 2</u>.

On July 12, 1971, female 65 was released on a fire lane and watched as she moved to B-33 (Figure 6). She frequently pushed her nostrils to the ground and to leaves and fallen twigs along the way, and to the sand of the burrow mound before entering. This female had occupied B-33 at least since mid-June 1971, and at the time of this observation the burrow was also inhabited by male 58 (Case 3). Another large female pressed her nostrils to living leaves while moving to her burrow upon her release on July 15, 1971. Tortoise 189 (sex undetermined) moved to B-106 upon release on July 9, 1973 and entered after some sniffing at the entrance; male 299 had just entered the burrow (the two adults had been found together in the burrow nine days earlier). Twice while male 201 was emerging from B-157 to dig or bask on March 22, 1975 I saw him push his nostrils to the sand of the burrow mound; this burrow was later occupied by female 374 (June and August 1975).

Male 96 paused occasionally during various forays and at times was heard to breathe more heavily than usual; this sometimes involved pulsing of the throat and a whistling sound from the nostrils upon inhalation. This behavior was observed as he paused to investigate the trail to B-46 (containing female 185) on August 6, 1971 and as he arrived on the mound of B-172 (containing female 185) on August 8, 1975. His investigation of the entrances of certain old burrows appeared to have involved olfaction as well as vision (Case 1). When released on the mound of B-171 on August 26, 1975, male 96 refused to enter. He backed out and circled around the mound, frequently pressing his nostrils to the ground, then moved quickly and steadily south with occasional pauses to touch his nostrils to the ground. He arrived and paused on the mound of B-188 and head-bobbed at the occupant male (161) as if challenging (full account in Case 1). This incident apparently involved scent-trailing of 161 by male 96. The smaller male was a subordinate individual attempting to establish himself as a breeder in the home range of 96. Male 161 co-occupied B-128 with female 185 in July 1974 and visited this female at B-172 in August 1975; the two males apparently competed for opportunities to breed with her.

Tortoises presumably rest in their own excrement at the ends of burrows (Hubbard 1894, Hallinan 1923, Brode 1959, Hansen 1963), and scent is no doubt distributed on the surface simply by movement of sand onto burrow mounds and repeated trampling of favored routes in the course of foraging and other activities. Following of scent-trails might enable males to locate females or other males in some cases.

Several observations suggest that scat deposition and penis-dragging may serve as forms of scent-marking as well. The remains of six tortoise scats were found around the edge of the mound of B-98 about 1.6 m outside the entrance on July 4, 1973. This burrow was inhabited by an adult male (263) and female (183) at the time. A single, dried dropping was found on the mound of B-119 about 1.3 m outside the entrance on August 5, 1973. The burrow was in use by an adult female (57) and had been used by an adult male (56) in August 1974 (it is not known whether or not a second individual was sharing the burrow with the female at the time this observation was made). One scat was found on the mound of B-33 about 1 m outside the entrance on July 15, 1974; the burrow had been inhabited by an adult male (58) and female (65) in the summer of 1971. On September 11, 1975 I found three fresh droppings on the mound of B-167 about 1 m from the entrance. The burrow was in its third week of use by male 96 and had been inhabited by an adult female (214) the month before. The three scats dried gradually but remained in place on the mound through October 3, 1975; a fresh dropping was found with the others on September 26, 1975. The male almost certainly detected the presence of these scats in his basking area and had apparently deposited them there: when they were only one day old I watched him bask with his head a few centimeters from them for over an hour.

Brode (1959) observed *G. polyphemus* backing out of their burrows in late summer dragging and scraping dung and trash to several feet beyond the entrances; he also noted that in many cases tortoises moved a few feet outside of their dens to defecate and then returned. That scats would remain on the mound of a burrow without detection by an occupant tortoise is unlikely. Some burrow maintenance, involving moving of sand, occurs nearly every day in summer, and burrow mounds are generally kept clear of litter.

It is interesting that the only mounds on which droppings were found were at burrows inhabited at one time or another by an adult male and female. It is possible that scats deposited at co-occupied burrows serve to deter intrusion by other individuals. Deposition of scat by a dominant male on the mound of a burrow he is occupying might advertise his presence to other males (e.g. to 161, in the case of male 96) and thereby reduce the amount of energy expended in active assertions of dominance. In this connection, Patterson's (1971a) observations on *G. agassizii* captives are of interest: Fecal pellets deposited by dominant males caused dispersal of subordinate males from sleeping areas.

J. N. Layne (pers. comm.) observed what may have been marking activity while watching courtship behavior between an adult male and female *G. polyphemus* placed together in the laboratory at the Station on March 3, 1970. The male extruded his penis while moving over the floor and dragged it for 0.3-0.6 m at a time. The drag-marks on the floor consisted of a viscous fluid which had exuded from the penis; examination of a sample showed the fluid to have contained no sperm. On September 22, 1972 a large male was captured at a burrow entrance with his penis extended; marks in the sand showed that the penis had been dragged (C. E. Winegarner pers. comm.).

Head-bobbing as a signal

Chin glands have been described in all four species of the genus *Gopherus*; head-bobbing and chin-gland secretions have been found to function in sex and species discrimination and in courtship and combat in these animals (e.g. LeConte 1836; Agassiz 1857; Camp 1916; Grant 1936; Smith and Brown 1948; Woodbury and Hardy 1948; Legler and Webb 1961; Eglis 1962; Auffenberg 1965, 1966, 1969; Rose, Drotman, and Weaver 1969; Rose 1970; Weaver 1970). Auffenberg (1966) suggested that head-bobbing may serve as a means of wafting scent through the air as well as being a visual signal in *G. polyphemus*, and Rose, Drotman, and Weaver (1969) remarked on olfactory and visual cues provided by chin glands in tortoises of this genus. Examples of the vigorous head-bobbing of courting males in or near the burrow entrances of females are given under Mate-seeking (above) and in Cases 1 and 2 in the present study: it appears that under natural circumstances the signal transmitted is both visual and olfactory in nature.

The tendency of females in certain burrows to advance toward their burrow entrances in response to disturbance outside (e.g. "hand-bobbing") is mentioned elsewhere (Defense of burrows; Cases 1 and 2); female emergence sometimes occurred in response to head-bobbing by a male on the burrow mound. Advancement in the tunnel may have allowed these females to supplement visual information gained from the males' head-bobbing and other movements with olfactory cues about the identity of these intruders or potential mates. On March 23, 1975 I "hand-bobbed" vigorously at the entrance of B-152. Adult female 374 was about 0.6 m inside the tunnel facing out. With increasing intensity she inhaled and exhaled deeply and steadily through her nostrils, to the point where the skin at the base of her neck and forelegs bulged and retreated noticeably. Although this generally shy female may have been attempting to intimidate the supposed intruder or preparing to lunge and hiss at my hand, it seems more likely that her deep breathing represented an effort to draw in and test the scent of the simulated tortoise. Pawley (1975) reported that a large female *G. flavomarginatus* advanced slowly from inside her burrow in response to tapping of the ground and soft calling at the entrance.

In all of the cases observed in which *G. polyphemus* males head-bobbed at females inside burrows, the females were found to have been resting facing out within about 1 m of the entrances. Head-bobbing in burrow entrances probably serves primarily as a visual signal of a male's readiness to mate, and it is possible that from inside the tunnel the female is able to discriminate the sex and maybe even individual identity of the visitor based on visual and olfactory cues.

That head-bobbing by males may occur in response to stimuli primarily visual in nature was evident in several observations of bobbing at inanimate objects. Male 96 paused briefly on June 17, 1973 while moving over a fire lane near the former burrow of a female to head-bob at the fallen cone of a slash pine. When male 261 was put on the floor of a truck on September 3, 1973 he engaged in vigorous and persistent head-bobbing and repeated biting at the rounded base of the shift stick, and male 273 head-bobbed persistently at the tip of my boot and bit at its edge while in the laboratory on August 15, 1975. The sight of a projecting knob or splinter on a fallen fence-post on the mound of B-168 elicited vigorous head-bobbing by male 201 at one point as he courted the occupant female (332). This bobbing continued for several seconds, with the head and neck of 201 audibly striking his anterior marginal scutes. This male head-bobbed at the wheel of an office chair and at the tip of a shoe in the laboratory on May 7, 1976.

The most vigorous head-bobbing observed in males 96 and 201 occurred in response to slight movements made by females at whose burrows they were courting (Cases 1 and 2). The head-bobbing of another male (24) at other individuals in his enclosure on July 1, 1971 seemed to have been triggered by the sight of a head or limb of another individual; he followed certain individuals persistently, occasionally touching his nostrils to their limbs or shells.

My presentation of the cloacal area of female 185 to the nostrils of male 96 at one point elicited immediate and vigorous head-bobbing and biting of her marginal scutes by the male, and this seemed clearly to have involved olfactory recognition. Male 299 was covered with the urine and feces of female 390 when I placed him with male 96 on August 8, 1975. Male 96 head-bobbed vigorously at 299 (to the point where his neck thumped on the ground) and at the nearby female, but when he was put head to head with 299 he appeared to recognize this individual as a male and rammed and chased him.

It appears from these examples that head-bobbing serves primarily as a visual signal elicited by certain visual stimuli. Olfactory discrimination of sex, based on chin-gland secretions or cloacal scent, often follows or may itself induce bobbing at close range. The relative importance of these sensory modalities of the head-bob signal is apparently a consequence of the tendency for tortoises to be seen before they are smelled by others in the wild. This is interesting in light of the suggestion that certain head movements now having functions as visual signals originated as olfactory motor patterns (Eglis 1962, Auffenberg 1965).

Head-bobbing has been noted in females far less often than in males; in the five cases observed, it has been far lower in intensity as well. Female 185 exhibited one brief series of weak horizontal head-bobs on July 18, 1971 as she was resting in the entrance of B-46 being courted by male 96. Male 201 head-bobbed at female 35 and bit at her marginal scutes and forelegs in the laboratory on July 9, 1974; she repeatedly tried to move away but occasionally returned some weak head-bobs. When courted by male 27 in the laboratory on April 8, 1976, she occasionally returned weak vertical and horizontal bobs. Female 256 head-bobbed weakly while being courted by 201 at B-206 on May 7, 1977. Female 210 (190 mm) head-bobbed slowly (ca. 1 bob/sec) in the laboratory on June 19, 1971 with no apparent stimulus. The chin glands of adult females in this population are generally well-developed but usually less swollen than are those of sexually active males.

Descriptions are given elsewhere of head-bobbing between males preceding fights (Combat); it seems that head-bobbing by a male at a burrow entrance may be recognized as a challenge if the burrow occupant is a male and as a sort of summons if the occupant is a female.

Auffenberg (1969) noted that during courtship, female G. *polyphemus* sometimes rubbed their chins against their outstretched forelegs in order to transfer scent. Similar behavior was observed by Weaver (1970) in males of this species, and in the present study it was seen in male 96 on three occasions as he basked on the mounds of burrows he occupied (July 1973, September 1975). The chin glands of male 397 were swollen and beaded with fluid when he was placed in an enclosure with male 209 and female 21 on April 20, 1976. Each of the latter animals rubbed their nostrils repeatedly against the lower jaw, gular projection, and forelegs of this male with side-to-side movements of their heads, apparently investigating scent which had been distributed to these areas from his chin glands.

Age at sexual maturity

The wild male and female G. *polyphemus* found copulating by Kenefick (1954) were estimated to have been about 25 yr of age. Simkiss (1961) found ova in the ovary of a female only 350 g in weight. Auffenberg (1974) stated that sexual maturity is reached in about 5-7 yr in tortoises of this species, but six specimens (carapace lengths, 143-226 mm, including one male) examined by Jackson, Holcomb, and Jackson (1974) were sexually immature; two large females (241 and 275 mm) were mature, with eggs. Goin and Goff (1941) observed that sexual differences in plastron length were most pronounced in individuals greater than 150 mm in length.

Estimates of ages at sexual maturity in G. *agassizii* range from 10-20 yr (e.g. Woodbury and Hardy 1948, Miles 1953, Miller 1955, Berry 1974a). Grant (1936) noted that male secondary sex characters appeared as captive juveniles exceeded 120-140 mm in shell length; Miller (1955) observed that these characters began to develop at 16-17 yr and were complete at 20 yr of age in captives. In G. *berlandieri*, attainment of breeding age has been estimated to occur at 15-20 yr (Anonymous 1967, Texas Parks and Wildlife Department n.d.). Auffenberg and Weaver (1969), however, estimated that sexual maturity was attained at only 3-5 yr of age in animals of this species, at straight line carapace lengths of 105-128 mm. Scanty data suggested to Legler and Webb (1961) that sexual maturity in G. *flavomarginatus* was attained at carapace lengths of 220-300 mm in both sexes (at about age 11 in one female).

The smallest G. *polyphemus* females to have induced courtship behavior in males in the present study were 392 (131 mm), 384 (136 mm), 391 (202 mm), 390 (208 mm), and 400 (209 mm). The smallest males to have exhibited courtship behavior were 161 (222 mm), who visited female 185 at her burrows, male 397 (211 mm), who courted female 21 in the laboratory, and possibly male 455 (190 mm), who was found by J. N. Layne (pers. comm.) visiting female 332 (?) at a burrow. Male 363 (201 mm) occupied burrows near those of females in the old fields and extruded his penis in the laboratory, but it is not known whether or not he engaged in courtship activities during the study period. The smallest male to have extruded his penis in the laboratory was 184 mm in plastron length.

Breeding season

Kenefick (1954) reported having found a pair of G. *polyphemus* copulating in Lee County, Florida, on April 23, 1953, and spring was indicated as the mating season in this species by Hutt (1967) and Ernst and Barbour (1972). Courtship activity was observed by Auffenberg (1966) between captives from north central Florida on May 24, June 1, and June 3, 1964 and on May 18, 1965. J. N. Layne (pers. comm.) reported having found mated pairs only during May in open, turkey oak woods in Alachua County, Florida.

The monthly distribution of 34 recorded male visits to the burrows of females in the present study (based on evidence from tracks, trapping, and direct observations) was: March 2, May 2, June 2, July 10; August 14, September 3, and November 1. In addition, courtship of females was observed in the laboratory on 13 occasions involving 7 different males. The monthly distribution of these episodes was: March 2, April 3, June 1, July 2; August 3, September 1, and November 1. Although these distributions are probably not representative of actual frequencies of courtship episodes or visits to burrows because of irregularities in observational effort, they do indicate that mating behavior may occur at any time from early spring (perhaps earlier) to late fall at this locality.

Studies of reproductive histology have not been reported in any species of the genus *Gopherus*, and details of the reproductive physiology of these animals remain unknown. This situation is regrettable in light of the fact that hundreds of tortoises are slaughtered for use as food each year in Florida, and their reproductive tracts discarded. A study of reproductive physiology in *G. polyphemus* would yield knowledge of spermatogenesis and egg formation and of sperm storage if this occurs, and might aid in interpretation of some of the behavioral observations reported here.

Mounting attempts

Actual mounting attempts have been seen on only six occasions; in none of these was the penis of the male visibly extruded. In the laboratory, male 96 courted and tried to mount female 35 on April 10, 1972 (C. E. Winegarner pers. comm.), male 201 tried to mount female 400 (209 mm) on September 12, 1975, male 273 (231 mm) tried to mount 392 (sex undetermined, 131 mm) on August 15, 1975, and male 397 (211 mm) tried to mount female 21 (231 mm) on April 20, 1976. Accounts of male 201's attempted mounting of female 332 at B-168 (July 24, 1975) and of female 256 at B-206 (May 7, 1977) are given under Mate-seeking (above) and in Case 2, respectively.

Other than in cases of combat between males (accounts under Combat), two tortoises have been found within sight of each other outside of burrows on only two occasions. In both cases, an adult male and female were involved. Male 58 and female 3 were found in an open area only 15 m apart on June 23, 1973 (Case 3), and male 75 (251 mm) and female 78 (260 mm) were found on a fire lane about 30 m apart on July 25, 1974 (C. E. Winegarner pers. comm.).

Penis extrusion

Although the penis of males was not apparent in the six mounting attempts observed, struggling males sometimes extruded and briefly flared their penises when overturned or handled. Penis extrusion in the laboratory has been recorded on 25 occasions at the Station; these incidents involved 18 different males, ranging from 184 to 270 mm in plastron length. The monthly distribution of these observations was: January 1, March 2, April 1, May 4, June 3, July 3, August 2, September 4, October 1, November 3, and December 1.

It is possible that extrusion of this moist and highly vascularized organ might augment heat loss in males overturned (e.g. in combat) and exposed to unfavorably high temperatures; in the cases observed, however, the behavior seemed to reflect general excitement and appeared to have been elicited by factors other than environmental temperature. If penis extrusion is indicative of sexual vigor or readiness to mate, its occurrence in nearly every month of the year may be further evidence of year-round sexual activity in males. It was suggested above that extrusion and dragging of the penis may serve as a method of scent-marking as well.

AGONISTIC BEHAVIOR

Territoriality is not widely known in turtles and is apparently unusual in this group (Cagle 1944, Auffenberg and Weaver 1969, Brown and Orians 1970, Brattstrom 1974). Combat has been described in all four living species of the genus *Gopherus*, but the relationship of agonistic behavior to space or to the availability of food or mates has received little attention.

Defense of burrows

As previously mentioned, adult *G. polyphemus* in the population studied each made regular use of one to several deep burrows; the tunnels and mounds of sand outside were focal points of their activity (Douglass and Layne 1977). Observations made in this study clearly indicate that defense of burrows does occur, by dominant males and by certain females. In most cases, at the approach of an observer, tortoises retreated far down their burrows; the following cases are notable exceptions.

Male 201 exhibited marked animosity when I approached and bobbed my hand or hit the sand at the entrances of certain burrows he occupied. At these times he advanced hissing from inside the tunnel and lodged himself sideways in the burrow entrance. When I moved closer or touched him he often lunged and hissed explosively or braced himself in the tunnel with extended legs. This behavior clearly represented burrow defense and would have been a formidable obstacle to entry of the tunnel by another tortoise. It was observed in male 201 in 1975 at B-139 (January 25), B-105 (April 18, 19, and 20, June 17), B-158 (June 18, 20, and 29, July 23), B-159 (July 22 and 25, August 7, 9, 18, 21, and 24), and B-164 (July 28 and 29, August 1 and 3), in 1976 at B-182 (March 16 and 19) and B-204 (May 7 and 13), and in 1977 at B-189 (May 7) and B-169 (May 13).

J. N. Layne (pers. comm.) observed similar behavior in a male inside a burrow in slash pine-turkey oak woods at the Station on April 21, 1957. The animal hissed and advanced toward the entrance when tapped and could not be intimidated. Legler and Webb (1961) reported that the image reflected from a mirror placed in front of a burrow of *G. flavomarginatus* caused the occupant to come out and fight.

Male 96 was often found lodged sideways in the tunnel of B-95 near the entrance in June and July 1973; he entered B-167 as I approached on September 2, 1975 and turned sideways, but did not lunge or hiss when tapped. Although observations made on only two individuals do not really permit meaningful comparisons to be made, it is possible that the higher levels of aggressiveness seen in the burrow defense of male 201 in the old fields were related to higher population density and/or competition for burrows in that area (Case 2).

Observations in both areas indicated that subordinate males use certain burrows in the absence of the dominant male but that the latter may assert his dominance and occupy these burrows when he is using that part of his range.

Weaver (1970) thought it possible that, in meetings between *G. polyphemus* males, noncombative recognition of the dominant individual may result in retreat by the subordinate tortoise. Support for this suggestion may be found in the following observations.

On August 8, 1975, male 299 (234 mm) was seen retreating rapidly westward toward B-173 (Figure 4) upon sight of male 96 (246 mm); 96 was approaching from the north to visit and court female 185 at B-172 nearby (Case 1). I captured male 299 and put the two males head to head for several minutes; 299 remained withdrawn and no fight developed. I later put the two males together with female 390 (captured earlier) on the Jeep trail between B-104 and B-153 (Figure 4). Male 96 head-bobbed at the smaller male and then rammed and chased him south along the trail. When put together at the laboratory, no fighting occurred; each male moved off separately. Each of them head-bobbed at female 390 when she was placed nearby.

The following day, 299 moved steadily to B-173 and tried to enter upon being released; 96 tried to run into this burrow when I placed him alone on the mound. The two males were then put together on the mound of B-173. Male 96 rammed 299 repeatedly and the smaller male tried to run into the burrow. When I prevented this, 299 moved off the mound and, with continued ramming from 96, moved to B-174. When I again released 299 at the point of his capture the day before (between B-173 and B-172) and prevented him from moving in the direction of B-173 and B-174, he led me fairly directly to B-172 (containing female 185) and tried to enter without head-bobbing. Males 96 and 299 were then put together on the mound of B-172. The larger male rammed 299 and pushed him from the mound, and 299 moved off in the direction of B-173.

An account is given elsewhere (Case 1) of a visit by male 96 to B-188 (containing smaller male 161) and of the ramming dealt 161 when he was removed from this burrow. The smaller male tended to associate with one of the females (185) courted by male 96 at various burrows (Case 1).

Male 363 (201 mm) was taken from B-139 on March 23, 1975 and placed about 1 m outside the burrow in a Tomahawk Live Trap containing male 201. Male 201 had just been taken from B-105 (Figure 5); he had previously occupied and defended B-139, however (July and August 1974, January 1975). Introduction of the smaller male elicited powerful ramming thrusts from 201, who pushed 363 out of the trap into the field. Male 363 retreated rapidly to the south and east, followed closely by 201, and entered B-158. Whenever 363 paused in his retreat the larger male rammed the rear or sides of his carapace and shoved at him with lifting movements as if trying to overturn the subordinate. The ramming continued even onto the mound of B-158, as 363 continued his retreat into the burrow. The entire chase lasted 8 min; 201 rammed 363 a total of 25 times. Male 201 later occupied B-158 himself (June and July 1975, Case 2).

I recaptured both males at B-158, brought them back to B-139, and put them together on the mound facing the burrow entrance: in this way they were given an equal opportunity to enter the burrow. Male 201 advanced steadily into the burrow as 363 veered away and began to move again toward B-158: the presence of the larger male deterred 363 from trying to re-enter the burrow out of which the latter had been taken earlier the same day (363 walked steadily into the tunnel when he was later released on the mound of B-139 in the absence of 201). When placed together several times in the laboratory later in the day, 201 and 363 moved off in separate directions with no ramming or pushing, further suggesting that the spatial contexts of encounters are important in determining the incidence of fights.

Male 363 was in B-159 on April 19, 1975, and advanced when I "hand-bobbed" at the entrance; this burrow was later occupied by male 201 (July and August 1975, Case 2). Number 363 was observed in another burrow (B-161) on June 18, 1975. This burrow had apparently been constructed in a marginal site, suboptimal with respect to drainage characteristics: deep ruts formed in the tunnel floor during a heavy rain two days later, and the burrow was abandoned. Temporary use of this inferior burrow by 363 may have resulted from restrictions imposed by male 201 on his use of other burrows in the area.

These observations indicate a pattern of burrow defense by dominant males and assertions of dominance over other males at various burrows, including those of females. Subordinate males apparently visit and may co-occupy the burrows of certain females in the absence of the dominant male (Case 1).

Fractures and partial flaking of the pleural and marginal scutes has been noticed on some males (e.g. two individuals examined in May 1977: 161 (225 mm), flaking of marginals 5-7 on each side; 461 (267 mm), flaking of left marginals 5-7, right marginals 5-9, left pleural 2, right pleurals 2-4). This condition probably results from rammings received during burrow defense (i.e. when lodged sideways in tunnels) or in combat.

Observations suggest that differences in temperament may exist between adult males and females. Females generally remained deeper inside their burrows and withdrew into them more readily when approached. In light of the general timidity of females in their burrows, the following observations are of interest.

The prevention of entry of courting male 96 by female 185 at B-46, by female 390 at B-171, and by female 391 at B-175 is described in Case 1. Each of these females advanced or turned sideways hissing in their burrow entrances at the approach of this head-bobbing male. The latter two females each turned sideways when released into their respective burrows in August 1975 and lunged and hissed when tapped. In addition, male 96 showed reluctance to enter certain burrows he visited, even when put in the entrances and goaded. This was evident at B-171 (containing female 390) on August 8, 1975, at B-175 (containing female 391) on August 9, 1975, and at B-172 (containing female 185) on August 9, 1975.

Several observations made in old field habitats (Figure 5) also have relevance here.

Although male 201 readily entered B-105, B-139, B-156, and B-157 when placed on the mounds of these burrows on March 23, 1975, he refused to enter B-152, which contained large female 374.

Female 256 occupied B-152 in April 1975; she advanced toward the entrance from inside this burrow in response to "hand-bobbing" and other disturbance at the entrance on April 18 and 19. Similar behavior was noted at B-206 on May 16, 1977 and on several succeeding days, and these responses seemed to represent burrow defense or a tendency to investigate disturbances on the mound. This female held her position inside B-204 as male 201 courted her there and tried to enter the tunnel on May 13, 1976.

Female 256 occupied B-164 in June 1975; this burrow came to be preferred by male 201 in late July 1975, however, and at that time 256 again occupied B-152. On July 29, 1975, male 201 emerged from B-164 and began feeding on vegetation 1-2 m southwest of the burrow entrance. He halted abruptly, however, and moved directly back to B-164 and entered just as female 256 emerged from B-152 to feed in the same area. The two tortoises were only 3 m apart when the male returned to B-164, and his retreat was clearly triggered by his having sighted the emerging female. His rapid return to B-164 may have served to prevent her re-occupation of this, one of her former burrows (Case 2).

Co-occupation of a burrow by two females is reported elsewhere (Burrow occupancy); it seems that this arrangement was temporary and that mutual hostility probably existed.

Female 66 (233 mm) wandered to within 2 m of B-165 while foraging on July 21, 1975. When placed on the mound of this burrow, she tried to escape into it. Female 35 advanced immediately from 1-2 m inside, however, and rammed and shoved 66 to the entrance. Three times I placed 66 in the entrance, and each time 35 advanced hissing slightly and pushed 66 out onto the mound, ramming and kicking at her with her forelegs. Female 35 also clawed at the top of the intruder's head with her forefoot several times. After her last expulsion, I watched as 66 fled north from B-165 through tall grass, closely followed by 35. Whenever 66 paused in this retreat, 35 persisted in ramming and shoving, and 66 moved quickly away. Number 35 stopped about 6 m north of B-165 as 66 continued running, and after a short pause 35 returned to and entered the burrow. Female 66 came to rest in the shade in a dense clump of shrubbery ("X", Figure 5). This encounter demonstrated both an attempted use of the burrow of another individual for escape and expulsion of an intruding female by an occupant female. On later dates when B-165 was approached, 35 advanced and turned sideways in the entrance, lunging and hissing at my hand when touched (July 22, 24, 25, and 28, August 17, 1975). Female 66 defended B-189 when I approached on May 13, 1977, bracing herself sideways in the tunnel when tapped.

On May 2, 1977, three attempts to pull 374 from B-157 failed as this timid female withdrew down the tunnel. I captured female 256 at B-206, placed her in the entrance of B-157, and curbed her attempts to back out and move away. After 4 min, 374 began slow but steady, repeated ramming of 256 from inside; in this way the larger female was drawn to the entrance and captured.

Female 332 escaped into B-205 upon her release on May 18, 1976. When about 1 m inside the burrow she turned sideways, lunging and hissing when touched.

Certain females are thus known to defend their burrows against males and against other females in some cases. Relaxation of this hostility may occur in cases of co-occupation of certain burrows by a male and female, or the male may simply impose himself upon the occupant female for varying periods of time. Female 185 exhibited no defense reaction against male 161 as he pushed himself past her upon his release into B-128 on July 20, 1974, nor did female 65 when she was followed into B-33 by male 58 upon their simultaneous release on July 18, 1971.

Combat

Combat between males has been described in *Gopherus agassizii* (e.g. Camp 1916, Miller 1932, Grant 1936), *G. berlandieri* (Weaver 1970), *G. flavomarginatus* (Legler and Webb 1961), and *G. polyphemus* (Carr 1952, Weaver 1970). The precise spatial and social contexts of fights have seldom been reported, however; combat between males has generally been said to represent rivalry for females during breeding activities (Weaver 1970; additional references in Douglass, 1975, 1977). That fighting is not associated only with sexual rivalry in *G. agassizii* was suggested by Miller (1932), who observed a hatchling lunging at a companion, and Jaeger (1950), who noted fights throughout the season of activity.

Aggressiveness between captive tortoises of this genus apparently functions in the establishment of dominance-subordinance relationships (e.g. Lampkin 1969, Weaver 1970). That assertion of a male's dominance over another may actually lead to enhancement of his own breeding success has been reported in *G. agassizii* (e.g. Lampkin 1969).

Weaver (1970) described two types of combat in male *G. berlandieri* (hereafter called Types I and II, respectively). In Type I combat, neither male is subordinate; both are initially aggressive, and dominance is established when one opponent flees or is overturned. Type II is combat in which only one member of the pair is aggressive; it is characterized by avoidance or retreat by the nonaggressive male.

Type I combat between *G. polyphemus* males has been seen in both the field and laboratory at the Station. Males 58 (254 mm) and 201 (243 mm) fought repeatedly when placed together in the laboratory on March 26, 1973 (J. N. Layne pers. comm.). Fighting bouts occurred for several minutes at a time, and both head-to-head and broadside ramming were observed. Attempts were made by each attacking tortoise to overturn the opponent; the gular projection was positioned under the other's shell with the hind legs extended and forequarters low, and powerful upward thrusts were delivered by sudden extension of the forelegs. Male 58 eventually succeeded in overturning 201 by forcing him against the doors of the laboratory.

J. W. Lang (pers. comm.) witnessed similar combat behavior between males 312 (216 mm) and 313 (234 mm) from 1655 to 1707 h on October 17, 1973 at this locality. On two occasions between bouts, male 312 scooped sand with his forefeet while positioned perpendicular to 313. Number 312 then retreated along a fire lane, closely pursued by 313. The larger male (313) succeeded twice in overturning his opponent, and in each case head-to-head ramming continued after 312 had righted himself. Finally, 312 retreated along the fire lane as 313 remained stationary.

A. R. DeGange (pers. comm.) observed a fight between males 398 (228 mm) and 399 (236 mm) from 1040 to 1105 h on September 11, 1975. Male 398 succeeded twice in overturning the larger male and pursued him upon his retreat. Mutual ramming continued when 399 was overtaken, and this male was again overturned. The fight resumed when 399 righted himself, then 398 moved rapidly away. Upon their release at this location later in the day, the two animals moved in opposite directions and entered separate burrows (pers. obsv.).

T. Allen and D. Austin (J. N. Layne pers. comm.) observed a fight between two tortoises of undetermined sex in Alachua County, Florida, at about 1000 h on May 3, 1959. The smaller of the two tortoises was overturned by the larger individual, but repeated ramming by the latter righted the smaller animal and head-to-head ramming continued. When frightened by the observers, the larger individual moved rapidly to an active burrow nearby and entered. The smaller tortoise moved away from this burrow when placed on the mound, but entered when placed again at the entrance.

Biting was not observed in any of the cases of combat described above. The jaws of the fighting males watched by DeGange remained open, but biting was not seen. Although Rose (1970) reported that biting is characteristic of courtship behavior but not combat in *G. berlandieri* males, biting was observed during Type II combat between animals of this species by Weaver (1970). Woodbury and Hardy (1948) reported ramming and biting of the legs and shells of male *G. agassizii* by conspecific males.

Type II combat between *G. polyphemus* males was induced near various burrows at the Station during March and August 1975; it occurred between males 96 and 299, 96 and 161, and 201 and 363 (<u>Defense of burrows</u>, above).

Head-bobbing between males has been seen on two occasions preceding fights. In both cases, the aggressor bobbed at and then rammed a subordinate. Male 24 began to head-bob when he was placed with male 26 by C. E. Winegarner (pers. comm.) on August 4, 1972. The two rubbed heads a few times, then 24 rammed 26 and moved off. An account is given elsewhere (<u>Case 1</u>) of head-bobbing by male 96 at a burrow occupied by smaller male 161, and of the ramming dealt 161 when he was removed from this burrow. In addition, males 209 (211 mm) and 397 (211 mm) head-bobbed vigorously at each other when placed in an enclosure with female 21 on April 20, 1976; male 209 then attempted to leave the area. In *G. agassizii*, combat between males is often preceded by head-bobbing (e.g., Camp 1916), and Grant (1936) thought it possible that males recognize one another by the scent of chin-gland secretions. The importance of chin-gland secretions as olfactory cues eliciting combat behavior and not courtship between male tortoises of this genus has been outlined by Rose, Drotman, and Weaver (1969) and Rose (1970). Weaver (1970) found that head movements and olfactory stimuli (chin-gland secretions and cloacal scent) are the chief releasers for courtship and combat in *G. berlandieri*, and suggested that in *G. polyphemus* head-bobbing serves as a visual cue prior to combat. Differences between challenging and courting head-bob signals were noted in *G. flavomarginatus* captives by Eglis (1962).

The conclusion of Patterson (1971b, cited by Brattstrom 1974, and Wilson 1975) that certain sounds produced by a male *G. agassizii* overturned in combat may cause an opponent to assist him in righting lacks supporting evidence. Righting of silent *G. polyphemus* males by continued ramming from their opponents is reported above, and the righting of overturned *G. agassizii* males by continued ramming has been reported elsewhere (Miller 1932, Lampkin 1969, Switak 1973). That this behavior truly represents assistance by the dominant male is highly questionable.

Combat between *G. polyphemus* males has been observed in the months of March, August, September, and October at the Station; Weaver (1970) observed ramming between male captives during spring and summer. Male-male combat has been reported to occur most frequently during the breeding season in *G. agassizii* (e.g., Woodbury and Hardy 1948, Carr 1952, Switak 1973) and *G. berlandieri* (Weaver 1970).

The occurrence of fights between *G. polyphemus* females was mentioned by Fletcher (1899) and Carr (1952). Aggressiveness between females has been noted occasionally in *G. agassizii* (Lampkin 1969, Switak 1973), but Weaver (1970) reported combat in *G. berlandieri* to occur only between males (the single instance of agonistic behavior between females he observed involved only pushing).

Combat between *G. polyphemus* females has been observed on five occasions at the Station. In each case, Type II combat occurred when two females were placed together. Female 223 (148 mm) persistently rammed female 278 (125 mm) when the two were placed together in an enclosure on 27 and July 28, 1973. The larger female lunged at 278 at intervals of several seconds, attempting to overturn her by thrusting suddenly upward after working her gular projection under the smaller female's 8th to 10th marginal scutes. Female 278 tried repeatedly to escape the assault, which in each case lasted several minutes. Female 374 (305 mm) rammed female 256 (260 mm) vigorously and repeatedly when the two were placed together in an enclosure on May 7, 1977. F. V. Brach (pers. comm.) observed persistent ramming of female 291 (196 mm) by female 157 (270 mm) on September 24, 1975 when these two individuals were placed together in an enclosure. The expulsion of female 66 from the vicinity of B-165 by female 35 and of female 256 from B-157 by female 374 is described above (Defense of burrows).

Agonistic behavior between the sexes is apparently of low frequency and intensity in tortoises of the genus *Gopherus*. Male aggressiveness toward females has been reported in *G. agassizii* (Jaeger 1950), as has female aggressiveness toward males (Beltz 1954, Lampkin 1969). Weaver (1970) noted that the upward thrust characteristic of ramming between opposing male *G. berlandieri* is not seen in courtship ramming in this species. It was not clear whether the ramming he observed between a captive male and female *G. polyphemus* was part of courtship or of combat. The defense of burrows by certain female *G. polyphemus* against entry by males is described above (Defense of burrows). In addition, it appeared that female 66 was rammed by male 201 inside a burrow in one instance (Case 2, May 7, 1977, in B-189).

Burrow occupancy

The burrows of *G. polyphemus* have often been described as permanent structures inhabited by single individuals for long periods of time (e.g. Hubbard 1893, 1894; Carr 1952; Hansen,1963; Auffenberg and Weaver 1969). Fletcher (1899) reported having never found two individuals in the same burrow, and knew of no visits to occur between burrows; individuals he placed in burrows not their own backed out and moved away. Agassiz (1857), Bumpus (1885), and Pratt (1935) reported that burrows are inhabited by single pairs. Allen (1932) reported excavation of a number of burrows in October and November 1930 in Harrison County, Mississippi, and noted that two individuals (sexes not indicated) were frequently found occupying the same burrow. Pope (1939) observed that no more than two individuals occupy a given burrow, but pointed out that it has not been determined whether pairs occupying single burrows are mated males and females. Kenefick (1954) found a copulating pair about 0.3 m inside a burrow on April 23, 1953 in Lee County, Florida.

In the present study, burrows of *G. polyphemus* were generally inhabited by single individuals at a given time. Many animals made use of one to several additional burrows in a given season, and the location of the preferred burrow of a particular animal usually changed from year to year. Reasons for the regular abandonment of burrows at this locality are considered elsewhere (Douglass and Layne 1977).

Examples of male-female co-occupation of various burrows are described in Cases 1 through 3. Five additional cases have been recorded in the course of burrow-checking and the release of animals. Most of these appeared to represent actual short-term co-occupation of burrows rather than use by two different animals at different times in a single season. Male 26 (246 mm) occupied B-23 in August 1970 and July 1971; female 157 (271 mm) entered this burrow on June 22, 1971. Male 207 (178 mm) occupied B-28 in June and July 1971; female 174 (182 mm) entered the burrow on August 7, 1971. Male 51 (254 mm) and female 160 (214 mm) both used B-55 in July 1971. Male 263 (207 mm) occupied B-98 in July and August 1973; female 183 (262 mm) was taken from this burrow on July 10, 1973. Male 336 (203 mm) occupied B-135 in July and August 1974; female 143 (228 mm) was taken from this burrow on July 19, 1974.

In addition, three cases have been recorded in which males have been found occupying burrows used previously by females. Male 336 occupied B-97 in June 1974; female 143 had used this burrow in August 1973. Male 56 (247 mm) used B-119 in August 1974; the burrow had been used by female 57 (230 mm) in August 1973. Male 261 (223 mm) used B-54 in September 1973; female 98 (257 mm) had used this burrow in July 1971. As outlined in Cases 1 and 2, some of the burrows used by males 96 and 201 had been occupied previously by large females.

Only two cases of possible male-male co-occupation of burrows were recorded. Male (?) 189 (195 mm) and male 299 (233 mm) occupied B-106 together in late June and early July 1973. Male 161 (222 mm) and 201 (256 mm) were trapped simultaneously from B-144 on July 24, 1974 (M. R. Ziegler pers. comm.). In addition, B-43 was occupied by male 205 (180 mm) in June 1971 and by male 241 in July and August 1973. B-195 was used by male 273 (233 mm) in November 1975 and by male 426 (232 mm) in April 1976.

That animosity may exist in cases of male-male co-occupation of burrows was evident in 201's assertions of dominance over smaller male 363 at B-139 and B-158 (Defense of burrows) and by the ramming dealt male 161 at B-188 by male 96 (Case 1). Also, as mentioned under Combat, T. Allen and D. Austin (J. N. Layne pers. comm.) watched two tortoises of undetermined sex enter the same burrow following a fight in Alachua County, Florida.

A single instance of co-occupation of a burrow by females was recorded. Female 66 (233 mm) was found in B-189 (Figure 5) deep to larger female 374 on September 2, 1975. This burrow was the size of 374 in cross section, and the large female had moved to it that day from her preferred burrow nearby (B-157). It appeared that 66 was a wanderer attempting to establish herself in this burrow; she inhabited it through early October 1975 and during May 1977. A few other observations deserve mention here. Female 374 occupied B-152 between March 23 and 26, 1975; female 256 had occupied this burrow in January 1975, and re-occupied it by mid-April 1975. B-60 was occupied by female (?) 199 (172 mm) in July 1971 and by female (?) 291 (152 mm) in June

1973. That animosity probably exists between certain females at co-occupied burrows was demonstrated on July 21, 1975, when female 35 vigorously defended B-165 against female 66, and on May 2, 1977, when female 374 defended B-157 against female 256 (Defense of burrows).

The duration of male-female co-occupation of burrows apparently ranges from several minutes to several days in this population of G. *polyphemus*. The tendency for burrows to be occupied by single individuals at a given time is probably associated in part with traffic problems in the unbranched tunnels. I have found no evidence of winter aggregations, and while the exact tenancy of burrows during periods of inactivity is generally not known, most burrows appeared to have been occupied singly during these times as well.

Which individual(s) actually dug particular burrows in the study area is generally not known (see also Gourley 1969), but some evidence is available regarding the relative roles of males and females in maintenance of favored burrows.

That a female may occupy a burrow dug, or at least maintained, by a male was indicated by the extended digging efforts of male 201 at B-157 and probably at B-204 and later occupation of these burrows by females 374 and 256, respectively (Case 2). It also appeared that B-178 was maintained by male 96 and later occupied by female 185 (Case 1).

Males sometimes occupied burrows formerly maintained by females (above, and Case 1). The use of B-24, B-167, and B-171 by male 96 and of B-164 and B-182 by male 201 indicated that males may use burrows dug or enlarged by females.

Examples in Cases 1 and 2 indicate that small males sometimes co-occupy burrows dug or inhabited by larger females (e.g., 161 at B-128) and make use of large burrows of the dominant male in his absence. In addition, males have been seen on several occasions beginning renovation of abandoned burrows.

Information on actual patterns of burrow co-occupation in other species of the genus *Gopherus* is meager. In studies of G. *agassizii*, Woodbury and Hardy (1940, 1948) found that summer holes were seldom inhabited by two tortoises simultaneously. In the few cases noted, pairs (male and female) were found together. Additional cases of male-female co-occupation of burrows in G. *agassizii* were reported by Jaeger (1950) and Gates (1957), and two individuals of undetermined sex were seen together at a burrow in May 1938 by Johnson, Bryant, and Miller (1948). Rose and Judd (1975) sometimes observed G. *berlandieri* trying to push themselves into occupied "pallets". Despite reports of communal use of burrows in G. *flavomarginatus*, Pawley (1975) found three single burrows to have had no interconnections.

Discussion

Agonistic behavior in G. *polyphemus* is involved in burrow defense by large males and certain females and in the establishment of dominance-subordinance relationships. In some cases, victory in combat between males appeared to have had real benefits for the victor in terms of access to females or to burrows in strategic sites. Combat and assertions of dominance in these situations were manifestations of competition for opportunities to breed.

Although territoriality is generally not known in turtles (Cagle 1944, Auffenberg and Weaver 1969, Brown and Orians 1970), Brattstrom (1974) indicated that a few species are territorial over retreats and food. The observations presented in this section include the first reported instances of active burrow defense in G. *polyphemus* and the first descriptions of the spatial and social contexts of fights in this species in the wild. It is perhaps not surprising that defense of retreats should be pronounced in a species like *G. polyphemus*, in which burrows are distinct and energetically costly structures.

Woodbury and Hardy (1948) reported overlap of the home ranges of *G. agassizii* in southwestern Utah, and found no evidence that home ranges, dens, or summer holes were defended as territories; social aggregation occurred in winter dens in the population studied. Similarly, Auffenberg and Weaver (1969) noted broad overlap of activity ranges in *G. berlandieri* in southeastern Texas; they concluded that there is generally very little competition between individuals for space and shelter, and that living space is not exclusive. Rose and Judd (1975) observed tortoises of this species trying to push themselves into occupied "pallets", but never saw one attempt to dislodge an occupant.

Auffenberg's (1966) citation of the work of Woodbury and Hardy (1948) as substantiation of "strong territorial behavior in the genus *Gopherus*" is unfounded, and although Weaver (1970) claimed that *G. polyphemus* individuals typically maintain "more or less well-defined territories", he offered no supporting observations. Weaver (1970) stated that these animals occupy "more or less mutually exclusive areas where contact with other tortoises is restricted", and noted that certain *G. polyphemus* males were dominant both in their own pens and in those of other animals.

The question of whether or not classical territoriality exists in *G. polyphemus* is difficult to answer. Seldom are two individuals seen together in the wild, and the feeding forays of neighboring individuals often do not overlap in time or space. Considerable temporal isolation of individuals may exist despite broad overlap of home ranges.

In animals such as birds, in which an entire territory is sometimes watched from a single perch and rapid expulsion of an intruder can be accomplished at any boundary, the limits of territoriality are more easily discerned. The limitations imposed by an awkward mode of locomotion on the maintenance of well-defined territories are considerable, and it appears that in the tortoise population studied, territories are spatiotemporal rather than absolute.

The mating system described herein seems best characterized as a loose or incipient harem system. Maintenance of a harem by a particular male is impeded by his slowness of movement relative to the dispersion of the females he visits. The harems of *G. polyphemus* are less well-defended than those known in certain other vertebrates, in large part, it seems, because of the problems inherent in patrolling of a large area by a slow-moving animal. Other males, including subordinates, infiltrate in the absence of the dominant male and probably even mate with preferred females. By assertion of his dominance whenever other males are encountered, a large male establishes a sort of spatiotemporal territory in which other males recognize his dominance and retreat in his presence. Indeed, although a subordinate male may co-occupy a burrow with a female in the absence of the dominant male, the latter may restrict the use of certain burrows by other males when he is in the area.

Selection may be maintaining spatiotemporal territoriality in these tortoises merely through the exclusion of less aggressive individuals from opportunities to breed; this mechanism has been suggested in the evolution of territoriality in birds (Brown 1964). Sheer size and weight appear to confer advantages on certain males in agonistic encounters, and in a particular population there may be a minimum size at which successful functioning in these encounters can begin. Size alone might thus indirectly enhance reproductive success in males, and rapid growth might be advantageous in this regard.

GENERAL DISCUSSION

Among animal societies, harems are systems in which groups of females are guarded by a male who prevents other males from mating with them (Brattstrom 1974, Wilson 1975). Inclusion of the territories of two or more females in the territory of a dominant male is often involved. Brattstrom (1974) indicated that among reptiles, harem systems are known only in a few species of lizards. The mating structure of the population of *Gopherus polyphemus* studied seems best characterized as a loose or incipient harem system. Each of two large males studied intensively courted several females at separate burrows and asserted his dominance over smaller males when the latter were encountered.

Various studies have outlined correlations between modes of social organization and resource use in land vertebrates (Crook 1965, 1970a, 1970b; Eisenberg 1966; Verner and Wilson 1966; Rand 1967; Geist 1974; Jarman 1974). For purposes of comparison with *G. polyphemus*, examination of the socioecology of other burrow-inhabiting vertebrates which graze on the surface is appropriate.

Among living reptiles, relatively few forms outside the Testudinidae are actually herbivorous; these include several species of lizards in the families Iguanidae, Agamidae, Scincidae, and Teiidae (Szarski 1962, Ostrom 1963, Bellairs 1970). Harems and "incipient harems" have been reported in several species of iguanids (Carpenter 1967, Brattstrom 1974). Carpenter (1967) noted that these harems are not necessarily fixed associations, and Wilson (1975) observed that many of those described are not true harems in the strict sense applied to birds and mammals: multiple females are tolerated within the territories of males, but they are not specifically recruited or defended. Brattstrom (1974) and Wilson (1975) indicated that the closest approach to true harem maintenance in lizards is found in the chuckwalla, (*Sauromalus obesus*); the social behavior of this herbivores, rock-dwelling iguanid was described by Berry (1974b). Large, dominant males ("tyrants") held extensive territories within which subordinate males were restricted to small territories around rock-piles and basking sites. Females also had territories within those of "tyrants". During the breeding season, dominant males patrolled their territories, visiting females and restricting the activities of subordinates. Possession of a territory conferred distinct advantages on "tyrants": (1) exclusive access to females within it; (2) access to food resources; (3) priority at rock crevices (protective cover). An important difference between the system described in *G. polyphemus* and that in these lizards is that, although only "tyrant" chuckwallas mated with females in their territories, subordinate male tortoises visited and probably even mated with some of the female tortoises visited by dominant males.

Among living mammals, the large, burrowing squirrels of the genus *Marmota* are those most similar to *G. polyphemus* in terms of sheltering and feeding relationships, and the social behavior of these animals has been the subject of a series of careful studies (Armitage 1962; Bronson 1964; Downhower and Armitage 1971; Barash 1973a, 1973b, 1974a, 1974b; Armitage and Downhower 1974). Harem systems are well-established in some forms. Barash (1973a, 1973b, 1974b) noted that the social systems of *Marmota monax, M. flaviventris,* and *M. olympus* are characterized by progressively decreasing aggressiveness and increasing social integration: *M. monax* are generally solitary and highly aggressive (Bronson 1964), while *M. olympus* are intensely socialized and tolerant. Barash suggested that there is a correlation between types of social organization in these animals and duration of the growing season, noting that increased sociality is associated with shorter growing seasons (e.g., *M. monax* in southern Pennsylvania, vegetative growing season 150+ days; *M. olympus*, 40-70 days). Exposure to progressively shortened growing seasons apparently favors the development of less aggressively-organized social systems, which permit animals to disperse at increased ages. Although parental care and its cessation is an important factor in this connection in marmot societies, it may be that levels of aggressiveness in populations of *Gopherus polyphemus* also vary under exposure to differing environmental rigors. In terms of such social features as den occupancy (solitary) and levels of aggressiveness (generally high), the tortoise population studied showed greatest similarity to *M. monax* (Bronson 1964).

Because mechanisms optimizing individual reproductive success are the primary influences on the evolution of social systems in animals, mating strategies of males and females in the system of *G. polyphemus* are discussed here. The patterns of mate-seeking and aggression described in this paper are perhaps not surprising when one considers that parental care is unknown in these animals and that males invest only courtship efforts, seminal fluid, and spermatozoa in the production of young.

For adult males of all sizes, there is an advantage to mating with as many females as possible. Fertilization of eggs in numerous females can directly increase the reproductive success of a male, and this was reflected in burrow visitation patterns in the population studied. In addition, there are apparently advantages to mating with the largest females in a given area. In reptiles generally, large, old females tend to produce the largest clutches of eggs (Bellairs 1970), and this appears to be true in *G. polyphemus* as well (Case 2, Douglass 1978a). Investment of a given amount of energy on courtship of a larger female capable of producing a larger number of eggs would clearly have advantages for a male. Advanced age and large size are themselves indications of favorable traits in females, and mating with these individuals is probably advantageous to males in this respect alone in that similar advantages may be conferred on their progeny. It is also possible that reproductive experience or greater receptivity in older females increases their value as mates for males. Both of the large, dominant males studied intensively showed marked preferences for the largest females in their areas, and smaller males sought these females as well (Cases 1 and 2).

There are advantages to smaller males in remaining in areas inhabited by large females despite domination by larger males. Subordinates may occasionally mate with larger females in the absence of dominant males, and with increasing size may themselves become dominant upon the death or expulsion of older males.

In addition, there may be advantages to males in allowing females to occupy burrows the males have dug or maintained (Burrow occupancy, Case 2). In this way, females might be encouraged to remain in particular areas and are easily found by the courting male. This feature of the system shows some of the elements of recruitment seen in the harem systems of other animals. In a loose sense, it seems that energy not expended by females in burrow construction may be directed into greater egg production in some cases.

Because of growth characteristics (gradually increasing size over the years) and expulsions which may result from dominance-subordinance interactions, certain areas are dominated by one large male at a given time. Dominance in males is probably associated with other favorable characteristics, and large size and advanced age are themselves indications of favorable traits in males. Mating with large, dominant males probably has advantages to females for these reasons. The fact that mating inside burrows is generally not feasible in this population may allow for some degree of mate selectivity by female *G. polyphemus*: visual and olfactory examination of courting males takes place as females remain inside their burrows. There are advantages to a female in remaining within walking distance of the dominant male in her area: this helps ensure that she will be among the females he visits and can help increase the frequency of courtship visits to her burrow. The tendency of females to remain within easy visiting distance of certain large males in different areas and the "tracking" of particular females by males from year to year may account in part for the colonial tendencies reported in this species by Holbrook (1836), Auffenberg and Franz (1975), and others.

In order to determine whether or not greater reproductive success really accrues to large, dominant males in this population and gain some further idea about whether or not the mating system described is actually functioning in the manner suggested, the application of non-destructive biochemical tests of paternity or relatedness might be considered. One obstacle to the collection of samples for this purpose would be that hatchlings and juveniles are very seldom found at this locality (Douglass 1978b, Douglass and Layne 1978).

In sedentary, slowly-reproducing animals such as *G. polyphemus,* harem-tending probably even further retards gene flow and rates of genetic recombination, especially when closely-related females (e.g., siblings 390 and 391 in the harem of male 96) are involved.

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APPENDIX

Case 1

Male 96 (246 mm) inhabited slash pine-turkey oak woodlands; his home range, as determined by the minimum polygon method, was 4.2 ha in area (Figure 4). Occasional observations were made on the activities of this male from July 1971 through April 1976. A list of all individuals found within his home range during the study period is provided in Table 1. Male 96 is known to have courted four different females at their burrows; accounts of some of his movements follow.

On July 1, 1971, male 96 was captured on the mound of B-5; he tried to run into the burrow when approached. Female 214 (240 mm) was inside this burrow and had occupied it during the previous month. When released at this point the next day, 96 moved to the entrance of B-5 and began digging into the burrow. When touched, however, he emerged, moved into the woods to the south, and tried to enter B-46, which at this time was inhabited by female 185 (245 mm). Male 96 was then released again on the mound of B-5; he moved to the entrance and began vigorous head-bobbing. When I approached, he turned and left the burrow, moved into the woods to the southeast, and tried to enter B-24. This burrow had been occupied by female 185 in August 1970. When released a third time on the mound of B-5, 96 moved to the entrance and paused, then entered slowly.

Male 96 was captured at the east end of the East Fire Lane two weeks later. When released there on July 18, 1971 he moved steadily west on the fire lane and then directly south on a well-worn tortoise trail to B-46. This burrow had been entered by female 185 upon her release less than a half hour before. Number 96 entered the burrow to about 0.3 m (1540 h) and was

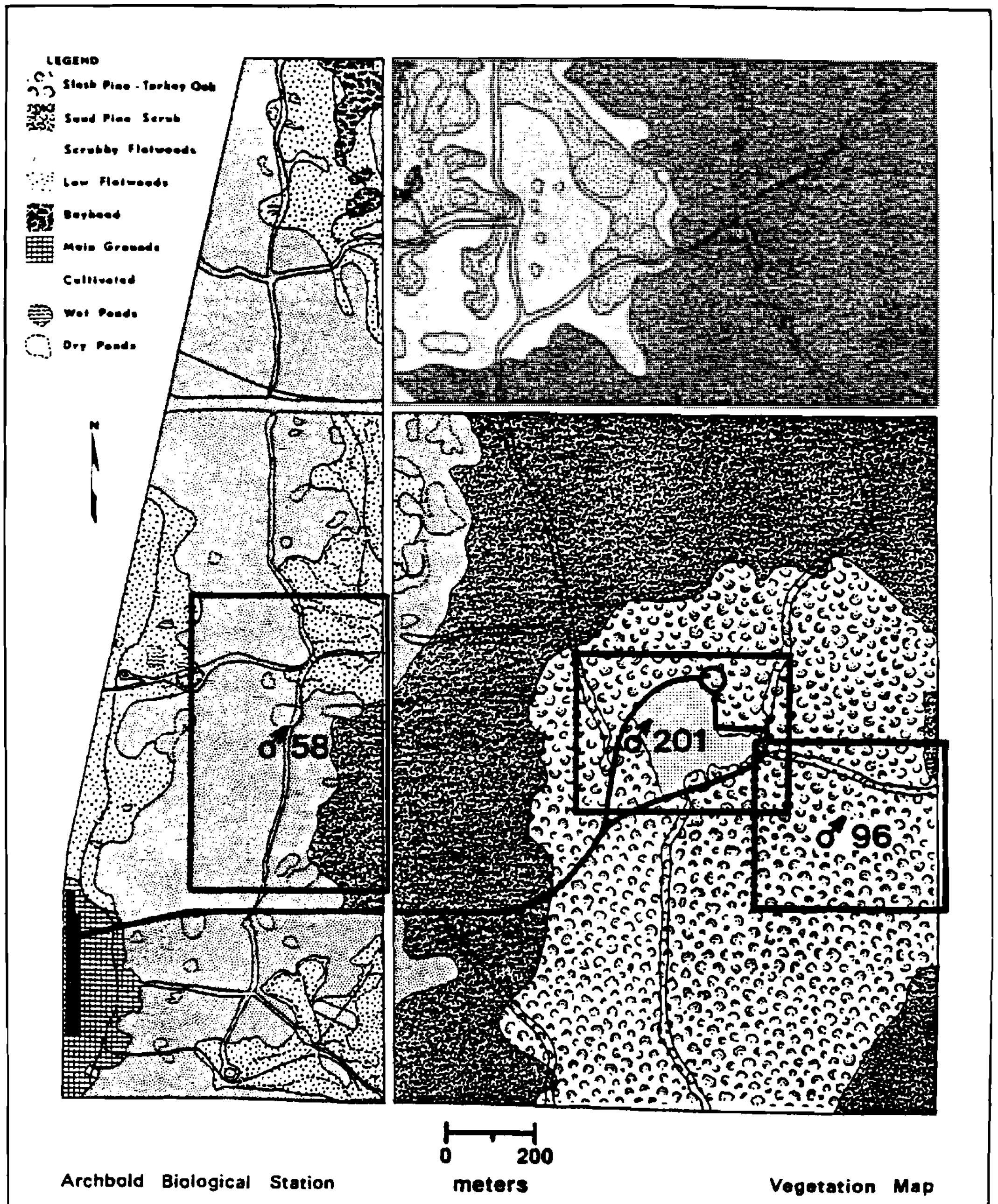

Figure 3. The overall study area, showing locations of the tracts enlarged in Figures 4-6. Within each tract is the home range (not shown) of the *Gopherus polyphemus* male indicated.

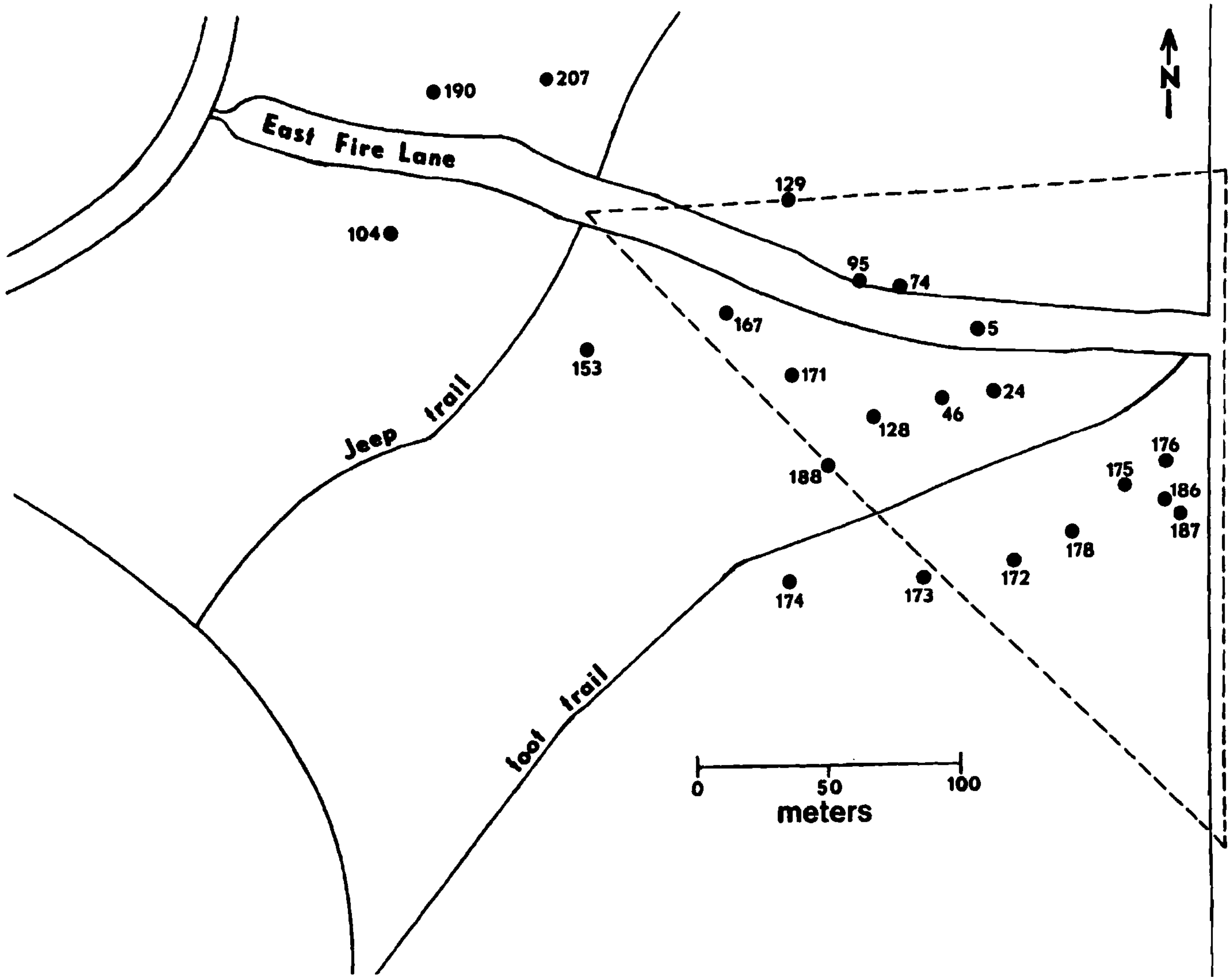

Figure 4. Dashed lines represent boundaries of the home range of *Gopherus polyphemus* male 96 as suggested by extreme points of capture. Shown are the burrows of adult tortoises mentioned in the text (the locations of B-172 through B-176 and of B-178 are approximate); several other burrows found within this area are not shown.

Table 1. Individuals captured in the home range of *Gopherus polyphemus* male 96, in order of decreasing size.

	Number	Plastron length (mm) at time of most recent capture	Inclusive dates of known presence in home range of 96
Males:	96	246	May 1969 - April 1976
	299	234	August 1975
	161	225	June 1970 - August 1975, May 1977
	141	202	January 1975
	189	192	May 1973
	401	190	September 1975
	215	180	June 1971
Females:	185	251	August 1970 - August 1975
	214	240	June 1971 - June 1972, August 1974 - August 1975
	106	230	June 1971
	390	208	August 1975
	391	202	August 1975

immediately pushed out by 185, who came to the entrance and stopped. Male 96 bit at her anterior marginal scutes as she pushed him out, then walked backwards quickly and directly to the far slope of the mound and stopped about 1 m from the entrance, facing it. He then engaged in vigorous, persistent head-bobbing at intervals of from 15 sec to 1 min or more; each burst of head-bobbing included several horizontal and vertical bobs.

Female 185 remained in the entrance of B-46 and showed little response. The slightest movements of her head or body elicited vigorous head-bobbing by the male. Twice she moved her head to her forefoot to remove gnats from an eye and 96 responded strongly, head-bobbing and moving back and forth between 0.6 and 1 m from the entrance. When the female was motionless at the burrow entrance, he repeatedly moved a few steps forward onto the level part of the mound, head-bobbing persistently in her direction. Whenever 185 moved her head or body slightly, 96 backed up quickly to the far slope of the mound (to a point about 1 m from the entrance) as if to allow 185 room for emergence onto the open, level part of the mound. During these movements his head-bobbing was continuous, and apparently served to beckon the female.

At 1604 h 185 turned 180° in the entrance of the burrow and dug her way down the tunnel. The male moved quickly to the entrance and head-bobbed vigorously for 2 min. He then returned to his former position on the mound, 0.6 m from the entrance, head-bobbing occasionally. At 1615 h he again moved to the entrance and head-bobbed into it, then backed up head-bobbing with active movement of his hind legs as 185 appeared at the entrance facing out. Twice the female gaped her jaws widely for several seconds; this elicited vigorous head-bobbing by the male. At 1625 h 185 head-bobbed weakly, and at 1630 h she emerged completely from the entrance and paused about 0.3 m outside. The male responded to her appearance on the mound with vigorous, continuous head-bobbing.

I observed this entire episode from the edge of the mound about 2 m from the burrow entrance. The two animals were frightened at 1638 h, when the female suddenly withdrew into the entrance. Male 96 tried to run into the burrow, but the female immediately emerged and forced him out onto the mound.

Many fresh tortoise trails were found daily on the mound of B-5 and vicinity in late July 1971. On July 26, I found fresh trails from the burrow entrance to nearby edges of the fire lane. About 5 m east of the entrance of B-5 was a circular, trampled area with many trails and deep footprints in groups and circles which probably represented the "male orientation circle" described in the courtship of *G. polyphemus* by Auffenberg (1966). It seems likely that female 214 had emerged from B-5 sometime that afternoon and a male, probably 96, had courted her there.

In early August, scaffolding was erected on the fire lane overlooking the entrance of B-5, and activity at this burrow and at B-46 was monitored from a platform 2.4 m above the ground. Male 96 came to court the females in both of these burrows on August 6, 1971.

Female 214 was inside B-5 and 185 was inside B-46 when a day-long watch was begun at 0820 h. Female 185 basked intermittently on the mound of B-46 beginning at 0846 h.

Male 96 was first seen at 1040 h as he moved north from the vicinity of B-24, feeding. He crossed the fire lane and moved toward B-5, feeding as he walked. He arrived at B-5 at 1050 h and paused on the mound about 0.6 m from the burrow entrance, then moved to within 0.3 m of it, head-bobbing vigorously at intervals of a few seconds to a minute or more. He backed up to about 0.6 m outside the entrance at 1107 h, and only occasional bursts of head-bobbing followed (e.g., at 1118 and 1120 h). At 1136 h he moved again to within 0.3 m of the burrow entrance and scooped sand with alternate forefeet while head-bobbing. He moved off the mound at 1142 h and walked south over the fire lane feeding, pausing occasionally to head-bob when about 5 m from B-5. At one point he paused for 4 min when facing in the direction of B-46, head-bobbing and feeding occasionally. He walked back to B-5 at 1148 h and paused about 0.3 m from the entrance, head-bobbing and scooping sand. He backed up to about 0.6 m outside the entrance at 1150 h, but was frightened into the burrow by the brief approach of a person on foot 2 min later. Male 96 was seen again at 1215 h just outside the burrow directing slow, horizontal head-bobs into the entrance. He backed up to about 0.6 m outside at 1222 h. At 1232 h he left B-5 and walked south to the edge of the fire lane, where he paused for 3 min sighting and sniffing down the trampled path to B-46. At 1240 h male 96 left the fire lane and began moving along the path toward B-46, just as female 214 emerged to several centimeters outside the entrance of B-5.

Number 96 arrived at B-46 at 1242 h and head-bobbed vigorously while moving actively around the far edge of the mound. He advanced at 1246 h and head-bobbed for 6 min into the entrance. At 1252 h he moved off the mound and nestled into a damp, shady pocket under the fallen trunk of a pine about 2 m from the burrow entrance. He remained there through the night and 185 remained inside B-46. (Female 214 was found occupying B-74 five days later.)

Male 96 was again captured at the east end of the East Fire Lane 22 months later, on June 16, 1973. When released the next day he moved west on the fire lane, feeding. He walked slowly across the mound of B-5 with no head-bobbing, then continued west; the burrow was collapsed and overgrown as a result of disc-harrowing of the fire lane the previous fall. The male entered a large, newly-dug burrow (B-95) at the north edge of the fire lane, and was seen entering this burrow on subsequent days as well. In late June, scaffolding was erected overlooking B-95, and the activities of 96 were watched for three day-long periods. At this time female 185 still occupied B-46, but female 214 had moved to B-104; 214 occupied the latter burrow through June and July 1973. Tracks from B-95 indicated that male 96 made fairly direct visits to B-46 on July 4 and 5, and crossed the inactive mound of B-5 while returning to B-95 in each case.

Number 96 occupied B-95 through early September 1973. He was found in a Tomahawk Live Trap set at the entrance of B-46 on September 3 and again on September 4, 1973, indicating his persistence in visiting the female at B-46.

In July and August 1974, male 96 occupied another burrow (B-129). Female 185 occupied B-128 during this period and female 214 occupied B-153. When taken from B-129 on July 19, 1974 and put on the East Fire Lane nearby, 96 walked steadily south into the woods and nestled into the litter about 3 m from a tortoise trail connecting B-128 and the fire lane; in this position he would have seen any other tortoises moving along the trail. When placed on the trail itself he veered away from it and wandered widely through the woods west of B-128, pausing frequently as if in orientation. (A smaller male [161, 222 mm] had been found in B-128 with female 185 the day before.) Female 185 was then taken from inside B-128 and placed on the burrow mound with male 96. He followed her persistently, head-bobbing vigorously and biting her at marginal scutes. The male was released into B-129 the next day.

Female 214 occupied B-167 in early August 1975; she was trapped there on August 3. Male 96 was found feeding on the East Fire Lane north of this burrow on August 5, 1975. When disturbed he moved along a tortoise trail through the woods to the vicinity of B-167 and wandered in wide circles near the burrow without approaching it. He then moved southeast to B-171 and tried to enter. When placed on the mound of B-167 he repeatedly tried to turn around and move toward B-171.

When released on the fire lane north of B-167 three days later, 96 moved eastward, feeding steadily. He walked to within 1 m of B-95 and over the mound of B-5 (inactive), then moved south through the woods along the trampled path to B-46. He crossed the mound of B-46 (then in use by an armadillo, *Dasypus novemcinctus*) without stopping, then moved to the vicinity of B-128 (in disuse) and stopped about 5 m from the latter burrow without crossing the mound. Then, with many pauses, 96 moved southwest to B-171; he stopped on the mound of this burrow and head-bobbed toward the entrance from about 0.3 m outside. Female 390 (208 mm) was resting just inside the entrance facing out, and as the male moved to the entrance head-bobbing she gradually turned sideways, blocking his entry into the tunnel. When I removed the male and "hand-bobbed" in the burrow entrance, the female, who had withdrawn suddenly, advanced hissing and turned sideways in the entrance. The two tortoises were then placed together on the mound; 96 head-bobbed weakly at the female and tried to follow her. He soon moved off the mound, however, and walked steadily and directly far through the woods to the south. He encountered a smaller male (299, 234 mm) between B-172 and B-173. Number 299 retreated at the approach of the larger male and moved quickly to B-173 (full account in <u>Defense of burrows</u>). (Male 299 had occupied B-106 and B-108 far to the southeast in July 1973.) Male 96 continued moving to B-172, which at this time was inhabited by female 185. He paused on the mound about 0.6 m outside and sniffed and head-bobbed at the burrow entrance. He tried to escape into the burrow when approached. Male 299 had been returning from a foray to the vicinity of B-172. The two males apparently competed for opportunities to breed with female 185, and 96 was clearly dominant at her burrow (<u>Defense of burrows</u>).

When released on the mound of B-172 the next day (August 9, 1975), 96 did not head-bob or try to enter the burrow, despite the presence of 185 inside. He turned and moved off through dense scrub in a wide arc, pausing on the mounds of each of two recently-abandoned burrows to investigate visually and olfactorily. He moved fairly directly to B-175 and stopped on the mound about 0.6 m outside, head-bobbing toward the entrance and moving slightly for 4 min, then moved off. When he was retrieved and placed at the entrance of this burrow, he struggled steadily and refused to enter. Female 391 (202 mm) responded by advancing from inside hissing slightly and turning sideways in the entrance. The contours of her carapace and peculiarities of scutellation suggested strongly that she was a sibling of 390, visited nearby by male 96 the day before.

Male 96 moved to B-176, paused on the mound with no head-bobbing, and began digging his way in; he tried to run into the burrow when approached. When placed on the mound he moved off and wandered west, pausing along the way on the mounds of each of two recently-abandoned burrows. I retrieved him when he had moved to within 60 m of B-172 and B-173.

On August 10, 1975 male 96 was released on the foot trail north of B-172 and B-173. He moved east through the woods and paused on the mounds of each of three different burrows to investigate (no head-bobbing). At two of these he began digging his way into the entrance, but moved on when I prevented his entry. The last of these burrows was B-178; from there he moved to B-172 and paused on the mound. Female 185 had been captured in a Tomahawk Live Trap upon her emergence from B-172 that day, and when 96 saw her inside the enclosure he wandered over the mound around the trap, head-bobbing at intervals.

When released again on the foot trail north of B-178, 96 moved steadily in a wide arc to B-171. He paused on the mound of this burrow about 0.6 m from the entrance, investigated without head-bobbing, and began digging his way in; female 390 was not seen inside. The male tried to escape into the burrow when approached, but when his entry was prevented he moved to a shaded area between B-171 and B-167 and dug a shallow pocket ("pallet" of Auffenberg and Weaver 1969) by scooping at the substrate and churning into the litter. When removed from this shelter, he wandered near B-167 and B-129 without investigating, then paused on the mound of B-95 (inactive).

On August 12, 1975, when released on the fire lane south of B-95, 96 moved directly to B-129 and began digging his way in. He was found in B-167 ten days later. Tracks on the East Fire Lane on August 18, 1975 indicated that he had moved near B-95 and B-74 while foraging, then east across the old mound of B-5 and back. When released on August 23, 1975 he followed an almost identical route, feeding steadily: this was apparently a routine circuit. When a brief rain began, 96 moved along a well-worn tortoise trail from the fire lane to B-24 and dug his way in after investigating the burrow from the mound; he tried to run into the burrow when approached.

When released on the East Fire Lane on August 24, 1975, 96 moved through the woods to the north, pausing to investigate the mounds of each of two inactive burrows (one of them B-74) without head-bobbing. When released again on the fire lane he moved directly south to B-178 and began digging his way in. When released on the foot trail north of B-172 and B-173, he moved directly to B-173 and began digging his way in without head-bobbing.

On August 26, 1975, male 96 was released on the East Fire Lane near B-95. He moved to the east end of the fire lane, then southwest on the foot trail and through dense woods. He crossed the mounds of each of three inactive burrows on his way to B-176 and paused briefly on the mound of B-176 before moving on. He paused on the mound of another active burrow (B-186), head-bobbing briefly or elevating his head in investigation, then moved to an inactive burrow nearby (B-187) and began digging his way in. When released later on the mound of B-171 he refused to enter, even when goaded. He backed out and circled around the mound, frequently pressing his nostrils to the ground, then moved quickly and steadily south with occasional pauses to sniff the ground. Number 96 arrived at B-188, having crossed the mounds of two inactive burrows along the way. He paused momentarily on the mound of B-188 about 0.6 m from the entrance with sudden elevation of his head as if investigating, then tossed a few scoops of sand as he moved to the entrance. Smaller male 161 was resting about 1 m inside the burrow, facing out. Male 96 directed two or three bursts of head-bobbing into the entrance, and after less than a minute moved again to about 0.6 m outside. He turned around to face the entrance and tossed a few scoops of sand with his forefeet. He tried to run into the burrow when held at the entrance. Male 161 remained in place inside the tunnel when I "hand-bobbed" at the entrance. He was captured, and the two males were put head to head on the mound and then about 1 m from it; each time, 96 ran at the smaller male and rammed him vigorously and repeatedly as the latter tried to run toward B-188. This episode provided an example both of scent-trailing by an adult male and of head-bobbing by a male at a burrow occupied by another male. It is possible that 96 had not discerned the sex or identity of the occupant tortoise and was summoning it for purposes of sex or individual identification, or the head-bobbing may have represented a challenge to the smaller male. When released later on the mound of B-167, 96 dug his way vigorously into the tunnel; he occupied this burrow through early October 1975, and used B-171 during April 1976.

When released on the foot trail south of B-188 on August 28, 1975, male 161 moved north into the woods and paused on the mounds of each of two inactive burrows. When released again on the trail he moved steadily and directly along worn tortoise trails to B-172. He paused about 1 m outside with a burst of head-bobbing, then advanced slowly and paused about 0.3 m from the entrance with another burst of head-bobbing, then moved to the entrance and began digging his way in. He tried to run into the burrow when approached. Upon his third release on the foot trail, 161 moved steadily to B-188 and dug his way in. He later used B-190 (in mid-September 1975, when female 185 was occupying B-178) and B-207 (May 1977). This male had been trapped at B-144 (Figure 5) with a larger male (201) on July 24, 1974 (M. R. Ziegler pers. comm.), and was apparently a wanderer who made opportunistic use of burrows. As indicated, he co-occupied B-128 with female 185 in July 1974 and visited her at B-172 in August 1975; he and male 96, as well as 299, competed for opportunities to breed with this female.

In summary, male 96 maintained burrows of his own and made courtship visits to particular females at their burrows. He visited females 185 and 214 intermittently from July 1971 through August 1975 despite changes in the locations of their preferred burrows. In addition, two smaller females, probably siblings, were visited at separate burrows in August 1975. Two smaller males (161 and 299) apparently made occasional visits to female 185 at her burrow(s); male 96 was hostile toward both of these males and asserted his dominance when they were encountered.

Case 2

Male 201 (256 mm) inhabited old fields west of the home range of male 96 throughout the study period; his home range, as determined by the minimum polygon method, was 6.3 ha in area (Figure 5). Occasional observations were made on the movements and behavior of this male from August 1971 through May 1977. All individuals found within his home range during the study period are listed in Table 2. Male 201 is known to have courted four different females at their burrows. Periodic mowing of the old fields resulted in the collapse of various burrows during this period, and as a result changes in burrow use probably occurred somewhat more frequently than in less-disturbed areas. Male 201 is known to have occupied B-73 in August 1971 and B-105 in June 1973.

Female 332 (248 mm) occupied B-142 during June, July, and August 1974. Male 201 was found by M. R. Ziegler (pers. comm.) on the mound of this burrow on June 22, July 9, and July 14, 1974. Upon his release at B-142 on June 23, 201 moved to B-143 and entered (this burrow was occupied in July 1974 by male 283, 215 mm), and when released at B-142 on July 9 he moved steadily and directly to B-139 and entered. It appeared that he maintained B-143 and B-139 himself and made frequent visits to female 332 at her burrow (B-142).

Number 201 was found lodged in the entrance of B-117 on July 18, 1974 (M. R. Ziegler pers. comm.); a smaller male (27, 228 mm) had been taken from this burrow the day before. The burrow was occupied throughout July 1974 by female 66 (232 mm); she had occupied it during July 1973 as well. (Male 27 had occupied B-84 (ca. 194 m NNE of the junction marked "J", Figure 5) in September 1973; B-84 was occupied by a female (35) in April 1976.)

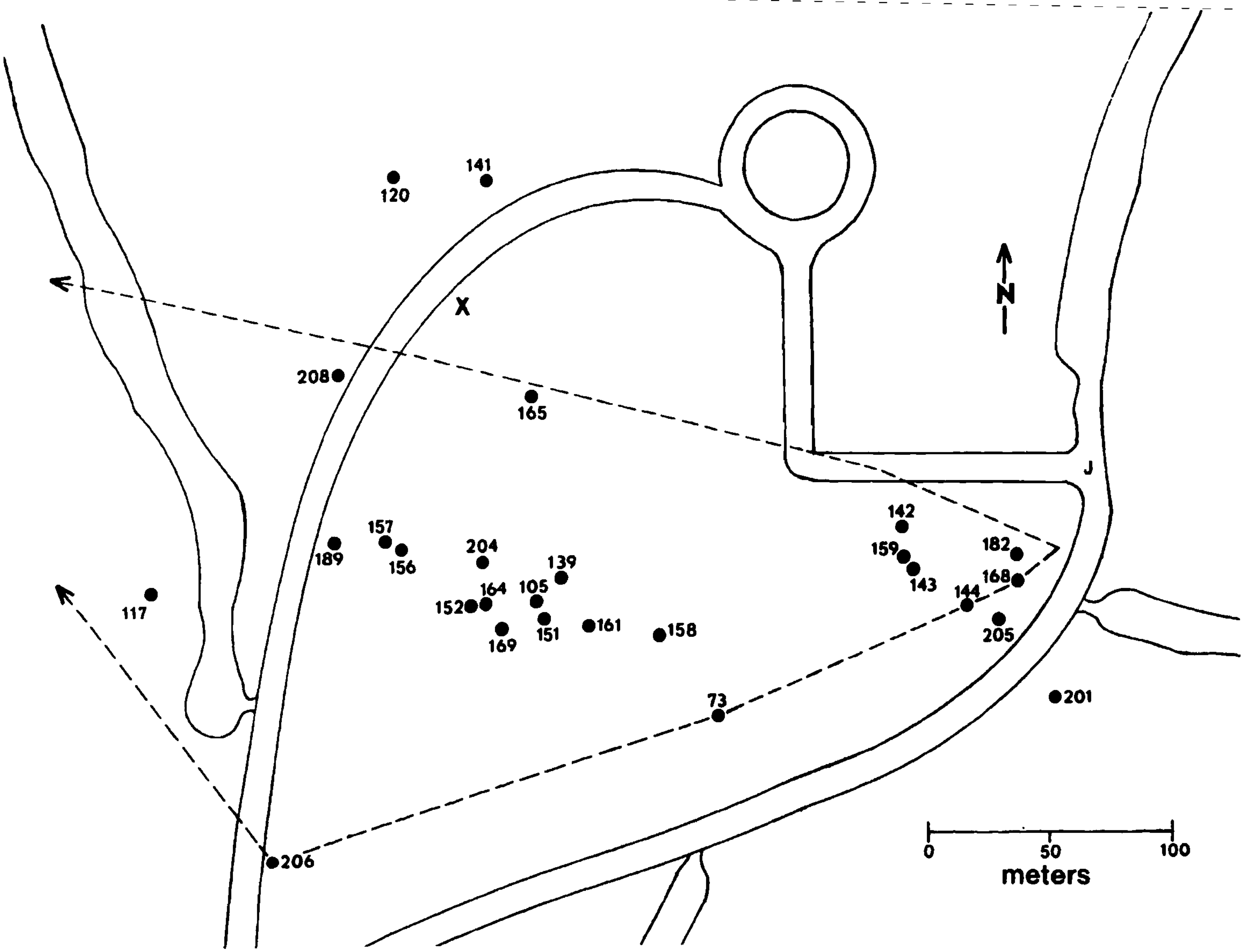

Figure 5. Dashed lines represent boundaries of the home range of *Gopherus polyphemus* male 201 as suggested by extreme points of capture. Shown are the burrows of adult tortoises mentioned in the text; several other burrows found within this area are not shown.

Table 2. Individuals captured in the home range of *Gopherus polyphemus* male 201, in order of decreasing size.

	Number	Plastron length (mm) at time of most recent capture	Inclusive dates of known presence in home range of 201
Males:	201	269	April 1971 - May 1976, May 1977
	273	233	August 1972 - August 1975, November 1975
	27	228	July 1974
	161	222	July 1974
	283	215	January 1973 - July 1974
	363	211	November 1974 - June 1975
	309	206	August 1973 - July 1974
	193	205	May 1973
Females:	374	305	March 1975 - May 1976, May 1977
	332	264	May 1974 - May 1976, May 1977
	256	260	June 1972 - May 1976, May 1977
	73	250	May 1970 - July 1972
	35	240	June 1975 - August 1975
	66	234	July 1974 - October 1975, May 1977
	143	208	April 1970 - March 1972
	253	184	June 1972 - May 1976
Sex undetermined:			
	50	259	June 1970
	265	197	July 1972
	385	196	June 1975 - March 1976
	393	168	August 1975 - March 1976
	343	163	August 1974
	298	145	November 1974
	392	131	August 1975
	348	98	August 1974
	347	85	August 1974
	441	79	June 1976
	425	68	March 1976
	423	58	March 1976
	424	58	March 1976

Male 201 used B-144 on July 21, 1974, and was trapped simultaneously from this burrow with a smaller male (161) on July 24, 1974 (M. R. Ziegler pers. comm.). As indicated in Case 1, male 161 was a wanderer who made opportunistic use of burrows. B-144 had been used in early and mid-July 1974 by male 309 (206 mm).

Male 201 was seen on the mound of B-139 on July 29, 1974, and was found inside this burrow deep to female 256 (242 mm) on August 3, 1974 (M. R. Ziegler pers. comm.). On August 26, 1974 he was found in B-151; female 256 was in B-152 at the time. When placed together, 201 followed the female persistently with head-bobbing and circling. Number 201 occupied B-151 through early September 1974. Tracks suggesting probable visits to female 256 at B-152 were found on January 26 and on August 3, 1975. Female 256 occupied B-152 continuously through March 1976, except for brief use of nearby B-164 in June 1975.

Male 201 was found occupying B-139 on August 28, 1974 and in late January 1975; his vigorous defense of this burrow is described elsewhere (Defense of burrows). Smaller male 363 (201 mm) occupied B-139 in late March 1975 when 201 was using B-105. Number 201 asserted his dominance over the smaller male at B-139 when the two were placed together on the mound on March 23, 1975 (full account in Defense of burrows). Male 363 was seen inside B-159 on April 19, 1975, and occupied B-161 in mid-June 1975. He made opportunistic use of burrows in the old fields, and larger male 201 apparently had his choice of burrows when he was in the area.

Number 201 occupied and defended B-105 intermittently from March through September 1975, and used other burrows during this period as well. He was inside B-105 when a day-long watch was begun at 0906 h on March 22, 1975. He emerged to bask on the mound at 0936 h, and re-entered the burrow at 1016 h. At 1156 h he emerged from the burrow and moved northwest across the field, feeding steadily, and at 1212 h turned directly into the woods to the west. He paused on the mound of an active burrow (B-156) at 1214 h, and for 6 min head-bobbed slowly into the entrance. He then turned away, moved directly to nearby B-157, and dug his way into this active-looking burrow without head-bobbing. Number 201 spent the remainder of the afternoon at B-157, emerging at regular intervals (once every 18-26 min) to dig on the burrow mound and into the tunnel. At 1434 h a large female (256 or 374) was seen resting facing out at the entrance of B-156; B-152, used previously by 256, appeared to have been in use by an armadillo at the time. Male 201 was captured the next day in a trap set opening into the entrance of B-156. As with male 96 at B-46 (Case 1, September 1973), this indicated his persistence in visiting the female in this burrow despite blockage of the entrance: 201 had apparently crashed into the trap from above the entrance on an attempted visit.

Male 201 occupied B-105 from April until June 18, 1975. During a day-long watch of the west field on April 19, 1975, he emerged at 1006 h and for 9 min dug on the burrow mound and into the tunnel. He emerged again at 1149 h and for 28 min wandered in a loop northwest through the field, feeding steadily, then returned to B-105 and entered. The maximum distance moved from B-105 on this feeding foray was about 20 m; 201 turned back when about 10 m north of B-152 and did not investigate this burrow despite the presence of female 256 inside. Tracks indicated that 201 visited female 374 at B-157 in mid-June 1975; this large female (303 mm) occupied B-157 continuously through May 1977, except for brief use of B-152 in late March 1975 and on May 13, 1977 and of B-156 in March and early May 1976.

By mid-June 1975, many plants in the west field surrounding B-105 had grown to over 2 m in height. On June 18, 201 began occupying and defending B-158, in a grassy area between the east and west fields; his preference for this burrow may have arisen partly from the difficulty of moving through dense vegetation in the west field. B-158 is the burrow to which smaller male 363 had retreated when chased and rammed by 201 on March 23, 1975 (Defense of burrows). During a day-long watch on July 24, 1975, 201 emerged from B-158, moved directly to B-168, and spent several hours courting female 332 at the latter burrow. A detailed account of his behavior on this excursion is included in Mate-seeking, above. Following this encounter, 201's use of B-158 decreased. He had expanded B-159 near the middle of the east field in mid-July, and occupied and defended this burrow for several days in late July (B-159 had been used by smaller male 363 in April 1975, as previously mentioned). The west field was not mowed until July 22, 1975; 201 may have preferred B-159 in the more open east field because of the relative ease of movement in the latter area in mid-July. Use of B-159 facilitated his frequent visits to the female in B-168 during this period.

Male 201 began occupying and defending B-164 in the west field on July 28, 1975, six days after the dense, woody forbs there had been mowed. This burrow had been constructed about two months earlier and was inhabited by female 256 in mid-June; her re-occupation of nearby B-152 in late July was synchronous with the occupation of B-164 by the large male.

A day-long watch of B-164 was begun at 0740 h on July 28, 1975. Male 201 first emerged from the burrow to bask on the mound at 0806 h. For 6 min he fed steadily on grass around the edge of the mound, and at 0840 h re-entered the burrow tossing sand. He emerged again at 0914 h and moved across the field feeding, then moved steadily northwest into the woods. He crossed the mound of B-156 and arrived at B-157 at 0924 h; female 374 was inside the latter burrow. Number 201 moved toward the entrance of B-157, head-bobbing occasionally, and stopped with his head in the entrance. At 0936 h he backed up head-bobbing vigorously to about 0.6 m outside and assumed his waiting posture (head elevated, forelimbs extended laterally) as at B-168 four days earlier (Mate-seeking). He advanced again to the entrance 4 min later, head-bobbed into it, and tossed a few scoops of sand. After 6 min he backed up suddenly to about 0.3 m outside head-bobbing, then advanced again to the entrance. Seven minutes later he backed up head-bobbing to about 0.6 m outside, and after 4 min advanced to the entrance with continued bobbing. At 0958 h the male turned around and left the mound of B-157. He paused on the mound of B-156 about 0.6 m from the entrance and, after moving briefly to the entrance to investigate (no head-bobbing), backed out and returned to B-164. He fed briefly near the mound of B-164, and entered the burrow at 1006 h. He emerged again at 1146 h, fed heavily for 11 min, and re-entered the burrow.

Male 201 used the west field as a base from which to visit and court female 374 during this period. Why he failed to visit the closer female (256, in B-152) is an interesting question. An indication that some animosity may have existed between him and female 256 was seen the next day, when 201 retreated to B-164 upon seeing 256 emerging from B-152. It seemed that he returned to B-164 to prevent her re-occupation of this, one of her former burrows (account in Defense of burrows); the male foraged from 1216 to 1238 h and the female from 1238 to 1256 h in the same area on that day.

Male 201 occupied and defended B-164 until August 5, 1975; tracks indicated another visit to B-157 on August 1. He emerged from B-164 on August 5, moved to and entered B-159 after investigating B-105, then emerged and visited female 332 at B-168 in the early afternoon (he was found in a trap set at B-168, having apparently entered from the side). Upon being released on the mound of B-168, 201 moved slowly to the entrance tossing sand, then stopped with his head in the entrance, bobbing occasionally. He then turned sideways in the entrance and remained there for over an hour before returning to B-159. Number 201 occupied and defended B-159 until mid-September 1975, when the burrow was partially collapsed by mowing. He apparently made frequent visits to B-168 during this period (e.g., he was found on the mound about 0.6 m from the entrance on August 17, 1975). Tracks indicated that he used B-158 and B-164 and visited B-157 on at least one occasion in mid-August as well. The partial collapse of B-159 in early September may have been a factor in his move back to the west field; he was captured in the west field on September 19 and entered B-105 upon his release.

Female 35 (240 mm) continuously occupied and defended B-165 in the northern part of the west field in June, July, and August 1975, but was apparently not visited by male 201. This female had occupied B-19 (ca. 291 m NNE of the junction marked "J", Figure 5) in August 1970, B-39 (ca. 183 m NNE of "J") in June 1971, B-120 in August 1973, and B-141 in July and August 1974, but I found no evidence of visits to these burrows by male 201. She was courted vigorously and persistently by 201, however, when the two were placed together in the laboratory on July 9, 1974, suggesting that his neglect of her may have had more to do with spatial factors than with individual repulsion. Female 35 was found inside B-82 (ca. 180 m NNW of "J") in late March 1976 and occupied B-84 during April 1976; she used B-141 during May 1976.

Blockage of the entrance of B-168 with a trap in early September 1975 apparently caused female 332 to move to nearby B-182. This burrow had been occupied by a smaller individual of undetermined sex (392, 131 mm) the month before, and was found greatly enlarged in mid-September. Tracks indicating a probable visit by 201 were found on the mound of B-182 on September 26, 1975. Female 332 occupied this burrow through January 1976; male 201 began occupying and defending it in March 1976, however, and at that time 332 again occupied B-168. She occupied B-201 during April and B-205 during May 1976.

In summary, male 201 visited 332 and each of three other females intermittently from June 1974 through September 1975; one of these females is known to have been visited by another male as well. Female 332 occupied three different burrows during this period, and each was visited by 201. The latter dominated at least one smaller male in the old fields. Two fall hatchlings (423, 58 mm; 424, 58 mm), found in separate burrows near B-152 in March 1976, were evidence of reproductive activity in the old fields the preceding spring/summer. Peculiarities of their scutellation suggested that these individuals were siblings; they were probably the offspring of female 374 or of 256.

Male 201 occupied and defended B-204 in early May 1976. This burrow had been occupied by a smaller individual (identity unknown) the month before, and was greatly enlarged by 201 during the first week of May 1976. Female 256 occupied B-152 during this time, but on May 12, 1976 was found resting inside the entrance of B-169. The original occupant of the latter burrow (459, 130 mm) was deep inside, and 256 had just enlarged the first 0.6 m of the tunnel. Two freshly-laid eggs were found just inside the entrance of this burrow the next day; female 256 was deep inside B-204 at the time, and male 201 was foraging near the paved road to the north. Upon returning to B-204, 201 stopped at the entrance, head-bobbing, then moved out onto the mound as the female advanced to the entrance. When I approached, 201 tried to enter the burrow, but the female held her position inside the tunnel and he remained lodged sideways in the entrance, lunging and hissing when touched. Female 256 was inside B-204 when the burrow was checked again two weeks later.

Female 374, in B-156 during early May and B-157 during late May 1976, was probably visited by male 201 during this period as well.

Female 332 was found feeding only 15-20 m east of B-152 on May 7, 1977. She refused to enter B-152 when placed on the mound, and instead moved far east to B-205 and entered. J. N. Layne (pers. comm.) had found male 455 (190 mm) on the mound of B-205 looking into the entrance of this burrow on November 27, 1976. The male had made no effort to escape when approached; another, larger individual (probably female 332) was seen just inside the entrance, and it seemed that some sort of interaction was in progress.

Female 256 occupied a large, newly-constructed burrow (B-206) during May 1977. She was being held in the laboratory when male 201 was captured on the mound of this burrow on May 7. The female was released into B-206 late that morning, and was resting just inside the entrance facing in when 201 was released on the burrow mound (1244 h). The male moved to the entrance, head-bobbing intermittently and tossing sand. At 1250 h 256 emerged steadily to about 1 m outside the burrow and 201 backed up on the mound head-bobbing vigorously. For 2 min the two exchanged head-bobs while remaining head to head and only a few centimeters apart. Those of 201 were vigorous and almost continuous, but 256 head-bobbed weakly and only occasionally. Although the head of 201 could not be seen when fully extended toward the female, it appeared that he occasionally bit at her marginal scutes and/or forelegs. At 1252 h 256 turned 180° and walked slowly into the burrow; 201 followed closely and mounted the female 0.3 m outside the entrance, but was scraped off by the overhang as she entered. The female emerged again at 1254 h and again at 1256 h, and at both times sequences nearly identical to that beginning at 1250 h followed. In each of the two latter sequences, male 201 uttered a single, high-pitched croak or whine while mounted on the female. Before re-entering the burrow in the third and final sequence, 256 pivoted in one full circle about 1 m outside the entrance while being closely followed by 201. Backing up and pivoting in a semicircle was described as part of the courtship behavior of female *G. polyphemus* by Auffenberg (1966).

Following these sequences, male 201 moved directly to B-189 and entered without head-bobbing (1310 h). From 1338 to 1420 h he engaged in weak but steady ramming of what sounded like the shell of another tortoise about 1.5 m inside the burrow. The ramming bouts were rather slow and occurred at intervals of several minutes. When tapped with a stick, 201 advanced immediately to the entrance and was recaptured; he was released three days later into B-189. Although attempts to trap the other occupant during the interim were unsuccessful, female 66 was pulled from the burrow on May 13; she had probably been the object of ramming by male 201 six days earlier. Number 201 was found inside B-169 defending this burrow on May 13, 1977, but moved to B-208 and entered without head-bobbing when I interrupted a feeding foray three days later.

Three large females from within the home range of male 201 were x-rayed on May 7, 1977, and each was found to contain well-formed, shelled eggs, as follow: 374 (305 mm), 9 eggs; 332 (264 mm), 8 eggs; 256 (260 mm), 7 eggs. Female 35 (241 mm), killed accidentally on May 27, 1977, contained 8 well-formed, shelled eggs.

Case 3

Male 58 (254 mm) inhabited scrubby pine flatwoods along the North Fire Lane (Figure 6). Female 65 (242 mm) occupied B-33 during June and July 1971. On July 15, she and male 58 were found together inside a trap that had been set opening outward at the entrance of B-33. The two tortoises had entered the trap simultaneously from outside, probably while copulating. Dried, whitish fluid, possibly representing ejaculate, was found around the vent of the female. When the pair was released on the mound of B-33 three days later, the female entered the burrow with male 58 close behind. The female was again seen entering the burrow on July 28, 1971; male 58 occupied B-16 on July 30, 1971. The latter burrow had been occupied by female 3 (240 mm) in August 1970.

Female 3 occupied B-69 in July 1971; this burrow was used by male 311 (214 mm) in September 1975. Number 3 occupied B-102 in June, July, and August 1973. She and male 58 were found only 15 m apart in an open area ("X", Figure 6) on the North Fire Lane on June 23, 1973. She was much more active than the male, and when placed next to him moved away with no response. Upon her release the next day she moved north on the fire lane and then slowly east and entered B-102. The male followed the same trails as used by female 3 upon his release 40 min later. He paused briefly on the mound of B-102 about 1 m from the entrance with no head-bobbing, and upon entering the burrow he collided with the female about 0.5 m inside. Before his capture the day before, 58 had tried to move east from the open area ("X"), and it is likely that he made use of some other burrow south of B-102 during this period as well. Female 3

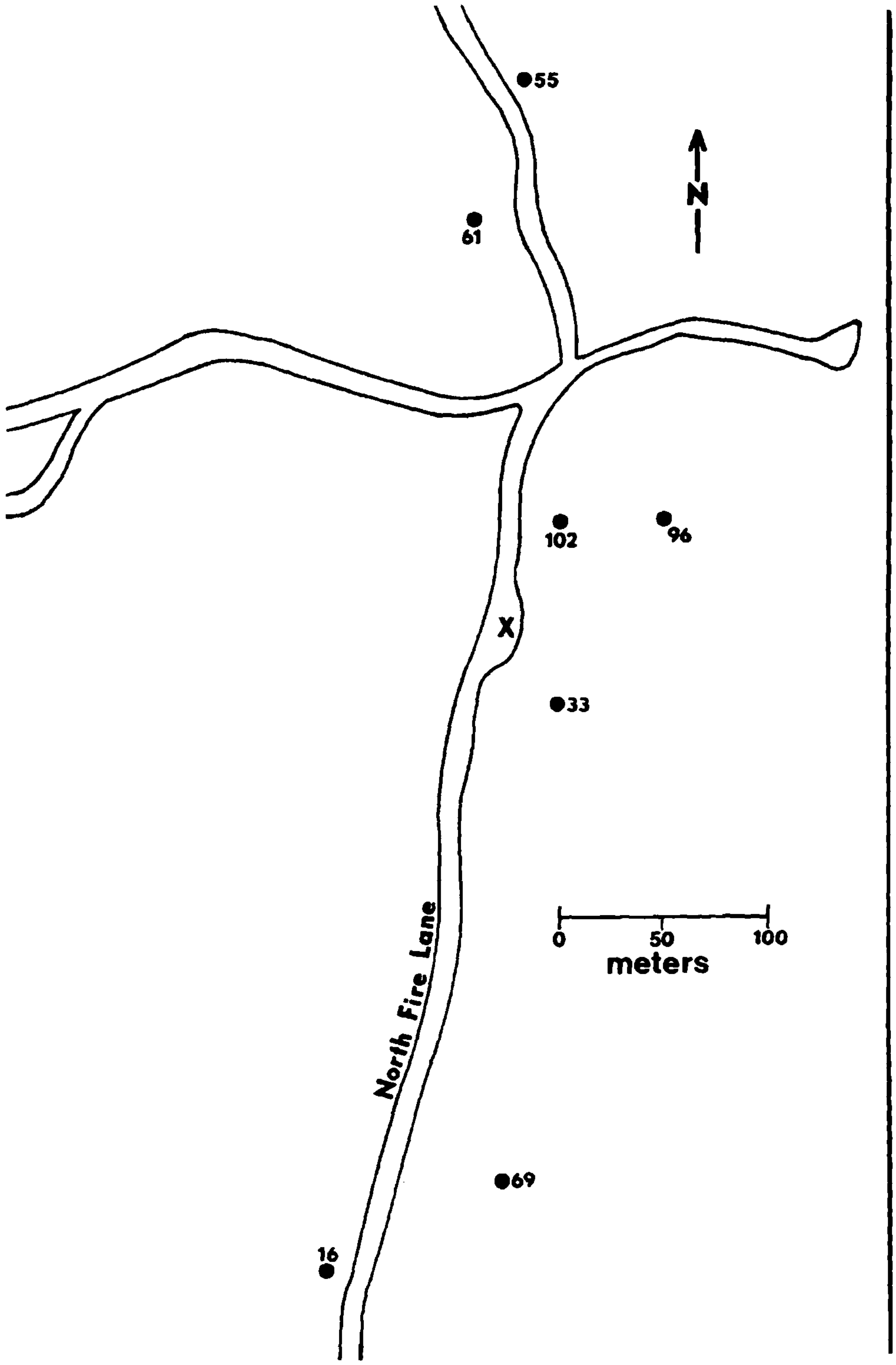

Figure 6. Locations of the burrows of adult tortoises mentioned in Case 3 in connection with the account of *Gopherus polyphemus* male 58. Several other burrows found within this area are not shown.

was again captured in the open area ("X") on July 26, 1973, and male 58 was found at this site the next day. Upon their release on July 29, 1973, the male and female followed identical trails to B-102 and entered. The female occupied B-102 through August 1973, and made use of it during April 1976 as well.

Male 58 had been found in the open area ("X") on January 3, 1973, and female 160 was found at this site (within 3 m of 58's point of capture) the next day (J. N. Layne pers. comm.). Female 160 occupied B-96 during June 1973. Male 58 used B-61 on August 26, 1974; this burrow had been occupied by female 160 (214 mm) in July 1971 and was entered by male 261 (204 mm) on July 20, 1972. Female 160 had also used B-55 in late July 1971; this burrow was used by male 51 (254 mm) on July 13, 1971.