LIBRARIES
UNIVERSITY OF WISCONSIN–MADISON

Ecology of giant tortoises (Geochelone elephantopus) in the Galapagos Islands. 1987

Cayot, Linda Jean
[s.l.]: [s.n.], 1987

https://digital.library.wisc.edu/1711.dl/F57OFKG2TAOKG9C

This material may be protected by copyright law (e.g., Title 17, US Code).

For information on re-use see:
http://digital.library.wisc.edu/1711.dl/Copyright

The libraries provide public access to a wide range of material, including online exhibits, digitized collections, archival finding aids, our catalog, online articles, and a growing range of materials in many media.

When possible, we provide rights information in catalog records, finding aids, and other metadata that accompanies collections or items. However, it is always the user's obligation to evaluate copyright and rights issues in light of their own use.

728 State Street | Madison, Wisconsin 53706 | library.wisc.edu

ECOLOGY OF GIANT TORTOISES

(*GEOCHELONE ELEPHANTOPUS*)

IN THE

GALÁPAGOS ISLANDS

by

LINDA JEAN CAYOT
B.S., Colorado State University, 1975
M.S., Colorado State University, 1978

ABSTRACT OF DISSERTATION

Submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy in Biology
in the Graduate School of Syracuse University
May 1987

Approved _____

Date _____

ABSTRACT

Feeding ecology and associated behavioral adaptations of giant tortoises (Geochelone elephantopus) in the Galápagos Islands were studied from June 1981 to July 1983. Seasonal extremes from a hot-dry period to the exceptionally strong El Niño of 1983, with its heavy precipitation, were included. Dome-shaped tortoises (G. elephantopus porteri) on Santa Cruz, and saddle-backed tortoises (G. elephantopus ephippium) on Pinzón were studied. Activity patterns of tortoises were determined from instantaneous observations of all individuals. Food items of feeding tortoises were compiled monthly to determine diet. Analyses of daily time budgets were based on 2-day watches of focal animals. Available food (g/m^2) was calculated bimonthly from a combination of cover estimates with harvest plots. Food preferences were analysed relative to water, nitrogen, and carbohydrate content.

Tortoise activity patterns changed seasonally and were related to temperature and moisture. Tortoises were most active during periods of high rainfall and food abundance. Daily activity patterns included a unimodal pattern during the cool garúa season when mid-day temperatures were moderate, and a bimodal pattern in the hot season when mid-day temperatures were extremely high.

Tortoises exhibited a feeding strategy of flexible selectivity, adjusting food preferences and diet to environmental conditions. Feeding selectivity was highest in the hot-dry season when food and water were scarce. Tortoises fed on most available plant species, but only a few species constituted most of the diet. Major foods included grasses, forbs, and seasonally available fruit in the highlands of Santa Cruz, and primarily cactus (dry season) on Pinzón, where grasses and forbs were eaten when available (wet season). Tortoises showed a preference for foods with a high water content, especially during dry periods. Neither carbohydrate nor nitrogen content of the foods was a major factor influencing food preferences.

Habitat selectivity for feeding was greater than for resting or traveling. Habitat preferences for feeding were related to abundance of preferred foods, while those for resting and traveling were related to sun:shade patterns and seasonal changes in ambient temperature. Tortoises concentrated in regions of high habitat diversity associated with areas of water flow or collection.

Precipitation, the controlling factor in most arid ecosystems, was the dominant factor affecting tortoise behavior, primarily due to its effects on the availability of food and water.

ECOLOGY OF GIANT TORTOISES

(GEOCHELONE ELEPHANTOPUS)

IN THE

GALÁPAGOS ISLANDS

To Gdan,
with many thanks,
and much love,
Linda

by

LINDA JEAN CAYOT
B.S., Colorado State University, 1975
M.S., Colorado State University, 1978

DISSERTATION

Submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy in Biology
in the Graduate School of Syracuse University
May 1987

Approved _____

Date _____

Copyright 1987

LINDA JEAN CAYOT

ACKNOWLEDGEMENTS

Many people, both in the Galápagos Islands and in the United States, helped to make this research possible, and I am grateful to all of them.

Most of all, I would like to thank Treesa Kineke, who, as my assistant in the islands from January 1982 to July 1983, helped both in the field and in the lab, and who, as my friend, played, laughed, and stayed on with me til the end of El Niño, in spite of the rain. Special thanks to Gayle Robinson and Gayle Davis, who did field work with us at La Caseta, El Chato, and on Pinzón. Ken Risenhoover, Lizabeth Menzies, Bets Stover, Linda Michelsen, and Donna Reynolds all helped in the early months of the study, many of them with the dreaded vegetation transects. Gary Robinson and Priscilla Martinez collected tortoise scat on Santa Cruz while I was on Pinzón. Vicky Seal made one trip to the nesting zone with us during El Niño, and monitored tortoises in the pouring rain. Ron Marlow, Larry Minden, and their fellow Earthwatchers helped Treesa with 2-day watches of focal animals in the summer of 1982. To all of these friends who provided invaluable help in the field I offer my heartfelt thanks.

Also in the Galápagos Islands, I would like to thank the personnel of the Servicio del Parque Nacional Galápagos (SPNG), especially Fausto Cepeda, Intendente, and Julio San Miguel, park warden in charge of La Caseta. SPNG kindly

allowed me to use the hut and kitchen at La Caseta throughout the study. Thank you also to the personnel of the Charles Darwin Research Station, especially Friedemann Koster, director, and Bob Reynolds, resident herpetologist. Little work could be accomplished in the archipelago without the boat crews who transport scientists among the islands. Of these, I would most like to thank Pancho and Efrain of the Beagle IV, and the continually changing crew of the Saturno. Señora Rosa and her family in Santa Rosa always made me feel welcome as I made my journeys to and from La Caseta. Lenín, Omar, and Carlos often helped to pack equipment in and out of the area on horseback, sometimes under terrible conditions. Thanks also to Ole Hamann who introduced me to the Galápagos flora during my first month in the islands, and who helped me with the final identifications and verifications at the end. Lynn Fowler, who studied giant tortoises on Alcedo, helped a great deal in preparing me for my initial journey to the Galápagos.

Of those who contributed to this research from the U.S., I would most like to thank Sam McNaughton, my advisor, for his encouragement in the grant proposal process, for his support upon my return from the islands, and for all of the stimulating discussions throughout the process of data analysis. Many thanks to Judy Tarrants who patiently taught me the laboratory techniques, and who did the majority of the graphics for my dissertation. She, along with her husband Charlie, handled the University paperwork for me

while I was gone. Thank you to Judy, Margaret McNaughton, and Bob Davis for doing some initial nitrogen analyses in 1981. Larry Wolf, Tom Starmer, and Dudley Raynal were all members of my committee. Larry and Tom both read and commented on my dissertation prior to its completion. Nancee Toft helped with statistics and computer analyses. Barb Carns spent hours typing the final tables.

I would also like to thank my parents who are supportive of all of my endeavors, and who took care of my mail, income taxes, etc., while I was in the Galápagos.

The California Academy of Sciences provided me with the use of their herbarium for species verification. This study was funded by the National Science Foundation under Grants No. DEB-7922991, DEB-8021409, and BSR-8505862, the Sigma Xi Grants-in-Aid Program, and The Explorers Club Education and Youth Activities Fund.

CONTENTS

Page

ACKNOWLEDGEMENTS....iii
LIST OF TABLES....viii
LIST OF FIGURES....xii

CHAPTER 1 - INTRODUCTION....1
THE GALÁPAGOS ISLANDS....4
GIANT TORTOISES....13

CHAPTER 2 - METHODS....20
STUDY AREAS....20
VEGETATION....23
Cover....23
Harvest Plots....26
Water, Nitrogen, and Carbohydrate Analyses....30
Species Verification....32
HABITAT TYPES....32
TORTOISES....34
Instantaneous Observations....35
Focal Animals....36
STATISTICS....38

CHAPTER 3 - STUDY AREAS....39
SANTA CRUZ....39
Uplands: La Caseta and El Chato....40
Lowlands: Santa Cruz Nesting Zone....71
PINZÓN....90
DISCUSSION....99

CHAPTER 4 - ACTIVITY PATTERNS....101
INTRODUCTION....101
RESULTS
Daily Activity Patterns....105
Daily Time Budgets....131
DISCUSSION....157

CHAPTER 5 - FEEDING BEHAVIOR....160
INTRODUCTION....160
RESULTS
Food Habits....167
Selectivity and Diversity of Diet....200
Food Preference Indices....214
Food Preferences....217
Food Preferences in Relation to Water Content....225
Food Preferences in Relation to Nitrogen....238
Food Preferences in Relation to Carbyhydrates....243
DISCUSSION....243

CHAPTER 6 - HABITAT PREFERENCES....253

INTRODUCTION.....253
RESULTS
Habitat Types - La Caseta/El Chato.....256
Habitat Types - Santa Cruz Nesting Zone.....266
Habitat Types - Pinzón.....274
Movement Among Habitat Types.....284
Habitat Selectivity.....294
Habitat Preference Indices.....300
Habitat Preferences - Feeding.....307
Habitat Preferences for Feeding in Relation to Habitat Characteristics.....319
Habitat Preferences - Resting.....348
Habitat Preferences - Traveling.....363
DISCUSSION.....379

CHAPTER 7 - CONCLUSION.....385

LITERATURE CITED.....390

LIST OF TABLES

Table — Page

1.1 - Monthly precipitation at CDRS.....8

1.2 - Monthly mean maximum air temperatures at CDRS.....9

1.3 - Monthly mean minimum air temperatures at CDRS.....10

2.1 - ANOVA results for 5% harvest plot data.....29

3.1 - Monthly tortoise counts at La Caseta and El Chato...42

3.2 - Plant species list - Caseta/Chato.....48

3.3 - Weather data - La Caseta.....58

3.4 - Tortoise counts and weather data - Santa Cruz Nesting Zone.....80

3.5 - Plant species list - Santa Cruz Nesting Zone.....84

3.6 - Tortoise counts and weather data - Pinzón.....91

3.7 - Plant species list - Pinzón.....95

4.1 - Number of instantaneous tortoise observations by activity.....107

4.2 - ANOVA results for activity data.....122

4.3 - Stepwise regressions - activity vs environmental variables.....125

4.4 - Correlations between activities and environmental variables.....128

4.5 - List of focal animals.....132

4.6 - Focal animals - Day 1 vs Day 2 (paired t-test).....137

4.7 - Time resting vs environmental variables.....139

4.8 - Time feeding vs environmental variables.....140

4.9 - Time traveling vs environmental variables.....142

4.10 - Time interacting vs environmental variables.....143

4.11 - Time drinking vs environmental variables.....144

5.1 - Food items of tortoises, based on the literature...163

5.2 - Percent diet and percent available food by species and season - La Caseta.....177

5.3 - Percent diet and percent available food by species and season - El Chato.....181

5.4 - Percent diet and percent available food by species - Santa Cruz Nesting Zone.....185

5.5 - Percent diet and percent available food by species and season - Pinzón.....187

5.6 - Importance of significant food items in the diet...189

5.7 - Food items constituting greater than 5% of the diet, by food type.....190

5.8 - Rare food items - La Caseta and El Chato.....192

5.9 - Rare food items - Santa Cruz Nesting Zone and Pinzón.....193

5.10 - Number of food items eaten by focal animals - La Caseta and El Chato.....195

5.11 - Number of food items eaten by focal animals - Santa Cruz Nesting Zone.....196

5.12 - Number of food items eaten by focal animals - Pinzón.....197

5.13 - Food items of focal animals - La Caseta and El Chato.....198

5.14 - Food items of focal animals - Santa Cruz Nesting Zone.....201

5.15 - Food items of focal animals - hot-dry season, Pinzón.....202

5.16 - Food items of focal animals - El Niño, Pinzón.....204

5.17 - Feeding selectivity by season and study area.....208

5.18 - Diet diversity and selectivity - analysis.....211

5.19 - Indices of feeding preference.....215

5.20 - Preferred foods - La Caseta and El Chato.....219

5.21 - Avoided foods - all study areas.....221

5.22 - Preferred foods - Santa Cruz Nesting Zone and Pinzón.....222

5.23 - Avoided plant species - all study areas.....224

5.24 - Food preferences vs water content of the food.....234

5.25 - Food preferences vs nitrogen content of the food..240

6.1 - Study area by habitat type - La Caseta and El Chato.....265

6.2 - Habitat characteristics by season - La Caseta and El Chato.....267

6.3 - Study area by habitat type - Santa Cruz Nesting Zone.....275

6.4 - Habitat characteristics - Santa Cruz Nesting Zone.....276

6.5 - Study area by habitat type - Pinzón.....283

6.6 - Habitat characteristics by season - Pinzón.....285

6.7 - Habitat use by focal animals - all study areas.....288

6.8 - Habitat selectivity vs activity, study area, and season.....296

6.9 - Monthly total of instantaneous tortoise observations by activity.....301

6.10 - Comparison of two types of habitat preference indices for resting, feeding, and traveling - all study areas.....304

6.11 - Use and preference indices of habitat types for feeding, by season - La Caseta.....308

6.12 - Use and preference indices of habitat types for feeding, by season - El Chato.....310

6.13 - Comparison of habitat preference indices for feeding, by season - La Caseta vs El Chato.....312

6.14 - Use and preference indices of habitat types for feeding - Santa Cruz Nesting Zone.....316

6.15 - Use and preference indices of habitat types for feeding, by season - Pinzón.....317

6.16 - Primary variable explaining habitat preferences for feeding - La Caseta and El Chato.....321

6.17 - Stepwise regressions - habitat preferences for feeding vs environmental variables - La Caseta....332

6.18 - Stepwise regressions - habitat preferences for feeding vs environmental variables - El Chato.....334

6.19 - Stepwise regressions - habitat preferences for feeding vs environmental variables - Santa Cruz Nesting Zone.....337

6.20 - Stepwise regressions - habitat preferences for feeding vs environmental variables - Pinzón.....344

6.21 - Use and preference indices of habitat types for resting, by season - La Caseta.....349

6.22 - Use and preference indices of habitat types for resting, by season - El Chato.....351

6.23 - Seasonal use of shaded and open habitats by resting tortoises - La Caseta and El Chato.....353

6.24 - Comparison of habitat preference indices for resting, by season - La Caseta vs El Chato.....354

6.25 - Use and preference indices of habitat types for resting - Santa Cruz Nesting Zone.....356

6.26 - Use and preference indices of habitat types for resting, by season - Pinzón.....358

6.27 - Habitat preference indices for resting vs % cover by rock, by season - Pinzón.....360

6.28 - Use and preference indices of habitat types for traveling, by season - La Caseta.....364

6.29 - Use and preference indices of habitat types for traveling, by season - El Chato.....366

6.30 - Seasonal use of shaded and open habitats by traveling tortoises - La Caseta and El Chato.....368

6.31 - Comparison of habitat preference indices for traveling, by season - La Caseta vs El Chato.....370

6.32 - Use and preference indices of habitat types for traveling - Santa Cruz Nesting Zone.....371

6.33 - Stepwise regressions - habitat preferences for traveling vs environmental variables - Santa Cruz Nesting Zone.....373

6.34 - Use and preference indices of habitat types for traveling, by season - Pinzón.....374

6.35 - Use of Opuntia habitat types for feeding, resting, and traveling, by season - Pinzón.....375

6.36 - Habitat preference indices for traveling vs % cover by rock, by season - Pinzón.....376

LIST OF FIGURES

Figure — Page

1.1 - The Galápagos Islands.....5

2.1 - Santa Cruz Island. Location of study areas.....21

2.2 - Pinzón. Location of study area.....24

3.1 - Habitat type map of La Caseta.....44

3.2 - Habitat type map of El Chato.....46

3.3 - Monthly precipitation and available food - La Caseta.....60

3.4 - Available food over time - El Chato, Santa Cruz Nesting Zone, and Pinzón.....62

3.5 - Available food vs precipitation - La Caseta and El Chato.....64

3.6 - Species richness (S_v) over time - all areas.....67

3.7 - Species diversity (H'_v) over time - all areas.....69

3.8 - Species richness (S_v) vs biomass of available food.....72

3.9 - Species diversity (H'_v) vs biomass of available food.....74

3.10 - Species diversity (H'_v) vs precipitation.....76

3.11 - Species evenness (J_v) over time - all areas.....78

3.12 - Habitat type map of the Santa Cruz Nesting Zone....82

3.13 - Habitat type map of South Crater, Pinzón.....93

4.1 - Seasonal activity patterns by hour - Caseta/Chato..108

4.2 - Activity patterns by hour - Santa Cruz Nesting Zone.....111

4.3 - Activity patterns by hour - Pinzón.....113

4.4 - Tortoise activity vs temperature - Caseta/Chato....115

4.5 - Tortoise activity vs temperature - Santa Cruz Nesting Zone.....118

4.6 - Tortoise activity vs temperataure - Pinzón.....120

4.7 - Carapace measurements of focal animals.....134

4.8 - Percent day in each activity - focal animals.....147

4.9 - Percent day feeding and resting vs maximum temperature - Pinzón.....150

4.10 - Percent day feeding vs precipitation and water content of the food - all areas.....152

4.11 - Distance traveled/day vs time traveling and precipitation.....154

5.1 - Available food and tortoise diet by food type - La Caseta.....168

5.2 - Available food and tortoise diet by food type - El Chato.....170

5.3 - Available food and tortoise diet by food type - Santa Cruz Nesting Zone.....172

5.4 - Available food and tortoise diet by food type - Pinzón.....174

5.5 - Diet richness (S_d) vs vegetation diversity (H'_v)...209

5.6 - Diet diversity (H'_d) vs vegetation diversity (H'_v).....212

5.7 - Water content of the available food and of the tortoise diet over time - La Caseta, Santa Cruz Nesting Zone, and Pinzón.....226

5.8 - Water content of the available food and of the tortoise diet over time - El Chato.....228

5.9 - Feeding selectivity vs water content of the food.....231

5.10 - Food preferences vs water content of the food - La Caseta and Pinzón.....236

5.11 - Food preferences vs nitrogen content of the food - Caseta/Chato and Pinzón.....241

6.1 - Habitat type map of La Caseta.....257

6.2 - Habitat type map of El Chato.....259

6.3 - Habitat type map of the Santa Cruz Nesting Zone....270

6.4 - Habitat type map of South Crater, Pinzón.....278

6.5 - Number of habitat types visited/day vs time feeding and traveling - Caseta/Chato.....290

6.6 - Movement among habitat types vs time traveling - Caseta/Chato.....292

6.7 - Habitat preferences for feeding vs % preferred-significant foods - La Caseta.....323

6.8 - Habitat preferences for feeding vs % preferred-significant foods - El Chato.....325

6.9 - Habitat preferences for feeding vs biomass of preferred-significant foods - La Caseta.....327

6.10 - Habitat preferences for feeding vs biomass of preferred-significant foods - El Chato.....329

6.11 - Habitat preferences for feeding vs biomass of significant foods - Santa Cruz Nesting Zone.....339

6.12 - Habitat preferences for feeding vs % preferred-significant foods - Santa Cruz Nesting Zone.....342

6.13 - Habitat preferences for feeding vs % cover by rock and biomass of signficant foods - Pinzón.....346

6.14 - Habitat preferences for resting vs % cover by rock - Pinzón.....361

6.15 - Habitat preferences for traveling vs % cover by rock - Pinzón.....377

CHAPTER ONE - INTRODUCTION

Arid ecosystems are defined as "water-controlled ecosystems with infrequent, discrete, and largely unpredictable water inputs" (Noy-Meir 1973). Although temperature can play an important role in these systems, precipitation is so low that water becomes the dominant controlling factor for biological processes. Precipitation often comes in pulses, and organisms at the higher trophic levels must adopt a pulse-reserve pattern, by creating their own reserves, using the reserves of other organisms, or by having flexible feeding habits that allow them to use whatever pulse or reserve is available (Noy-Meir 1973).

Herbivores living in arid ecosystems tend to have a fairly generalized feeding behavior, and consume a wide range of plant species, plant types, and plant parts (Noy-Meir 1974). They often maintain a strategy of flexible selectivity, with their preferences shifting seasonally in response to the composition and the phenological state of the available food (Noy-Meir 1974). Optimal foraging models predict that these seasonal changes will be evident in the level of specialization, with animals feeding more selectively or specializing when food is abundant and then feeding on all potential food items when food is scarce (Ivlev 1961, MacArthur and Pianka 1966, Emlen 1966, 1968, Schoener 1971).

Establishment and survival ability of species are dependent upon the ecological conditions of the area to which they have dispersed. On oceanic islands, animals with wide food preferences appear especially favored for establishment, and in many cases a high tolerance for aridity seems advantageous (Carlquist 1974).

The Galápagos Islands are located within the "Galápagos Triangle" where the climatological pecularities of the dry zone of the eastern equatorial Pacific reach their peak (Palmer and Pyle 1966). Although there are occasional wet years, the Galápagos environment is considered xeric, having various modifications of xeric environments (Carlquist 1974). The islands provide a unique type of natural laboratory for ecological studies. Isolated from other land masses, the islands have a low diversity of both plants and animals. The combination of oceanic islands with extreme aridity in some years creates an environment in which establishment and survival of organisms is extremely difficult, and is dependent in part upon their adaptations to arid environments.

As the major large native herbivore in the Galápagos Islands, giant tortoises (Geochelone elephantopus) should exhibit adaptations to an arid ecosystem as described above. Many known characteristics of giant tortoises make them good candidates for dispersal to and establishment on oceanic islands. The chilensis group of Geochelone, which includes elephantopus, is generally better adapted to much more xeric

conditions than other tortoises (Auffenberg 1971). In addition, Galápagos tortoises are able to live without food or water for periods in excess of one year (Porter 1822, Van Denburgh 1914, Townsend 1925), are able to float long distances (Stewart 1911, Simpson 1942), and have a hard carapace and plastron that would provide some protection upon arrival on the extremely rocky shores of the Galápagos Islands. They also are long-lived, providing them with many years to achieve successful reproduction. Some turtle species have the possibility of sperm storage in females (Pritchard 1977, 1979a, Moll 1979), which, if true for Galápagos tortoises, would give females time to locate adequate areas for nesting. In addition, the slow rate of passage of food through the gut of Galápagos tortoises, between 1-3 weeks and probably longer (Rick and Bowman 1961), would allow tortoises to transport seeds of their continental food species to the islands, and then deposit them in feces, thereby improving their chances for successful germination and growth on the lava-covered islands (see Hnatiuk 1978).

This study was designed to examine the present ecology of Galápagos tortoises, emphasizing their activity patterns, feeding behavior, and habitat preferences, in an effort to determine how tortoises are behaviorally adapted to the Galápagos environment, what external factors are controlling or triggering their behavior, and whether tortoise behavior differs due to differences in humidity or aridity among the islands. The role of precipitation, in terms of its effects

on both the habitat and behavior of giant tortoises, was examined to determine whether it could be considered the variable "driving" the system. The effects of temperature were also examined, due to its potential importance for ectothermic animals.

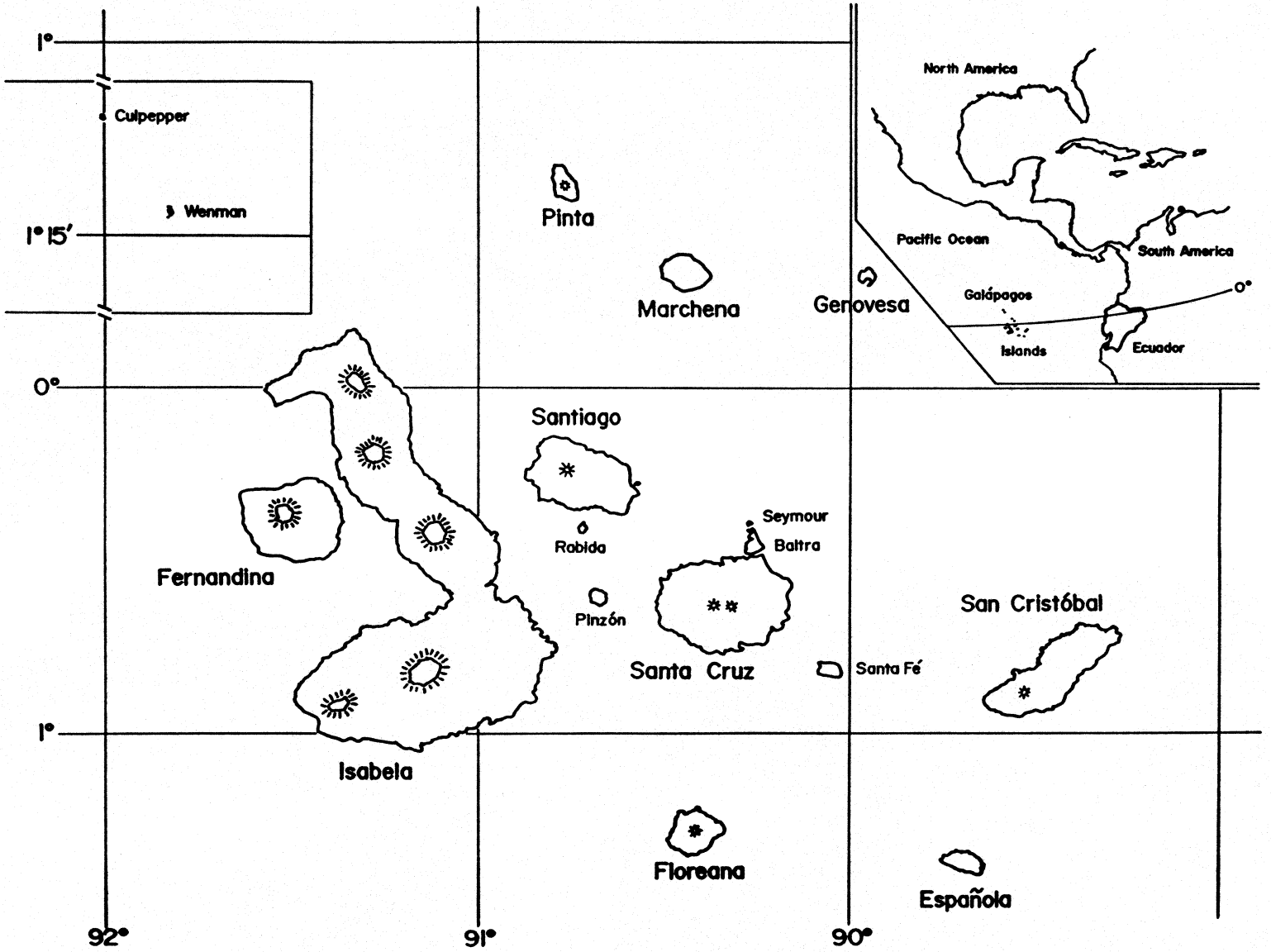
As the single large native herbivore with no major competitors and no natural predators, tortoises are essentially free to live in all areas of the islands on which they occur. The heterogeneity of the environment, with patches differing in "quality," should effect some degree of habitat selection (Wiens 1976), with tortoises preferring habitats of highest quality. Tortoises should exhibit a hierarchy of selection, with selection for the most favorable regions for living, selection for the most optimal habitats, and selection for the highest quality foods. In addition, seasonal changes in diurnal air temperature patterns should produce changes in tortoise activity patterns, with tortoises selecting the more optimal times of day to be active.

THE GALÁPAGOS ISLANDS

> "Nothing could be less inviting than the first appearance. A broken field of black, basaltic lava, thrown into the most rugged waves, and crossed by great fissures, is everywhere covered by stunted, sunburnt brushwood, which shows little sign of life." (Darwin 1860)

The Galápagos Islands lie astride the equator, 960 km off the coast of Ecuador (Fig. 1.1). The first islands of this volcanic archipelago emerged above sea level between 3

Fig. 1.1. The Galápagos Islands.


1°
1° 15'
0°
1°
92°
91°
90°
Culpepper
Wenman
Pinta
Marchena
Genovesa
Santiago
Rabida
Seymour
Baltra
Pinzón
Santa Cruz
Santa Fé
San Cristóbal
Fernandina
Isabela
Floreana
Española
North America
Pacific Ocean
South America
Galápagos
Islands
Ecuador
0°

and 5 million years ago (Cox 1983). Volcanic activity continues to this day, with several eruptions having occurred within the last decade. Simkin (1984) provides a good description of the geological history of the islands. Though the archipelago has no close geological affinity with the continental Americas, its native flora and fauna derive primarily from the American tropics (Wiggins and Porter 1971). Evolution of the unique terrestrial biota is thought to have occurred within the past 3 to 4 million years (Hickman and Lipps 1985).

The climate of the Galápagos differs from most other equatorial islands because of its location within the dry "Galápagos Triangle" on the eastern edge of the equatorial dry zone of the Pacific (Palmer and Pyle 1966). The climate is strongly influenced by the temperature of the surrounding sea. Seasonal changes are determined primarily by regular shifts in the position of water masses of different temperatures (Alpert 1963, Palmer and Pyle 1966, van der Werff 1979). There are two seasons, the hot or rainy season from January to April or May, and the cool dry or garúa season persisting the rest of the year (Tables 1.1, 1.2, 1.3).

During the hot season, the sea water, dominated by the warm current from Panama, is several degrees warmer than during the latter half of the year, effecting heavy local showers. The rainfall is irregular, with some years having a great deal of precipitation while others have very little (Table 1.1). In this study, the hot season has been sepa-

Table 1.1. Monthly precipitation (mm) at the Charles Darwin Research Station (CDRS, elevation 6 m) from 1965 through 1983 (data from CDRS weather reports).

YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC	TOTAL
1965	31.5	8.9	0.0	223.8	224.1	6.2	12.6	8.8	16.2	40.2	11.7	16.0	600.0
1966	69.7	41.8	0.0	0.0	0.0	8.5	13.8	10.4	15.6	19.1	14.0	10.4	203.3
1967	34.6	112.0	26.9	13.8	7.9	37.5	10.6	10.9	17.4	13.7	16.4	13.3	315.0
1968	5.7	32.9	30.2	0.0	0.1	1.0	18.6	19.1	23.5	14.1	11.7	6.6	163.5
1969	23.0	16.8	249.0	68.5	32.4	16.8	12.0	3.8	18.5	3.2	11.0	15.7	470.7
1970	20.4	0.0	1.2	0.7	4.6	8.1	8.7	10.0	6.2	10.1	8.7	5.6	84.3
1971	12.3	1.5	142.9	41.2	0.4	11.5	10.0	19.7	12.3	16.0	4.7	13.5	286.0
1972	46.9	70.8	49.1	241.9	31.2	123.5	7.2	8.0	5.5	8.1	1.7	75.2	669.1
1973	400.0	11.7	10.9	0.0	1.6	0.5	0.8	6.3	6.5	8.9	8.9	14.3	470.4
1974	7.2	54.4	16.2	15.2	19.7	14.4	6.0	12.1	9.6	6.1	6.1	7.4	174.4
1975	2.6	335.1	417.6	108.2	0.2	6.0	4.8	16.0	8.5	14.8	3.1	12.2	929.1
1976	45.2	81.8	0.0	43.4	239.2	10.4	30.9	22.1	10.4	3.9	10.2	8.9	506.4
1977	116.3	29.0	13.8	0.0	31.8	7.0	22.5	5.2	2.5	18.6	9.4	12.3	268.4
1978	158.3	63.4	99.6	0.0	0.0	0.0	3.7	7.9	2.3	7.3	9.9	64.8	417.2
1979	44.3	31.5	0.0	44.4	1.9	12.7	8.0	3.8	14.8	3.1	0.6	4.6	169.7
1980	23.4	69.2	0.0	139.4	0.0	1.2	4.7	3.0	3.6	5.8	4.5	1.0	255.8
1981	1.5	4.4	275.3	21.0	1.0	2.1	4.5	1.2	12.2	5.9	3.2	37.5	369.8
1982	13.2	22.2	11.5	6.8	8.5	4.2	9.0	5.7	6.1	8.9	34.7	508.6	639.4
1983	315.9	91.9	298.1	434.2	660.2	637.5	278.2	5.4	3.1	28.3	3.0	14.1	2769.9
$\bar{X}$	72.2	56.8	86.4	73.8	66.6	47.8	24.6	9.4	10.2	12.4	9.1	44.3	513.8
SD	109.2	75.0	127.8	114.5	160.3	145.4	61.8	6.0	6.1	9.4	7.6	114.1	586.8
MEDIAN	31.5	32.9	16.2	21.0	4.6	8.1	9.0	8.0	9.6	8.9	8.9	13.3	369.8

Table 1.2. Mean monthly maximum air temperatures (°C) at the Charles Darwin Research Station (CDRS, elevation 6 m) from 1965 through 1983 (data from CDRS weather reports).

YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
1965	27.3	29.5	31.1	30.1	28.4	26.9	26.2	24.9	24.7	24.8	25.9	27.2
1966	28.7	29.9	29.7	28.7	26.4	25.1	24.1	23.1	23.2	23.9	24.3	25.6
1967	27.7	28.2	31.0	30.1	28.5	26.3	24.6	23.4	23.2	24.0	25.2	25.6
1968	27.2	29.4	28.9	27.1	26.1	24.6	23.5	24.7	24.6	24.8	25.7	27.3
1969	28.4	30.4	31.7	31.4	30.5	28.9	26.4	26.2	26.3	27.8	28.3	28.4
1970	28.9	29.9	30.9	29.3	27.5	24.2	22.9	22.7	23.5	24.0	25.1	26.8
1971	29.3	31.8	31.9	32.8	26.5	25.7	24.3	24.5	22.8	-	24.0	25.3
1972	26.9	29.7	30.5	29.1	27.2	27.0	26.8	26.4	25.7	26.0	25.8	26.6
1973	27.6	28.6	29.1	26.5	25.2	23.1	22.3	21.2	20.8	21.7	22.9	23.9
1974	25.8	28.9	30.6	30.8	28.3	26.5	24.8	23.6	23.4	23.2	23.9	24.4
1975	27.0	28.4	29.7	29.0	26.4	25.0	23.9	23.0	23.0	22.7	23.5	24.8
1976	27.4	29.7	30.7	30.7	29.4	27.9	27.0	26.3	25.4	25.7	26.5	27.2
1977	29.1	30.9	31.0	29.1	28.0	21.2	24.6	23.0	23.0	23.8	25.0	26.2
1978	27.4	28.9	28.1	27.8	26.5	23.9	23.6	22.5	22.3	22.6	24.4	25.7
1979	28.0	28.5	29.6	28.9	27.2	25.8	24.9	23.9	24.6	24.6	25.3	25.8
1980	27.7	29.5	30.2	29.9	27.2	25.7	24.4	23.3	23.1	23.6	24.6	25.5
1981	26.5	28.6	29.2	28.4	27.4	24.5	23.8	23.3	23.0	23.7	25.0	26.6
1982	28.3	29.6	29.4	28.3	27.8	26.0	25.3	24.9	25.6	26.5	27.9	28.7
1983	30.6	31.0	31.1	30.7	30.0	29.3	28.5	26.8	25.3	25.4	25.6	26.5
$\bar{X}$	27.9	29.5	30.2	29.4	27.6	25.7	24.8	24.1	23.9	24.4	25.2	26.2
SD	1.1	1.0	1.0	1.5	1.4	1.9	1.5	1.5	1.4	1.5	1.4	1.2

Table 1.3. Mean monthly minimum air temperatures (°C) at the Charles Darwin Research Station (CDRS, elevation 6 m) from 1965 through 1983 (data from CDRS weather reports).

YEAR	JAN	FEB	MAR	APR	MAY	JUNE	JULY	AUG	SEPT	OCT	NOV	DEC
1965	22.1	23.0	23.6	23.4	23.9	22.9	21.5	20.3	20.6	20.2	21.3	23.5
1966	23.9	24.2	22.6	22.2	20.6	19.9	19.6	18.4	18.8	18.9	20.1	20.7
1967	22.6	22.4	21.8	21.5	21.8	20.8	19.8	18.2	17.4	18.3	19.4	19.3
1968	22.1	22.8	20.8	21.6	20.0	19.6	20.0	20.5	20.3	20.7	20.8	22.3
1969	22.6	23.5	24.1	24.5	24.6	23.7	20.6	20.0	20.2	21.1	21.9	21.7
1970	23.2	23.5	23.2	23.4	21.6	19.7	17.2	17.2	17.4	18.3	18.6	18.9
1971	20.4	18.7	20.4	22.7	21.4	20.5	19.9	18.6	18.7	-	20.4	20.6
1972	21.7	22.6	22.0	24.2	23.8	22.7	23.3	22.6	21.6	21.3	22.4	22.7
1973	23.4	22.8	22.1	21.6	20.8	17.8	17.0	16.8	16.8	16.8	17.9	18.9
1974	19.8	21.6	21.9	22.8	22.1	21.8	19.0	20.4	18.7	18.9	19.2	19.8
1975	21.9	22.9	22.6	21.9	20.3	20.0	18.9	18.4	18.3	18.0	18.6	18.7
1976	21.8	21.3	21.8	23.2	23.6	22.9	23.0	22.8	21.1	18.6	19.9	22.2
1977	23.4	22.7	22.6	22.3	21.1	20.4	20.1	18.6	18.2	20.0	20.7	22.0
1978	23.4	23.9	23.0	22.0	21.2	19.0	19.1	18.3	18.1	18.2	19.8	20.2
1979	23.0	23.0	23.3	23.4	22.1	21.2	20.9	19.7	18.6	19.6	20.9	20.5
1980	22.5	23.3	23.0	23.3	21.9	20.8	20.2	18.5	18.7	19.1	20.2	20.2
1981	21.9	23.3	24.1	23.5	21.2	20.7	19.5	18.6	18.4	19.3	18.6	20.7
1982	23.4	24.3	24.8	23.4	23.6	22.8	22.4	21.7	22.0	22.5	23.8	23.8
1983	24.2	23.7	24.2	23.9	23.7	23.6	24.1	22.4	20.3	20.6	20.7	20.8
$\bar{X}$	22.5	22.8	22.7	22.9	22.1	21.1	20.3	19.6	19.2	19.5	20.3	20.9
SD	1.1	1.3	1.2	0.9	1.4	1.6	1.9	1.8	1.5	1.4	1.4	1.5

rated into a hot-wet and a hot-dry season, depending on precipitation.

The cool dry or garúa season is dominated by the movement of antarctic water northward combined with an upwelling of cold water off the coast of South America (Palmer and Pyle 1966). This season is cooler in all areas of the islands. The lack of moisture, however, occurs primarily in the lowlands, while the uplands (above ∿200 m) experience a thick mist or drizzle locally known as garúa. In this study, all of the work during this season was done in the uplands. Therefore, the season will be referred to as garúa season.

In some years, an anomalous warming of surface water in the equatorial Pacific occurs, causing exceptionally high levels of precipitation. These events are known as El Niños, and occur at intervals of 2-10 years (Gill and Rasmussen 1983). Although occurring predominantly in the hot season, El Niños are know to extend into garúa season at either end of the hot season. The 1982-83 El Niño, experienced during this study, was the most severe Niño in the last 100 years, and affected weather patterns throughout the world (Naranjo 1985, Ramage 1986). Effects of the 1982-83 El Niño in the Galápagos have been well documented (Robinson and del Pino 1985). Descriptions of the event can be found in several sources (see Philander 1983, Ramage 1986). Although the anomalous warming of the sea around Galápagos began mid-way in garúa season 1982, for the purposes of this

study the season designated El Niño coincides only with those months of heavy precipitation, ie., from December 1982 to July 1983.

Only 13 islands of the Galápagos archipelago have an area greater than 10 sq km. These can be classified into two major categories (Bowman 1961). The first, including Isabela, Santa Cruz, Fernandina, Santiago, San Cristóbal, Floreana, and Pinta, are large (6 of the 7 largest), and include an extensive area above 450 m. The combination of large size with high elevation produces an increase in precipitation which results in a more diverse flora (Fernandina is an exception) divided into two or more vegetation zones. The second group, including Española, Santa Fé, Baltra, and Genovesa, are smaller, lower in elevation (all less than 200 m), and have a less diverse flora, all within the arid coastal vegetation zone. The two remaining of the 13 largest islands, Pinzón and Marchena, are both intermediate in elevation. Marchena, however, has only one vegetation zone, while Pinzón has two.

The concept of vegetation zones, defined primarily by elevation and the resulting precipitation, has been widely used in the Galápagos literature. These zones have been well described by Wiggins and Porter (1971), after work by Stewart (1911) and Bowman (1961). Major works on the Galápagos flora include Wiggins and Porter (1971), van der Werff (1978), and Hamann (1981). The flora, predominantly weedy, is derived primarily from plants on the South American con-

tinent (Porter 1979, 1983). Endemism in the indigenous vascular flora is between 37-43% (Porter 1979).

The Galápagos National Park, which includes over 95% of the land area in the archipelago, was established in 1959, in celebration of the 100th anniversary of the publication of Darwin's The Origin of Species (Hickman 1985). The park is administered by the Servicio del Parque Nacional Galápagos (SPNG), established in 1968. Research in the islands is carried out under the auspices of the Charles Darwin Research Station (CDRS), an international scientific station which acts in an advisory role to SPNG.

GIANT TORTOISES

> "The day was glowing hot, and the scrambling over the rough surface and through the intricate thickets, was very fatiguing; but I was well repaid by the strange Cyclopean scene. As I was walking along I met two large tortoises, each of which must have weighed at least two hundred pounds: one was eating a piece of cactus, and as I approached, it stared at me and slowly stalked away; the other gave a deep hiss, and drew in its head. These huge reptiles, surrounded by the black lava, the leafless shrubs, and large cacti, seemed to my fancy like some antediluvian animals." (Darwin 1860)

Giant tortoises were once widespread and common in the warmer parts of the Americas, Europe, Africa, and Asia (Van Denburgh 1914, Pritchard 1979a). Now natural populations of giant tortoises are confined to two groups of oceanic islands: the Galápagos archipelago in the Pacific Ocean (Geochelone elephantopus), and the Aldabra atoll in the Indian Ocean (Geochelone gigantea). Fourteen races or

subspecies of the Galápagos tortoise were originally found in the islands (Van Denburgh 1914, Snow 1964, MacFarland et al. 1974a). Ten of the fourteen were from separate islands, while a separate race occurred on each of the five major volcanos of Isabela.

When the islands were first discovered in the 1500s, the tortoises were so abundant and dominated the landscape that the Spanish named the islands "Galápagos," which was their word for tortoises (Townsend 1925). From that point on, tortoises were severely decimated by seamen who used them for food. First were the buccaneers in the late 1600s and 1700s, followed by whalers, fursealers, and crews of naval vessels from the late 1700s to the late 1800s (Townsend 1925, Slevin 1959, Hickman 1985). Townsend (1925) estimated, from a review of the logs of whaling ships, that American whalers alone took over 100,000 tortoises subsequent to 1830.

With the beginning of human settlement on the islands in the 1800s, the settlers also began slaughtering tortoises for food. In addition, oil hunters in the late 1800s and the 1900s killed hundreds of tortoises to export their oil to the continent (Beck 1903). Oil hunters were active on Sierra Negra, a southern volcano of Isabela, as late as 1959 (MacFarland et al. 1974a). Mammals introduced by the settlers, the oil hunters, and the seamen eventually became the major threat to the tortoise populations and remain so today, with some destroying habitat while others destroy

tortoise nests or consume hatchlings (Eckhardt 1972, MacFarland and Reeder 1975, MacFarland et al. 1974a).

Perhaps the least understood decimation of tortoises was carried out by scientists, in the early years of this century, who tried to take as many of the remaining tortoises as possible. Their justification for taking away hundreds of tortoises was that since the tortoises were in danger of extinction and were unlikely to survive unless protected, which was impossible at that time, it was better that they be killed and taken for study than left for the oil hunters (Hickman 1985).

In 1969, a study was begun to determine the status and reproduction of the remaining tortoise populations (MacFarland et al. 1974a, b). Several races thought to be extinct were rediscovered, and the population sizes of most of the surviving races were found to be much larger than expected. The total number of tortoises in the islands was estimated at 8,500-14,000. The three northern volcanos of Isabela and the island of Santa Cruz have the largest remaining populations of tortoises, and they all have at least some successful natural reproduction (MacFarland et al. 1974a). Three subspecies are extinct (Santa Fé, Floreana, Fernandina), and the Pinta race has only one surviving member. The remaining populations have relatively low numbers, some having zero natural reproduction.

The current conservation program, a result of the aforementioned study, has three primary objectives: 1) control

and extermination of introduced mammals; 2) protection of tortoise nests, primarily from pigs (Sus scrofa) ; and 3) egg incubation and subsequent raising of young tortoises that are returned to their "native" island when approximately 5 years of age, old enough to withstand predation (MacFarland et al. 1974b). This program was begun in the 1960s, and is run jointly by SPNG and CDRS.

That a majority of the subspecies survived the centuries of exploitation is extraordinary. Their survival can be attributed to the longevity of the tortoise and to the rough and inhospitable terrain in the archipelago that inhibited tortoise hunters in whatever guise from locating all individuals. The conservation program has already improved the status and reproduction of several populations, leaving only the Pinta race, represented by a single individual, on the brink of extinction (Reeder and MacFarland 1978, Reynolds 1982).

The tortoise races can be divided into two major morphological types, the first with a dome-shaped carapace, and the second having the anterior end of the carapace raised, resembling old Spanish saddles. Captain Porter (1822) of the U. S. Frigate Essex was the first to note the morphological differences among tortoises from different islands. This difference was pointed out to Darwin by the Vice-Governor of the islands in 1835 (Darwin 1860). A key to the different tortoise races was developed by Van Denburgh (1914), but it was not until the 1960s that this difference

in morphology was related to environmental conditions, the domed shape being more characteristic of tortoises from the higher, more humid islands, and the saddle-backed shape characteristic of tortoises from the smaller, more arid islands (Snow 1964). The domed shape is considered to be the ancestral shape with the saddle-backed shape having evolved on the more arid islands (Pritchard 1979a). Examining the genetic differences among seven of the extant races of tortoises, Marlow and Patton (1981) found that genetic similarity, extremely high in all cases, was unrelated to carapace shape. They suggested that the saddle-backed morphology was independently derived several times on separate islands.

The dome-shaped tortoises are very large, with males often weighing 250-300 kg. The low anterior end of the carapace, the smoother shell, and the shorter legs allow easier passage through the sometimes dense vegetation of the higher, humid islands (Pritchard 1979a).

Saddle-backed tortoises are smaller, with males generally weighing less than 100 kg. In addition to the elevated carapace above the neck producing the saddle shape, the carapace is often strongly flared above the hind feet. These tortoises have longer, thinner limbs, and their neck, if not longer than dome-shaped tortoises, appears so because the entire neck can be raised vertically due to the saddle-fronted shells (Pritchard 1979a). The combination of longer legs and the totally vertical reach of the neck allows

saddle-backed tortoises to reach to a much greater height than can dome-shaped tortoises.

Increased vertical feeding range has been the principal explanation for the evolution of the saddle-backed trait. Snow (1966) suggested that the increased vertical feeding range of the saddle-backed tortoises would be particularly advantageous on arid islands where tortoises must feed primarily by browsing on shrubs and from cactus pads that droop down from the tall cactus trunks; whereas, on the more humid islands, tortoises feed primarily on low growing herbaceous plants. In addition to the hypothesis that the evolution of the saddle-backed trait was in response to food limitations, Pritchard (1979a) suggested that it may also assist tortoises in traversing the extremely rugged terrain of the lower islands and improve their ability for thermoregulation (Pritchard 1979a).

Schafer and Krekorian (1983), however, suggested that success in agonistic interactions requiring tortoises to raise their heads as high as possible was more important than the increase in vertical feeding range in the evolution of the saddle-backed trait, basing this in part on the idea that all tortoises in the Galápagos feed primarily on grasses. They suggested that on arid islands there may have been more competition for food resources than on humid islands, strengthening selection for those traits that would allow tortoises to win agonistic interactions, thus causing the evolution of the saddle-backed morphology. Fritts (1983,

1984) reviewed the two major hypotheses for the evolution of the saddle-backed trait, that involving an increase in the vertical feeding range, and secondly, the improved success in agonistic interactions, and noted that no one had yet measured food availability or diet for these different morphological types to determine if the suppositions of the hypotheses were valid.

In this study, the race of dome-shaped tortoises on Santa Cruz (Geochelone elephantopus porteri), and the race of saddle-backed tortoises on Pinzón (G. elephantopus ephippium) were examined in their natural setting in an attempt to document whether there are major behavioral differences, and whether any differences noted would support the above hypotheses for the evolution of the saddle-backed morphology. Carlquist (1974) noted that although Galápagos tortoises from different islands have been separated into subspecies, the subspecies do not appear to differ in ecology, except in terms of what foods and habitats are actually available to them on the different islands. However, the amount of field work on the ecology of these tortoises is limited, especially in terms of quantifying food availability on the different islands and in different seasons, a major factor underlying both of the above hypotheses. Results from this study should enhance the understanding of these different morphologies, and of the evolution of the saddle-backed trait.

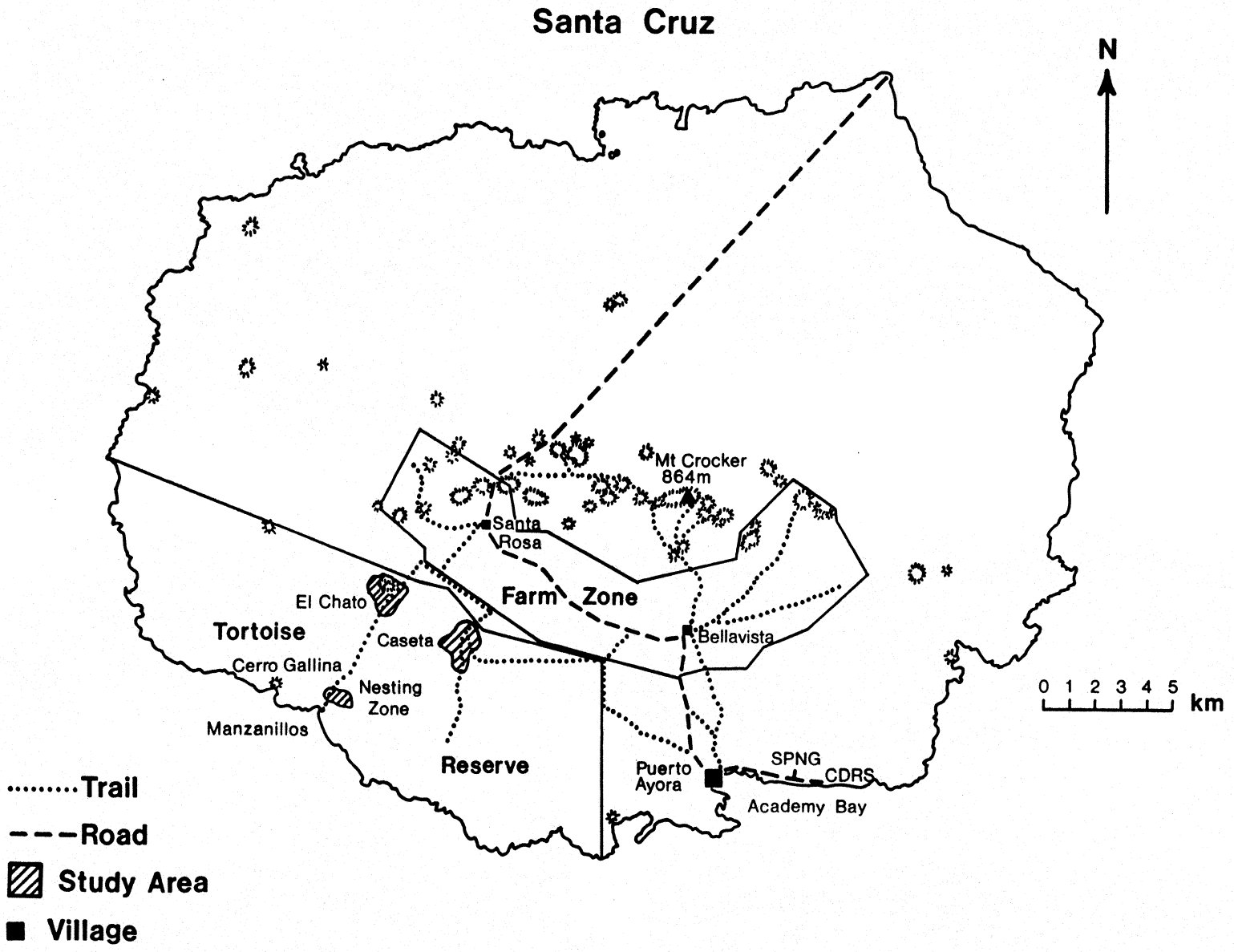
CHAPTER TWO - METHODS

STUDY AREAS

Selection of study areas was based on distributions of tortoises inhabiting the sites as well as environmental characteristics of the areas themselves. All of the tortoise populations that have remained relatively large and reproductively successful in the Galápagos Islands are composed of dome-shaped tortoises. Therefore, a population of dome-shaped tortoises was chosen for the continuous two-year study. An area with few introduced mammalian herbivores in potential competition with tortoises and few introduced plants was preferred. The logistics of doing research inland in the Galápagos Islands are difficult at best, so the accessibility of the area was also important. The Tortoise Reserve on Santa Cruz was selected for the continuous two-year study as it adequately fulfilled the ecological requirements and was by far the most accessible area.

Three study areas were selected for use on Santa Cruz. Two permanent sites, La Caseta and El Chato, were established in the highlands of the Tortoise Reserve in June 1981, in the main living area of adult tortoises (Fig. 2.1). Research was conducted in these areas continuously from June 1981 to June 1983. However, at the onset of El Niño (December 1982), the majority of tortoises inhabiting the farmlands and the upper regions of the Tortoise Reserve began a mass migration to lower elevations (Cayot 1985). In order

Fig. 2.1. Santa Cruz Island. Location of study areas at La Caseta, El Chato, and one of the Santa Cruz nesting zones. (After map prepared by CDRS 1972).


Santa Cruz
N
Mt Crocker
864m
Santa
Rosa
Farm Zone
El Chato
Tortoise
Caseta
Bellavista
Cerro Gallina
Nesting
Zone
Manzanillos
Reserve
Puerto
Ayora
SPNG
CDRS
Academy Bay
0 1 2 3 4 5
km
Trail
Road
Study Area
Village

to continue monitoring the adult population, a new study area was established in one of the traditional nesting zones for the duration of El Niño (Fig. 2.1). This area was visited for 3-week periods in February/March, April, and July 1983.

The population of saddle-backed tortoises on Pinzón was chosen for short-term studies for comparison purposes (Fig. 2.2). The population on Pinzón is the only substantial population of saddle-backed tortoises in the islands today, other than a little-known population on the lower slopes of Volcán Wolf, the northernmost volcano on Isabela. Pinzón was visited for 3-week periods in April/May and December 1982, and for 1 week in June 1983.

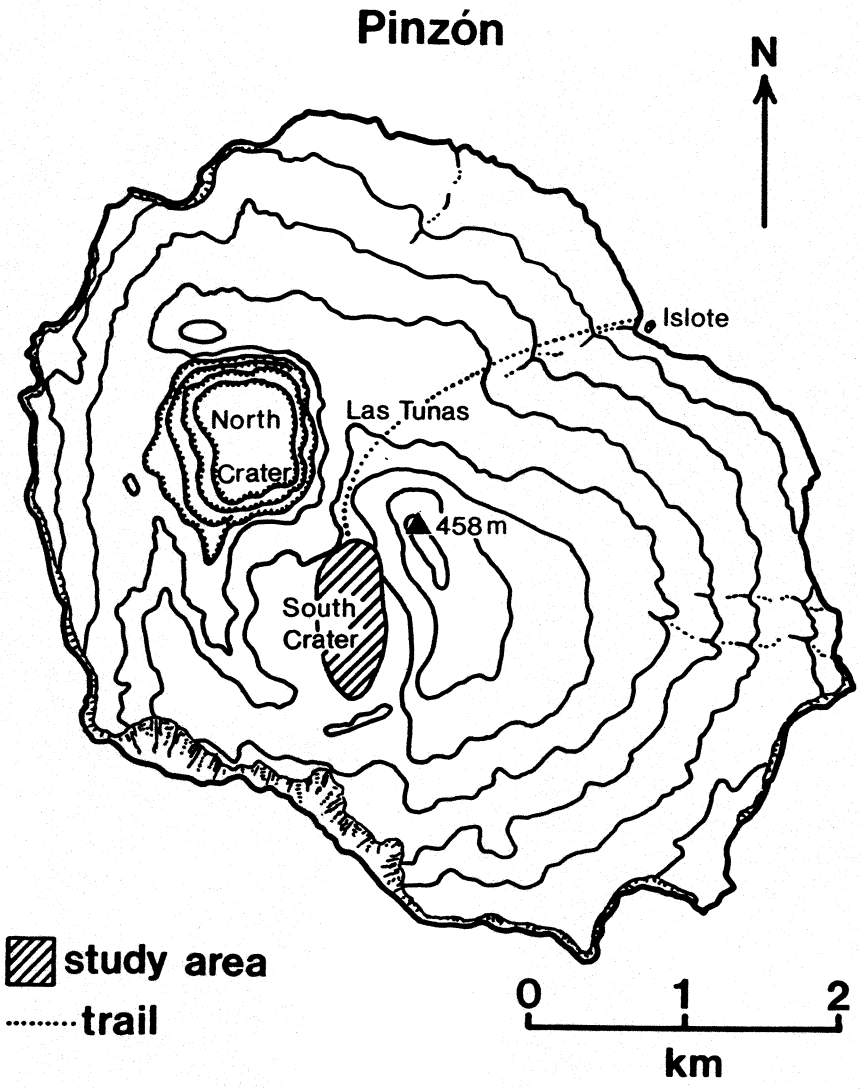
After the initial core areas were established, regions surrounding them were occasionally explored. If several tortoises were located in a new section, it was added to the study area for the duration of the project.

VEGETATION

Cover

A set of vegetation transects used to measure percent cover of food items was completed every two months at La Caseta and El Chato, in April and July 1983, at the Santa Cruz Nesting Zone (SCNZ), and in May and December 1982, on Pinzón. Fifty-meter, parallel transects were laid 25 m on either side of and approximately perpendicular to the major trail in the regions of greatest tortoise activity in each

Fig. 2.2. Pinzón. Study area located in the South Crater. (After map prepared by CDRS 1972).


Pinzón
N
Islote
North
Crater
Las Tunas
458 m
South
Crater
study area
trail
0
1
2
km

study area. Quadrats (1 m^2 , 6/transect) were placed 10 m apart, as were adjacent transects. Percent cover by food item was estimated for those plants below the maximum foraging height of tortoises. In most cases, each food item represented a separate species; however, some species were separated by plant part (eg., fruit and leaves) or by age of plant (eg., cotyledons and leaves). Rather than use complete canopy coverage as described by Daubenmire (1959), only that portion of the plant potentially edible by tortoises, based on feeding observations of tortoises in the wild, was included. Two hundred quadrats were sampled for each set of transects. If a quadrat was in a location that was too rocky or too dense to permit access by tortoises, it was eliminated and another quadrat was added at the end. Eight cover classes were used (I = 0-1%, II = 1-5%, III = 5-15%, IV = 15-25%, V = 25-50%, VI = 50-75%, VII = 75-95%, VIII = 95-100%). Using the mid-point of these eight classes, the average percent cover per m^2 of each potential food item was calculated. In addition, percent cover estimates were made for rock (all rock regardless of plant cover), litter, non-food regions (area not covered by available food), and water.

Harvest Plots

Biomass data provide more accurate information on the relative importance of species in a community than does cover (Humphrey 1985). Although cover can be used as a suitable index to herbage production by species (Payne 1974),

and due to the ease and speed of measuring cover it is often used in food selection studies of herbivores, cover becomes a less reliable estimator of forage availability as the diversity of food types increases, as in the case of giant tortoises. Cook et al. (1948), Anderson and Kothman (1982), and Humphrey (1985) developed methods to combine biomass and cover estimates to determine standing crop for western rangelands. The technique developed for this study combines cover measurements with harvest samples termed "5% plots" to estimate available biomass for all potential food items.

Harvest plots of each food item were used to calibrate cover data from the vegetation transects. A quadrat (20x25 cm), equal to 5% of 1 m^2, was placed over an area where a single food item filled the plot. The edible portion of the food item in the plot that was within the foraging reach of tortoises was harvested. For those food items that never occurred at densities equal to 5%, the edible portions were collected and placed in a 5% plot in a manner similar to their usual growth pattern until the entire plot was covered.

At La Caseta and El Chato, 5% plots were harvested during the initial four months of the study while the technique was being developed, then again in March, July, and October 1982, and February and May 1983. Harvest plots were collected concurrently with each set of vegetation transects at SCNZ and on Pinzón. Generally, two plots of each food item were collected per sampling period at La Caseta and El Cha-

to, and three plots at SCNZ and on Pinzón. Plant samples were air dried in the field when possible, transported to the Charles Darwin Research Station (CDRS) (maximum delay = 2 weeks), oven dried at 60°C to a constant dry weight, then weighed to the nearest 0.1 g.

To determine the effect of food item, location, and month on the biomass of the 5% plots at La Caseta and El Chato, only the 36 food items that had been collected in all time periods were included in the analysis. Of the 34 additional food items collected at least once, only moss and Hippomane mancinella fruit ever equaled greater than 4% of the total available biomass in either study area by season. An analysis of variance including food item, location, and their subsequent interaction, showed that only food item was significant ($F_{35,755}$ = 6606.3, $P < .0001$, R^2 = 0.64). Due to the lack of significance of the location term, the results of the 5% plots from La Caseta and El Chato were combined. The analysis of variance, using the same 36 food items and five collection periods (the two El Niño periods were combined) showed that food item, month, and the food item-month interaction were all significant (Table 2.1).

The other two study areas had similar results. For the nesting zone, only 16 food items were collected in both time periods. Again, food item, month, and the food item-month interaction were significant, with food item the most significant factor (Table 2.1). On Pinzón, 21 food items were collected during both time periods. The analysis of vari-

Table 2.1. ANOVA results of the effect of food item, month of collection, and their interaction on the 5% plot data (weight in grams, by food item) from all study areas. Data from La Caseta and El Chato have been combined (see text for explanation). F values based on Type III sums of squares. Results list F values at P <.05*, .01**, .0001****. Model R^2 equals 0.82, 0.67, and 0.92 for Caseta/Chato, Santa Cruz Nesting Zone (SCNZ), and Pinzón, respectively.

	CASETA/CHATO		SCNZ		PINZÓN	
SOURCE	df	F value	df	F value	df	F value
MODEL	179	16.3****	15	4.2****	41	24.5****
FOOD ITEM (FI)	35	64.6****	15	6.6****	20	47.7****
MONTH (M)	4	26.6****	1	5.6*	1	7.4*
FI x M	140	3.9****	15	1.8[a]	20	2.1**
ERROR	647		64		82	

[a] P <.06.

ance showed that food item, month, and the food item-month interaction were all significant, with food item again the most significant factor (Table 2.1).

For all study areas, the highly significant effect of food item on the biomass measurements resulting from the 5% plot samples indicates that these harvest plots are a good measure of relative biomass of different food items. The biomass data were thus incorporated into the cover data to increase the precision of the availability estimates. For each time period, average dry weight for food items when covering 5% of 1 m^2 was calculated, then converted to g/1% cover. Combining the transect data (% cover/m^2) with the biomass data (g/1% cover) resulted in an estimate of the dry weight of each food item per m^2 potentially available as food for tortoises.

Water, Nitrogen, and Carbohydrate Analyses

During the first year of the study, in addition to 5% harvest plots, samples of food items were collected monthly at La Caseta and El Chato for the determination of their water content. Plant samples were handled and processed as described above. Percent water was calculated. Similar samples were collected at SCNZ during February/March 1983. Otherwise, at SCNZ and on Pinzón, and during the second year of the study at La Caseta and El Chato, the 5% harvest plots were weighed in the field and used for the determination of water content of food items. Results of water content for food items from La Caseta and El Chato were combined.

Water content of the total available food was calculated by combining percent water by food item with percent total available biomass by food item. Moss, nearly 100% avoided by tortoises and having a water content that varied with daily weather conditions, was excluded from the calculations. Alternanthera filifolia, Maytenus octogona, and Prosopis juliflora were excluded from the data on Pinzón, due to the strong avoidance of these plants by tortoises. For those items with no water content measurements available in a given time period, measurements from the month most similar in amount of rainfall were used. The rarer species that were never harvested were given the average water content of the one to several species most similar to them morphologically.

Nitrogen analyses of plant tissues were completed at Syracuse University. Percent nitrogen was determined by the Kjeldahl method. Between 2 to 6 samples per food item were analysed for each time period. For La Caseta and El Chato, months for nitrogen analyses were selected based on seasonal changes in rainfall and composition of the tortoise diet. Samples were analysed from collections in July and September 1981, February, April, and October 1982, and January/February 1983. Results from the two study areas were combined. Percent nitrogen was analysed for SCNZ samples from April and July 1983. Plant tissues from Pinzón were analysed for the three visits in April/May and December 1982, and June 1983.

Percent total non-structural carbohydrates (%TNC) was determined for food items from Pinzón using a modified Dale Smith method (Smith 1969). Due to the lack of interesting results, %TNC was not analysed for plant samples from any other area.

Species Verification

Plant specimens for species verification were collected in all study areas. All species were collected with flowers and seeds if possible. The majority of verifications were done at the herbarium of CDRS on Santa Cruz, with the help of Dr. Ole Hamann. Verification of species not in the CDRS collection was completed at the herbarium of the California Academy of Sciences in San Francisco.

HABITAT TYPES

General descriptions of habitat types, defined mainly by dominant plant species, were made for each study area. Specific characteristics of the major habitat types were determined from the results of the vegetation transects. From January 1982 on, habitat types were recorded for each quadrat of the vegetation transects. For each set of transects, data from all quadrats of a single habitat type were combined to determine average availability of food items (biomass), as well as average percent cover by rock, litter, water, and non-food areas in that habitat. Data from La Caseta and El Chato were combined. Due to the seasonal con-

centration of tortoises at ponds, additional vegetation transects were completed bi-monthly in the large pond at La Caseta and in one of the large ponds at El Chato. Methods were similar to the regular vegetation transects, except that parallel transects were laid across each pond and were placed only 5 m apart, as were quadrats.

Composition of each study area by habitat type was determined using two methods. Percentage of quadrats in the vegetation transects for each habitat type gave an estimate of the breakdown of habitat types within the key tortoise areas. General landscape patterns of study areas were determined from vegetation maps. Trail systems were initially mapped using a combination of pacing and compass. Habitat types were then mapped onto the trail systems, again using pacing and compass. Final maps were made at the end of El Niño which allowed mapping of ponds and river systems which were usually dry. Maps were cut into separate habitat types. Total area in each habitat type at SCNZ and Pinzón was determined by use of a leaf area meter. In addition, the habitat pieces were weighed. A highly significant regression of area (cm^2) on weight (g) resulted from these data ($F_{1,38} = 699,095.7$, $P < .0001$, $R^2 = 1.0$). The resulting equation was used for determining area in each habitat type at La Caseta and El Chato from their weight data because many of the sections of habitat in these two study areas were too small for accurate estimates from the leaf area meter. Total area, as well as percent of the entire study area, by habitat type were determined for all sites.

TORTOISES

Both instantaneous observations of tortoises and continuous monitoring of focal animals were used to determine tortoise behavior (Altmann 1974). A majority of tortoises in all study areas had been previously marked and the number of each marked tortoise was noted when possible. National Park Service personnel have been marking tortoises using a system of notches in the marginal scutes of the carapace since the early 1960's (Snow 1960). However, due to wear and breakage of the marginal scutes, these markings are not always reliable. Questionable marks were noted and an attempt was made to determine which observations were of the same animal based on notes on the notches as well as carapace measurements. Carapace measurements included the curved length and curved width of the carapace, as described by Van Denburgh (1914). Curved length was the most accurate measurement taken in tortoise studies on Aldabra (Gaymer 1968). In a study of 20 morphometric variables from the carapace and plastron of both living tortoises and museum specimens, curved width of the carapace was consistently highly correlated with most variables and was emphasized on the first factor in principal component analyses (Fritts 1983).

Sex was determined for the larger tortoises by secondary sexual characteristics, primarily the size of the tail, the tail of males being much heavier and longer than that of females (Gaymer 1968, Staedeli 1972, MacFarland et al. 1974a). Adult males and females were easily distinguished

in the field. However, the sex of small and often of medium-sized tortoises was impossible to determine. Since the maximum size varies by race, the minimum size at which tortoises can be sexed also differs by race (MacFarland et al. 1974a), with the sex of Pinzón tortoises easily determined at a much smaller size than that of tortoises from Santa Cruz.

Instantaneous Observations

All tortoises encountered were recorded during periods of instantaneous observations. Tortoise number, sex, and carapace measurements were noted when possible. In addition, time, air temperature, habitat type, activity, and miscellaneous comments were recorded for each observation. Temperature was determined at the height of the tortoise. A minimum of 1 hour was maintained between succeeding observations of any one individual. A maximum of 10 observations per hour were allowed in any day. Observations were made between 0530h and 1830h. During the initial months of the study, observation periods were concentrated on hours in which more tortoises were feeding. Beginning in May 1982, a monthly goal of 50 observations per hour was initiated. In addition, a goal of 100 feeding observations per month was initiated in October 1981. In some months, due to an absence of tortoises or a cessation of activity, notably at La Caseta and El Chato during the hot-dry season 1982, and El Niño, these goals were impossible to reach.

Activities of tortoises included resting/sleeping, feeding, traveling, mating, agonistic interactions, and drinking. Resting included transition periods between resting and other activities, when tortoises were adjusting their position, dragging themselves forward, or making forms for sleeping. Observations of males mounted on females or on individuals of unknown sex were included in mating, while observations of males mounted on males were included in agonistic interactions. Drinking included mud-sucking by tortoises in areas where there was no free standing water.

Instantaneous observations of feeding tortoises were used to determine diet. Food items eaten were recorded for each observation. Each observation was given a value of one. If more than one food item was recorded for a single observation, each item was given a corresponding fraction of one. Percent diet by food item was determined monthly. Water content of the diet was calculated by combining percent water by food item with percent diet by food item. Substitute measurements of water content for food items with no water data were made in a manner similar to those made for determination of water content of the availablle food.

Focal Animals

During the first trip to Pinzón in April/May 1982, and subsequently at all study areas, constant monitoring of focal animals for 2-day periods was begun. Each tortoise was observed for two consecutive days for the 12 1/2 hours of daylight, generally from 0545h to 1815h with seasonal

shifts of 15 minutes in either direction. In some cases it was logistically difficult to reach the tortoise before daylight. Likewise, it was occasionally necessary to leave a tortoise prior to nightfall. However, tortoises generally bed down prior to nightfall and arise after sunrise, and most times the tortoises were found settled in a form. To make all day lengths similar, activity times for the unobserved minutes were conjectured from the available information. In the majority of cases it was obvious that the tortoise had not yet arisen (morning) or would remain in its form (evening). Questionable conjectures, when a tortoise was doing something other than resting, occurred in only 9 out of the 60 days of observation on Santa Cruz, and totaled only 1.3% of the total focal animal observation time. On Pinzón, questionable conjectures occurred in 9 out of the 38 days of observation, and constituted only 2.2% of the total focal animal observation time.

Focal animals were selected based on location and sex. An attempt was made to monitor tortoises in all regions of the study areas and to alternate sexes when possible. Tortoises were selected the evening before observation began, after they had settled into a night form. Tortoise number, sex, and carapace measurements were recorded.

During the 2-day period all changes in activity, habitat type, air temperature, and weather, as well as occurrence of defecations and urinations, were recorded. In addition, conditions were noted every half hour regardless of the lack

of obvious changes. Tortoises were observed from a distance and observer interference was minimal. Activities recorded were the same as those used in the instantaneous observations. Food items eaten were noted whenever possible. All occurrences of the finch-tortoise cleaning symbiosis, described by MacFarland and Reeder (1974), were included in resting behavior. Although MacFarland and Reeder noted that finches rarely attempted initiation of the symbiosis with inactive tortoises, of the 31 observations of the symbiosis during monitoring of focal animals on Pinzón, 26 involved tortoises at rest. Total number of minutes in the six activity categories were determined for each day of observation and converted to percents.

Beginning in October 1982, maps of tortoise movements with estimates of distance traveled were compiled throughout the two days of observation, resulting in a sum total of distance traveled per day.

STATISTICS

Standard statistical analyses (Snedecor and Cochran 1973) were used. Most analyses were performed using SAS software (SAS Institute Inc., Cary, North Carolina). All percentages were transformed to arc sine square root (Snedecor and Cochran 1973).

CHAPTER THREE - STUDY AREAS

SANTA CRUZ

The tortoise population on Santa Cruz numbers between 3,000 to 4,000 animals and lives predominantly in the Tortoise Reserve on the lower southwestern slopes of the island. The Reserve, established in 1963, encompasses 166 sq km, with an altitudinal range from sea level to approximately 200 m. Reeder and Riechert (1975) described the vegetational changes along this altitudinal gradient. Altitude, associated with changes in temperature and precipitation, and the percentage of ground covered by lava, related to the development of soil and the water carrying capacity of the ground, are the two main environmental factors affecting the formation of the vegetation and the resulting environmental complexity of the region (Itow 1965). The area encompasses parts of four vegetation zones as described by Wiggins and Porter (1971). The Littoral Zone, a narrow strip of vegetation along the coast, is essentially unused by tortoises. Immediately inland from the Littoral Zone and extending upward to an elevation of 80-120 m is the Arid Zone. Above the Arid Zone is the Transition Zone, ranging from about 80-180 or 200 m where it runs into the Scalesia Zone. The area encompassing the continuum between the Arid Zone and the Transition Zone contains the tortoise nesting zones. The upper edge of the Transition Zone and the lower-most Scalesia Zone encompass

the main living areas of the great majority of adult and subadult tortoises (Reeder and MacFarland 1978). The upper borders of the Reserve are adjacent to farmland. During this study, the tortoises moved up into the farmlands in large numbers when the lower areas became extremely dry.

The tortoise population on Santa Cruz contains moderately large numbers of small and medium-sized animals, as well as a large adult population, including an estimated 300-450 females sufficiently large for nesting (MacFarland et al. 1974a). Over 2200 tortoises have been marked by Galápagos National Park Service (SPNG) personnel as part of a marking program begun in 1962. Successful reproduction in this population has increased in recent years due to conservation efforts by SPNG.

Uplands: La Caseta and El Chato

Two permanent study areas, La Caseta and El Chato, were established in June 1981, in the main living area of adult tortoises. Both of these areas, at the upper edge of the Tortoise Reserve at an elevation of approximately 160-200 m, encompass the upper-most Transition Zone and the lower-most Scalesia Zone. Some tortoises remain in these areas throughout the year, although between June and December many of the larger females migrate to the lowlands to nest (Reeder and MacFarland 1978).

Many authors have suggested that tortoises migrate up and down the volcanos of Galápagos in response to environmental conditions (Darwin 1860, Heller 1903, Van Denburgh

1914, Townsend 1925, Snow 1964, Carpenter 1966, Rodhouse et al. 1975, Reeder and MacFarland 1978, Enriquez 1982, Fritts and Fritts 1982, Fowler 1983). Several of these indicated that tortoises remain in the lowlands when there is available water and food, and then migrate to the uplands when the lower regions become dry (Heller 1903, Van Denburgh 1914, Townsend 1925, Rodhouse et al. 1975, Fowler 1983). Perry (1964) observed tortoises moving more and more upward into the farmlands, and suggested that this was due to the dryness of recent years. However, Carpenter (1966) and Reeder and MacFarland (1978) indicated that when conditions became extremely dry tortoises moved to the lowlands where they were able to feed on cactus. Both types of migrations may occur.

During the period from June 1981 to January 1983, both sexes of tortoises were found using the upland study areas in all months (Table 3.1), although there was a noticeable movement of animals into the farmlands when conditions became dry. The consistent majority of males in both study areas is likely a result of the greater exploitation of females during the previous two centuries, due to their smaller size and their seasonal use of areas close to the coast for nesting (Townsend 1925), leaving the populations skewed toward males. At the onset of El Niño rains in December 1982, tortoises in the uplands began a mass migration to lower elevations (Cayot 1985). Although few tortoises remained in either study area, vegetation measure-

Table 3.1. Estimated number of different tortoises (TOTAL) at La Caseta and El Chato. Estimates are based on a compilation of observations of marked tortoises (marked numbers were often difficult to distinguish) and of unmarked tortoises that were separated by sex and carapace measurements. Number of observations (OBS) when tortoise markings were recorded is given.

	LA CASETA					EL CHATO				
			SEX					SEX		
MONTH	OBS	TOTAL	M	F	?	OBS	TOTAL	M	F	?
Jun81	126	66	45	7	14	60	35	23	6	6
Jul81	21	19	13	1	5	47	34	23	6	5
Aug81	35	23	12	3	8	23	19	12	5	2
Sep81	99	46	19	15	12	74	43	19	14	10
Oct81	110	37	14	12	11	90	47	18	24	5
Nov81	79	42	16	11	15	63	41	23	11	7
Dec81	258	85	47	15	23	254	70	37	20	13
Jan82	192	92	56	15	21	220	76	55	10	11
Feb82	125	62	36	10	16	70	42	30	8	4
Mar82	246	115	76	19	20	164	74	46	21	7
Apr82	151	79	62	7	10	83	32	19	8	5
May82	347	73	55	6	12	72	34	29	2	3
Jun82	533	115	84	12	19	136	57	47	5	5
Jul82	241	50	26	6	18	365	92	57	20	15
Aug82	349	63	33	13	17	248	71	34	23	14
Sep82	254	37	18	5	14	414	45	25	13	7
Oct82	236	40	16	9	15	415	63	35	17	11
Nov82	285	47	21	11	15	367	50	30	14	6
Dec82	150	29	25	1	3	75	22	18	3	1
Jan83	137	25	23	2	0	96	26	20	6	0

ments and tortoise searches were continued throughout El Nino.

Laruelle (1966) described an altitudinal zonation of soils along the south-central slope of Santa Cruz. La Caseta and El Chato fall at the break between his zones 2 and 3. The most common soil type of the second zone, from 100-180 m, is a brown-colored soil with an AC profile resulting primarily from weathering of the basaltic parent rock. The depth of the profile rarely exceeds 70 cm. In the third zone, associated with the Scalesia forest, the basaltic rock still occurs at a depth of less than 1 m. The increase in pyroclastic deposits at higher elevations (mostly ashes) with alteration products of the basaltic parent rock produces a soil type, sol brun or sol brun lessive, with an A(B)C or an ABC profile.

Both study areas were long and narrow with a mixture of habitat types (Figs. 3.1, 3.2). A total of 124 plant species was encountered at La Caseta and El Chato during the period from June 1981 to June 1983 (Table 3.2). A majority of these species was found at both study sites. The three most common tree species were Psidium galapageium, Zanthoxylum fagara, and Hippomane mancinella. Habitat type maps, completed at the end of El Niño 1983, also indicate the major drainages (Figs. 3.1, 3.2). Both study areas, initially set up in regions where tortoises tend to concentrate, followed exactly along the river drainages.

Fig. 3.1. La Caseta. Habitat type map of the study area. Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, OF - Open Forb, GL - Grazing Lawn, SCPT - Scleria Stand, SCAL - Scalesia Stand, and DWH I/WH I - Dry Water Hole/Water Hole (type I). Habitat types were interspersed in areas where habitat patterns and/or letters are combined. Rivers and flood ponds occurred only during El Niño. Trails are indicated only where they exit the study area.

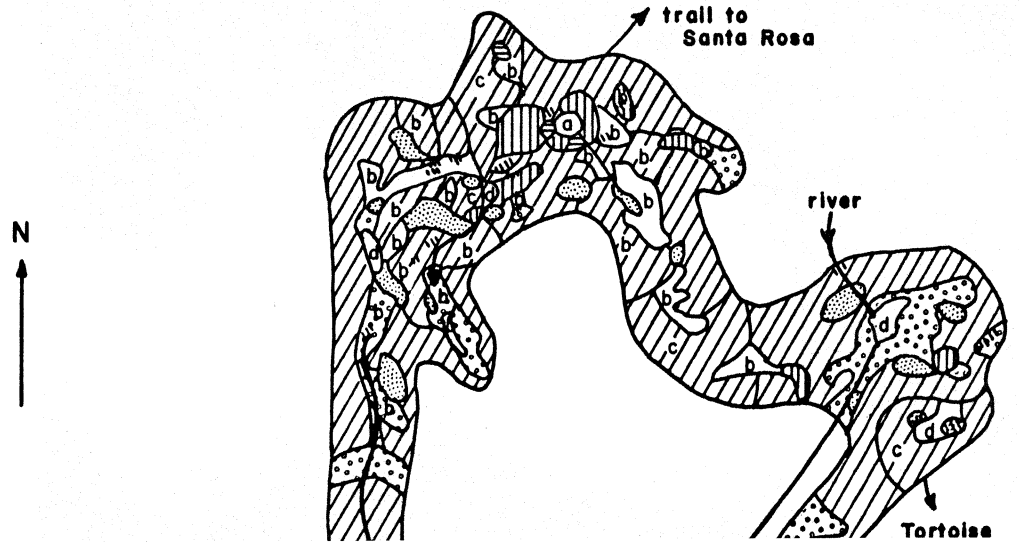

N
trail to
Santa Rosa
river
Tortoise

Fig. 3.2. El Chato. Habitat type map of the study area. Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, OF - Open Forb, GL - Grazing Lawn, SCPT - Scleria Stand, SCAL - Scalesia Stand, and DWH I/WH I - Dry Water Hole/Water Hole (type I). Habitat types were interspersed in areas where habitat patterns and/or letters are combined. Rivers and flood ponds occurred only during El Niño. Trails are indicated only where they exit the study area. Cerro Chato is a large hill dominating the area.

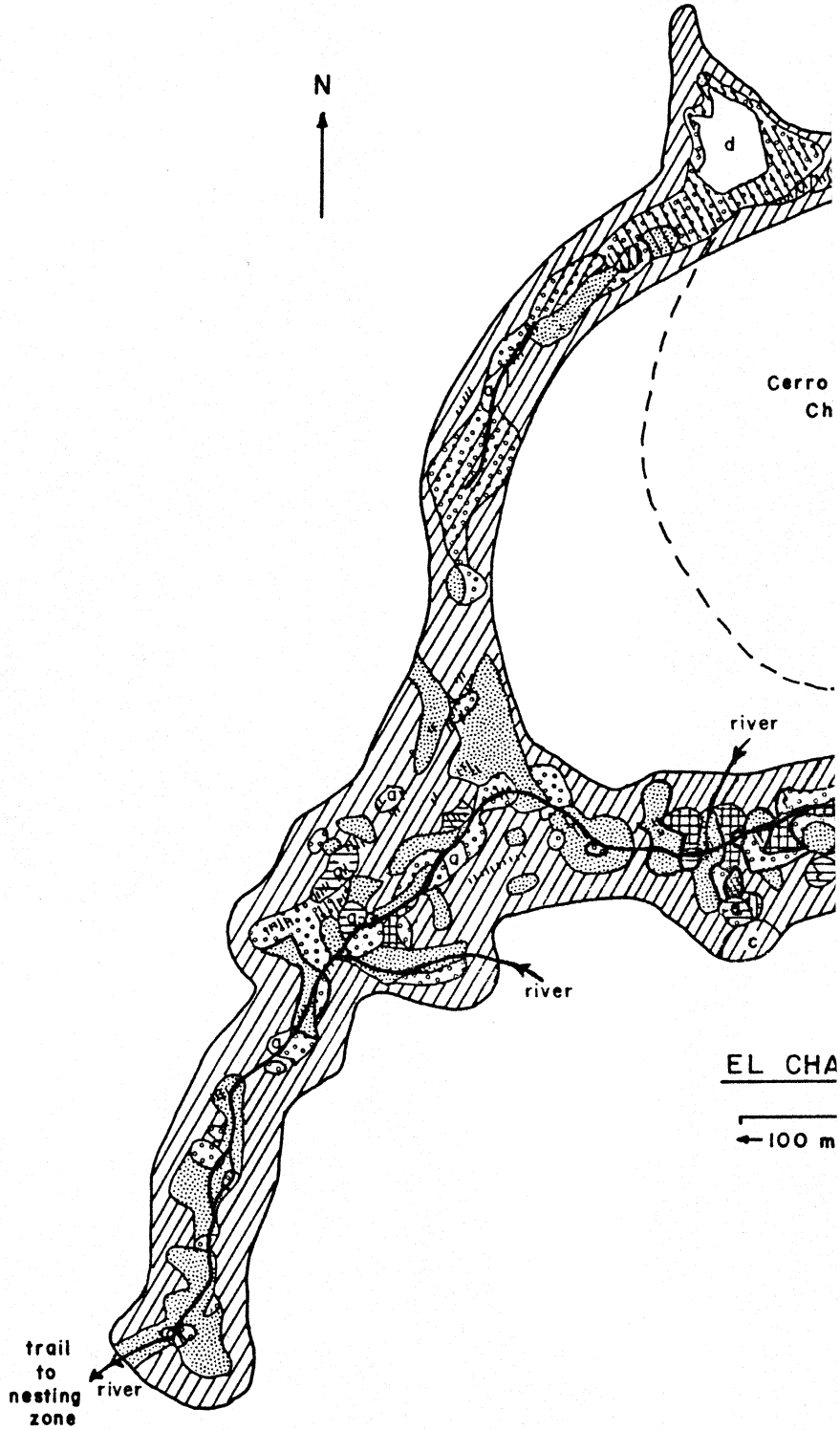

N
d
Cerro
Ch
river
river
c
EL CHA
100 m
trail
to
nesting
zone
river

Table 3.2. Plant species encountered at La Caseta and/or El Chato from June 1981 to June 1983. Plant types include trees (T), shrubs (S), forbs (F), grasses and sedges (G), ferns (FE), and other (O). Status includes endemic (E), indigenous (I), and introduced (INT). Species names, types, and status are from Wiggins and Porter (1971) unless otherwise noted.

FAMILY SPECIES	TYPE	STATUS
Acanthaceae		
Blechum brownei	F	I
Justicia galapagana	F	E
Amaranthaceae		
Alternanthera echinocephela	S	I
A. halimifolia	F	I
Amaranthus lividus	F	INT
Azollaceae		
Azolla microphylla	FE	I
Balanophoraceae		
Ombrophytum peruvianum	O	I[a]
Basellaceae		
Anredera ramosa	F	I
Boraginaceae		
Heliotropium indicum	F	I
Tournefortia psilostachya	S	I
T. rufo-sericea	S	E
Bromeliaceae		
Tillandsia insularis	O	E
Caryophyllaceae		
Drymaria cordata	F	I
Characeae		
Chara sp.	O	I[b]
Commelinaceae		
Commelina diffusa	F	I

Table 3.2 continued.

FAMILY SPECIES	TYPE	STATUS
Compositae		
Ageratum conyzoides	F	I[c]
Bidens pilosa	F	I[c]
Eclipta alba	F	I
Enydra maritima	F	I
Eupatorium pycnocephalum	F	INT[d]
Scalesia pedunculata	T	E
Spilanthes acmella	F	INT[a]
Synedrella nodiflora	F	INT[a]
Convolvulaceae		
Cuscuta sp.	O	E
Dichondra repens	F	I
Ipomoea triloba	F	I
I. spp. (*I. batatus* and/or *I. nil*)	F	INT[a,f]
Stictocardia tiliifolia	F	I[a]
Cucurbitaceae		
Momordica charantia	F	INT[a,e,f,g]
Cyperaceae		
Cyperus brevifolius	G	I
C. confertus	G	I
C. grandifolius	G	E
C. ligularis	G	I
Eleocharis fistulosa	G	I
Eleocharis spp.	G	I
Rhynchospora nervosa	G	I
Scleria pterota	G	I
Euphorbiaceae		
Acalypha sp.	F	E
Croton scouleri	S	E
Hippomane mancinella	T	I
Phyllanthus caroliniensis	F	I

Table 3.2 continued.

FAMILY SPECIES	TYPE	STATUS
Gramineae		
Digitaria horizontalis	G	INT[a]
Eleusine indica	G	INT
Ichnanthus nemorosus	G	I[c,h,i]
Panicum dichotomiflorum	G	I
P. geminatum	G	I
P. laxum	G	I
Paspalum conjugatum	G	I[c]
P. distichum	G	I
Stenotaphrum secundatum	G	I
Hypoxidaceae		
Hypoxis decumbens	F	I
Labiatae		
Hyptis rhomboidea	F	INT[a]
Salvia occidentalis	F	I
Teucrium vesicarium	F	I
Lauraceae		
Persea americana	T	INT
Leguminosae		
Acacia sp.	T	I
Caesalpinia bonduc	S	INT[e,f]
Cassia occidentalis	F	I
C. picta	S	I
Crotalaria incana	F	I
Desmodium canum	F	I[c]
D. limense	F	INT[a]
Galactia striata	F	I
Lablab purpureus	F	INT[a]
Phaseolus mollis	F	E
Piscidia carthagenensis	T	I
Vigna luteola	F	I

Table 3.2 continued.

FAMILY SPECIES	TYPE	STATUS
Lemnaceae		
Lemna aequinoctialis	O	I
Loasaceae		
Sclerothrix fasciculata	F	I
Lycopodiaceae		
Lycopodium dichotomum	O	I
Malvaceae		
Sida hederifolia	F	I
S. rhombifolia	S	I[c,j]
S. spinosa	F	I
Menispermaceae		
Cissampelos pareira	F	I
Myrtaceae		
Psidium galapageium	T	E
P. guajava	S	INT[a,g]
Najadaceae		
Najas guadalupensis	O	I
Nyctaginaceae		
Pisonia floribunda	T	E
Onagraceae		
Ludwigia erecta	F	I
L. leptocarpa	F	I
L. peploides	F	I
Orchidaceae		
Ionopsis utricularioides	O	I
Liparis nervosa	O	I
Oxalidaceae		
Oxalis corniculata	F	I[c]
Passifloraceae		
Passiflora colinvauxii	F	E
P. foetida	F	E
P. incarnata	F	INT[b]

Table 3.2 continued.

FAMILY SPECIES	TYPE	STATUS
Piperaceae		
Peperomia spp.	F	I
Plantaginaceae		
Plantago major	F	INT[a,f,g]
Plumbaginaceae		
Plumbago scandens	F	I
Polygonaceae		
Polygonum opelousanum	F	I
Polypodiaceae		
Adiantum macrophyllum	FE	I
A. villosum	FE	I
A. spp.	FE	I
Asplenium auritum	FE	I
Doryopteris pedata	FE	I
Polypodium dispersum	FE	I
P. insularum	FE	E
P. lanceolatum	FE	I
P. tridens	FE	E
Thelypteris tetragona	FE	E
Trachypteris pinnata	FE	I
Rhamnaceae		
Gouania polygama	F	INT[a]
Rubiaceae		
Borreria laevis	F	I[c,k]
Chiococca alba	S	I
Psychotria rufipes	S	E
Rutaceae		
Citrus spp.	T	INT
Zanthoxylum fagara	S	I

Table 3.2 continued.

FAMILY SPECIES	TYPE	STATUS
Scrophulariaceae		
Capraria biflora	S	I
Mecardonia dianthera	F	I
Solanaceae		
Capsicum frutescens	S	INT[f,g]
C. galapagoense	S	E
Physalis pubescens	F	I
Solanum nodiflorum	F	I[c]
Umbelliferae		
Apium sp.	F	I
Urticaceae		
Fleurya aestuans	F	I
Pilea baurii	F	E
Valerianaceae		
Astrephia chaerophylloides	F	INT[a]
Verbenaceae		
Clerodendrum molle	S	I
Phyla strigulosa	F	I
Priva lappulacea	F	I
Verbena litoralis	F	INT[a]
Viscaceae		
Phoradendron henslovii	O	E
Vitaceae		
Cissus sicyoides	F	I

[a]Status from Porter (1983).

[b]No reference.

[c]Considered introduced to the islands (Porter 1983), but not believed so by author based on observed distributions.

[d]Status from Hamann (1975).

[e]Status from Eckhardt (1972).

[f]Status from Haro (1974).

Table 3.2 continued.

---

[g]Status from Haro (1975).

[h]Status from van der Werff (1978).

[i]Status from Eliasson (1982).

[j]Introduced to Santa Cruz from San Cristóbal (Haro, 1974, 1975).

[k]Status from Colinvaux and Schofield (1976).

Introduced plants at La Caseta and El Chato include trees, shrubs, grasses, and forbs. The choice of whether a species is native or introduced is somewhat subjective (van der Werff 1983). Porter (1979) considered 192 species to be introduced to the islands, while van der Werff (1983) included only 113 species in that category. Based on distributions observed during this study, many of those considered introduced by Porter (1983) have not been included in that group (see footnote a, Table 3.2). Only 17% of the total number of species encountered at La Caseta and El Chato were considered introduced. The only abundant species listed as introduced was a liana, Momordica charantia. Momordica was introduced to Santa Cruz in 1935 (Eckhardt 1972). Stictocardia tiliifolia, another abundant liana, was considered "probably introduced" by Wiggins and Porter (1971); however, Porter (1983) later designated it indigenous. Both species cover much of the indigenous vegetation. Stictocardia became so abundant during the 1982-83 El Niño event that its weight caused damage to some of the indigenous tree species (Cayot 1985). Other introduced species that were not overly abundant but were important to tortoises included members of the Citrus family, mostly lemon and orange and occasionally grapefruit trees (Citrus spp.), and Sida rhombifolia, a shrub in the mallow family. Lemon and orange trees were usually found singly in the midst of the indigenous woodlands. Sida rhombifolia, indigenous to other islands in the Galápagos archipelago, was introduced onto

Santa Cruz from San Cristóbal (Haro 1974). On Santa Cruz, it exhibits the typical distribution of an introduced species, occurring along roadsides and trails, and has begun to make inroads into the Tortoise Reserve. Although the local farmers consider it a pest plant, it is a preferred plant in the tortoise diet, both on Volcán Alcedo where it is indigenous (Fowler 1983) and on Santa Cruz (this study).

Given the large number of plant species that have been introduced in the farmlands in this century, it is perhaps surprising that they have not made greater inroads into the indigenous flora of the Tortoise Reserve. A majority of the introduced species were recorded only at La Caseta, which is close to the farmlands and receives many tourists. El Chato has a larger stretch of forest between it and the farmlands, and thus has fewer roaming cattle (Bos taurus) and horses (Equus caballus), as well as fewer tourists visiting the site. The inability of introduced species to spread into the native flora in the Tortoise Reserve may be partially due to the fact that the indigenous flora of the islands is typically weedy (Porter 1979, 1983, Hamann 1981), and may therefore be somewhat resistant to competition from introduced species.

Introduced mammals seen during this study at La Caseta and El Chato included rats (Rattus rattus), mice (Mus musculus), pigs, cats (Felis catus), burros (Equus asinus), and occasionally cattle or horses that wandered onto the Reserve from the farmlands. Pigs were not abundant, although the

population increased following the heavy rains at the onset of El Niño. Pigs were occasionally hunted by both park guards and local residents. Burros were seldom seen in the area, and then only during extremely dry periods when they moved up from lower elevations. Although goats (Capra hircus) do still occur on Santa Cruz and were once abundant on the Reserve, neither they nor their sign were observed at any time during the study, due to an earlier eradication program by SPNG. In general, introduced mammals on the upper edge of the Tortoise Reserve play a minor role in the lives and habitat of giant tortoises. Hamann (1975), in a study of changes in vegetation, concluded that the vegetation in this region had been little affected by introduced mammals.

Climate at La Caseta and El Chato is as described for mid-elevations on the higher islands. The general pattern of precipitation appears to be that in dry years the rainfall is rather evenly distributed throughout the year, while in extremely wet years, there is very heavy precipitation in the hot season, and some garúa in the cooler season (Hamann 1979). Weather data, collected at La Caseta from August 1981 to May 1983, indicate the seasonal changes experienced during this study (Table 3.3). The latter half of 1981 was a typical garúa season following a late rainy season. Early rains in 1982 were soon followed by drought conditions that continued into June. Sea surface temperatures did not drop substantially in the latter half of 1982, due to the onset

Table 3.3. Precipitation and air temperatures measured at La Caseta[a], unless otherwise indicated. Temperature data reflect only those days in the field. Dates for precipitation measurements given in parentheses.

	TEMP (C^{o})		
MONTH	$\bar{X}$ MIN	$\bar{X}$ MAX	PRECIPITATION (mm) (dates)
Jun81	-	-	2.1[b] (6/1 - 6/30)
Jul81	-	-	4.5[b] (7/1 - 7/26)
Aug81	-	-	26.9 (7/27 - 8/30)
Sep81	-	-	68.8 (8/31 - 9/28)
Oct81	-	-	45.7 (9/29 - 10/18, 10/24 - 10/31)
Nov81	-	-	12.7 (11/1 - 11/30)
Dec81	-	-	67.3 (12/1 - 12/28)
Jan82	20.3	29.9	70.4 (12/29 - 1/30)
Feb82	20.7	35.5	68.3 (1/31 - 2/28)
Mar82	19.9	35.1	28.4 (3/1 - 3/30)
Apr82	19.2	35.3	3.0 (3/31 - 4/18)
May82	18.6	34.3	5.6 (4/19 - 5/31)
Jun82	19.1	30.5	31.8 (6/1 - 6/30)
Jul82	18.6	26.7	96.0 (7/1 - 7/31)
Aug82	18.3	25.3	75.2 (8/1 - 8/31)
Sep82	17.7	26.8	57.2 (9/1 - 9/30)
Oct82	18.4	26.8	34.8 (10/5 - 10/27)
Nov82	19.9	28.7	266.4 (10/28 - 11/26)
Dec82	21.6	29.0	750.3[c] (12/8 - 1/2)
Jan83	21.3	32.4	511.8[c] (1/3 - 1/31)
Feb83	21.1	31.7	417.8[c] 2/1 - 2/28)
Mar83	21.6	32.0	338.1[c] (3/1 - 3/22)
Apr83	22.5	31.5	434.2[b] (4/1 - 4/30)
May83	22.8	29.2	660.2[b] (5/1 - 5/31)
Jun83	-	-	637.5[b] (6/1 - 6/30)

[a]Mean annual rainfall = 990.3 mm (Hamann 1979).

[b]Recorded at the Charles Darwin Research Station; mean annual rainfall = 363.8 mm (Hamann 1979).

[c]Recorded at the Devine farm above La Caseta (at 360 m) (S. Devine, pers. comm.); mean annual rainfall = 1037.2 mm (Hamann 1979).

of El Niño, and temperatures at La Caseta were higher than normal. The 1982-83 El Niño event created flood conditions off and on from December 1982 to July 1983.

During the two-year study, both areas experienced extremes in rainfall and subsequent productivity of the flora. Vegetation transects, run monthly at both study areas from June to October 1981, and bi-monthly after that until May/June 1983, together with the harvest plots (dates of collections indicated in Fig. 3.3), resulted in estimates of the available biomass (Figs. 3.3, 3.4). Productivity of forage is generally dependent on amount of precipitation (Lauenroth 1979, McNaughton 1985a). In arid climates there is a nearly linear relationship between net primary productivity and annual precipitation (Whittaker 1970). The total biomass of available food at both La Caseta and El Chato showed a significant positive relationship to rainfall (Fig. 3.5). Data from El Niño were eliminated from the analysis because a majority of the increase in productivity during that period was vertical and therefore out of reach of tortoises and subsequently not measured in the vegetation transects.

Diversity of the available food can play an important role in determining feeding strategies of giant tortoises. The three indices of diversity examined, calculated bi-monthly from the biomass data, were species richness (S_v), species diversity (H'_v), and species evenness (J_v).

S_v = number of potential food items,

Fig. 3.3. Total biomass of available food and the corresponding rainfall at La Caseta. Accurate rainfall data were not available at La Caseta during El Niño. Measurements at the Devine farm, located just above La Caseta, are given for the months available (S. Devine, pers. comm.). The remaining rainfall data are from the Charles Darwin Research Station (CDRS), located on the southern coast of Santa Cruz. CDRS generally has less rainfall than La Caseta. Collection periods for 5% harvest-plots, described in Chapter 2, are indicated at the top of the graph for both La Caseta and El Chato.

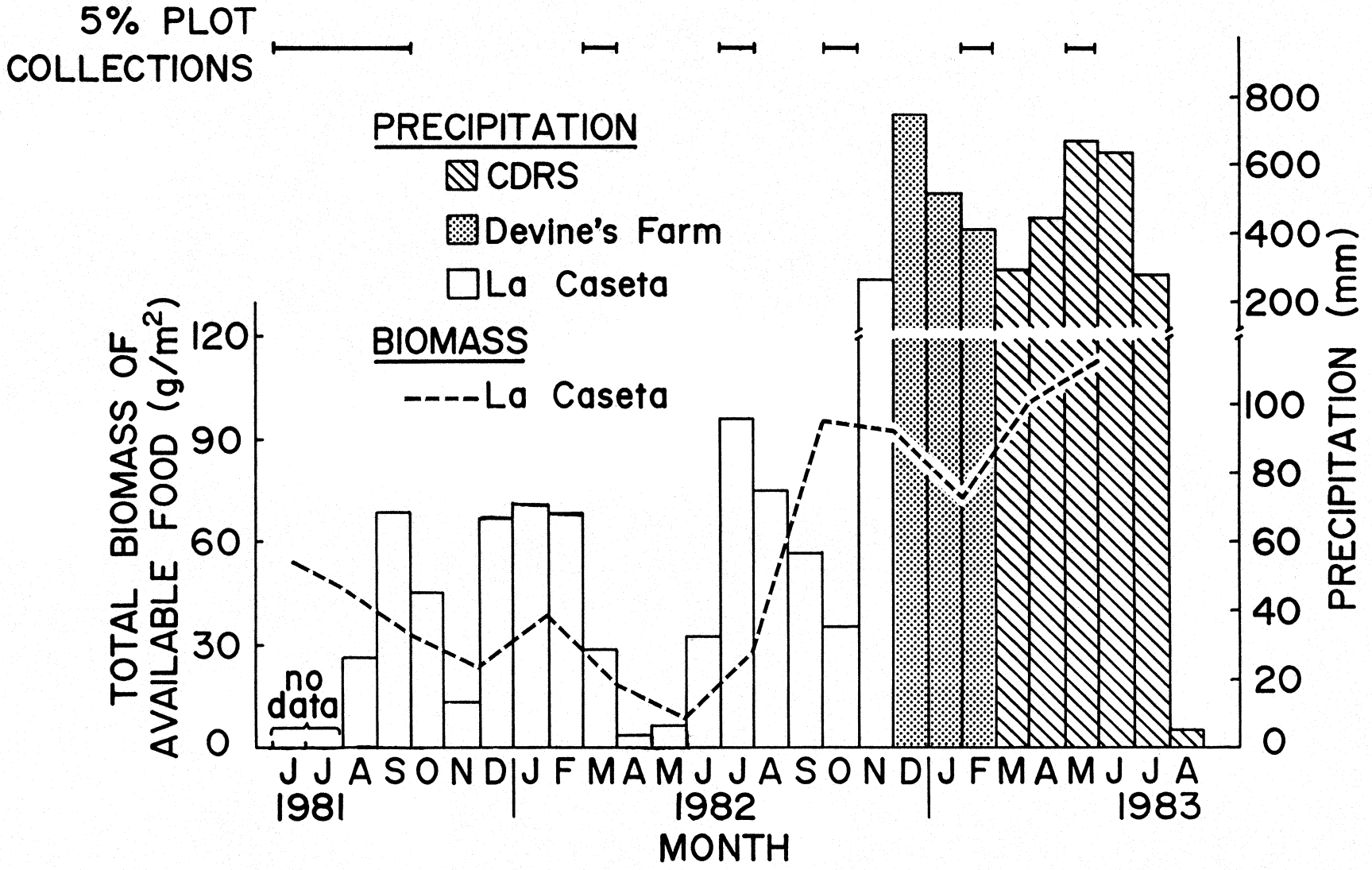

5% PLOT COLLECTIONS
PRECIPITATION
CDRS
Devine's Farm
La Caseta
BIOMASS
----La Caseta
TOTAL BIOMASS OF AVAILABLE FOOD (g/m²)
PRECIPITATION (mm)
no data
J J A S O N D J F M A M J J A S O N D J F M A M J J A
1981
1982
1983
MONTH

Fig. 3.4. Total biomass of available food at El Chato, the Santa Cruz Nesting Zone (SCNZ), and Pinzón. Measurements for Pinzon[a] exclude *Alternanthera filifolia*, *Prosopis juliflora*, and *Maytenus octogona* (see text for explanation).

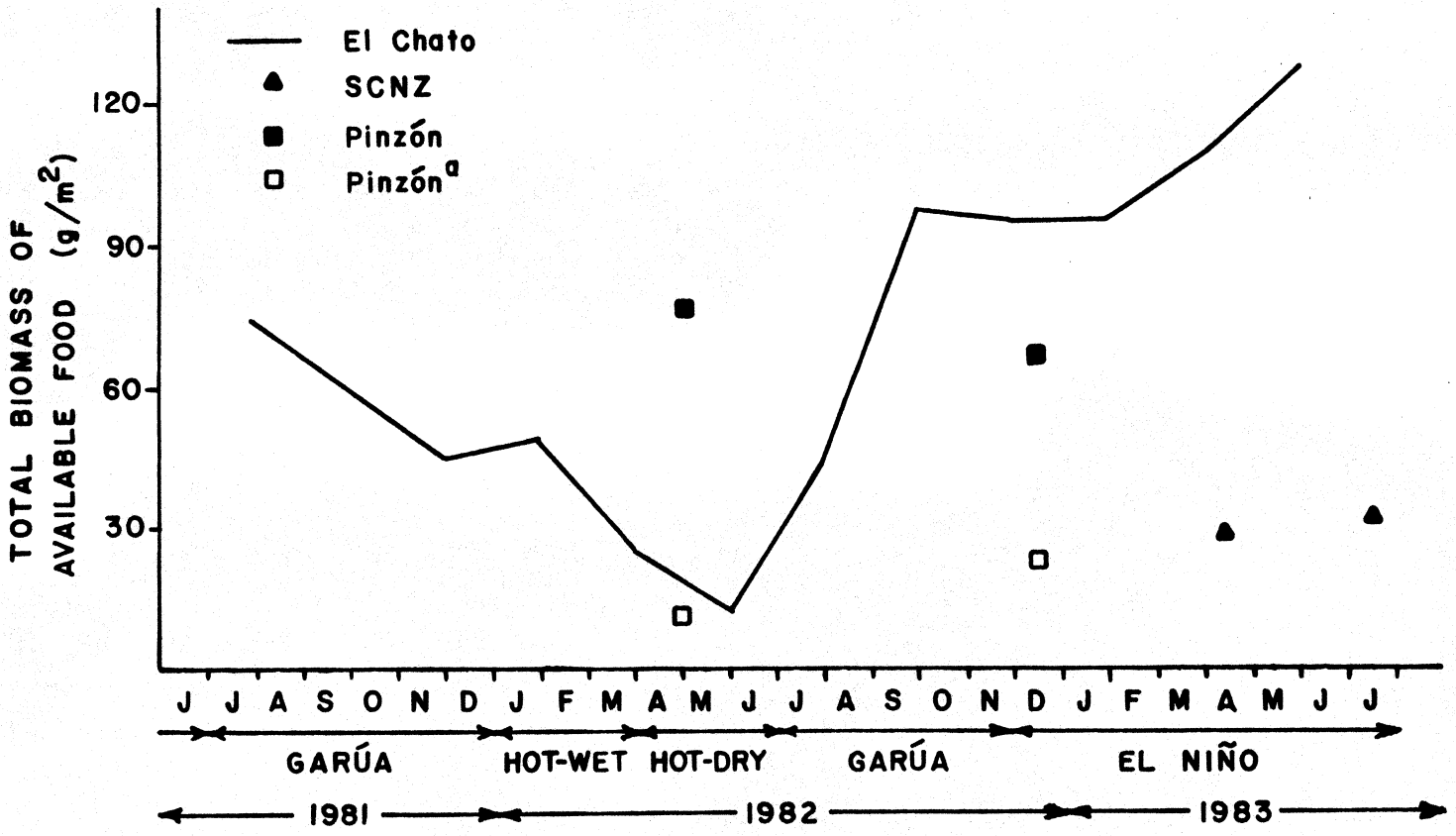
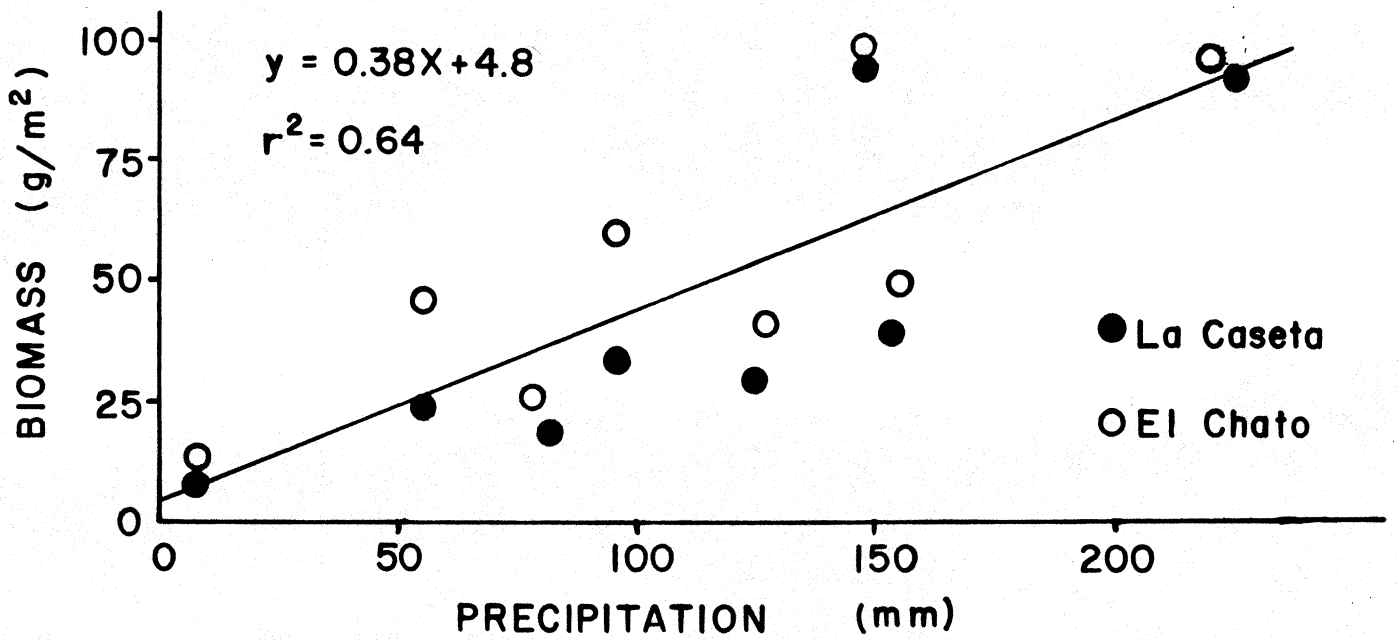

El Chato
SCNZ
Pinzón
Pinzón[a]
TOTAL BIOMASS OF AVAILABLE FOOD (g/m²)
120
90
60
30
J J A S O N D J F M A M J J A S O N D J F M A M J J
GARÚA
HOT-WET
HOT-DRY
GARÚA
EL NIÑO
1981
1982
1983

Fig. 3.5. Relationship between rainfall at La Caseta and total biomass of available food for tortoises at La Caseta and El Chato ($F_{1,14}$ = 24.96, P < .0002). Rainfall data reflect the period of time between sets of vegetation transects (range from 45 to 72 days). Data from El Niño, with its unusually high rainfall, were excluded from the analysis.


y = 0.38X+4.8
r² = 0.64
BIOMASS (g/m²)
100
75
50
25
0
0
50
100
150
200
PRECIPITATION (mm)
La Caseta
El Chato

$H'_V = -\Sigma p_i \ln p_i$, where p_i = proportion of potential food item i in the available biomass,

and $J_V = H'_V / \ln S_V$.

S_V includes all food items encountered in the vegetation transects, not just those that were included in the biomass data.

The large variation in S_V and H'_V over time (Figs. 3.6, 3.7), showed the same general trend exhibited by total biomass over time (Figs. 3.3, 3.4), suggesting that diversity was closely linked to total biomass. Due to the highly significant relationship between total biomass and precipitation, stepwise regressions were run for each index with total biomass and precipitation as the independent variables. Regressions included only the period from September/October 1981, to January/February 1983, when reliable rain data from La Caseta were available. Separate stepwise regressions were run for: 1) the total data set (September 1981-February 1983), and 2) a subset excluding periods with precipitation measurements greater than 250 mm (ie., excluding data from January/February 1983, the first set of vegetation transects following the initial rains of El Nino). Data from both La Caseta and El Chato were used in each regression.

Total available biomass was the major variable related to S_V and H'_V. S_V showed a stronger relationship to total biomass than to precipitation. For both the full data set and the subset excluding El Niño, total biomass was the only

Fig. 3.6. Species richness of the available food (S_v) at La Caseta, El Chato, the Santa Cruz Nesting Zone (SCNZ), and Pinzón over time. Line drawn freehand for data from La Caseta and El Chato.

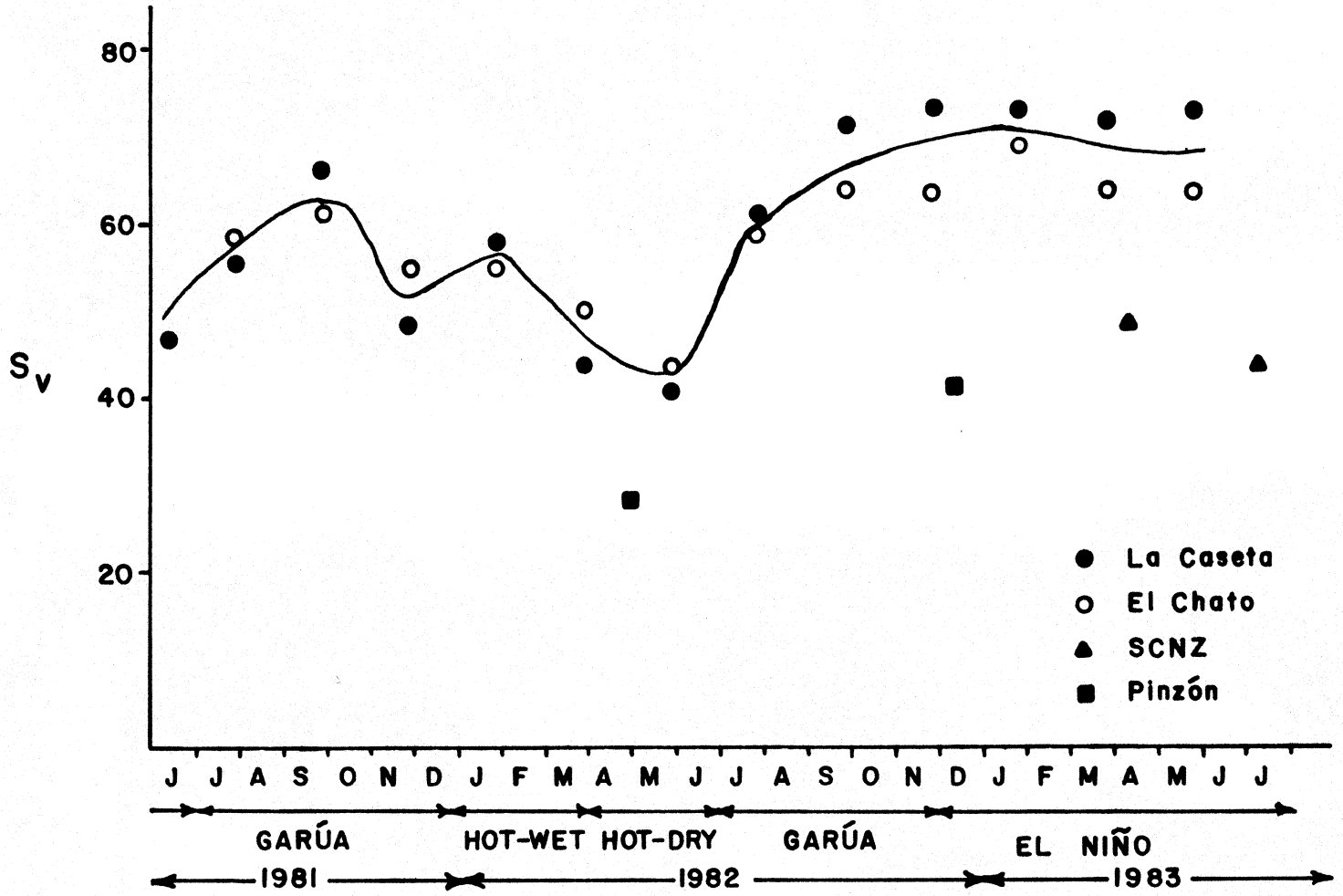
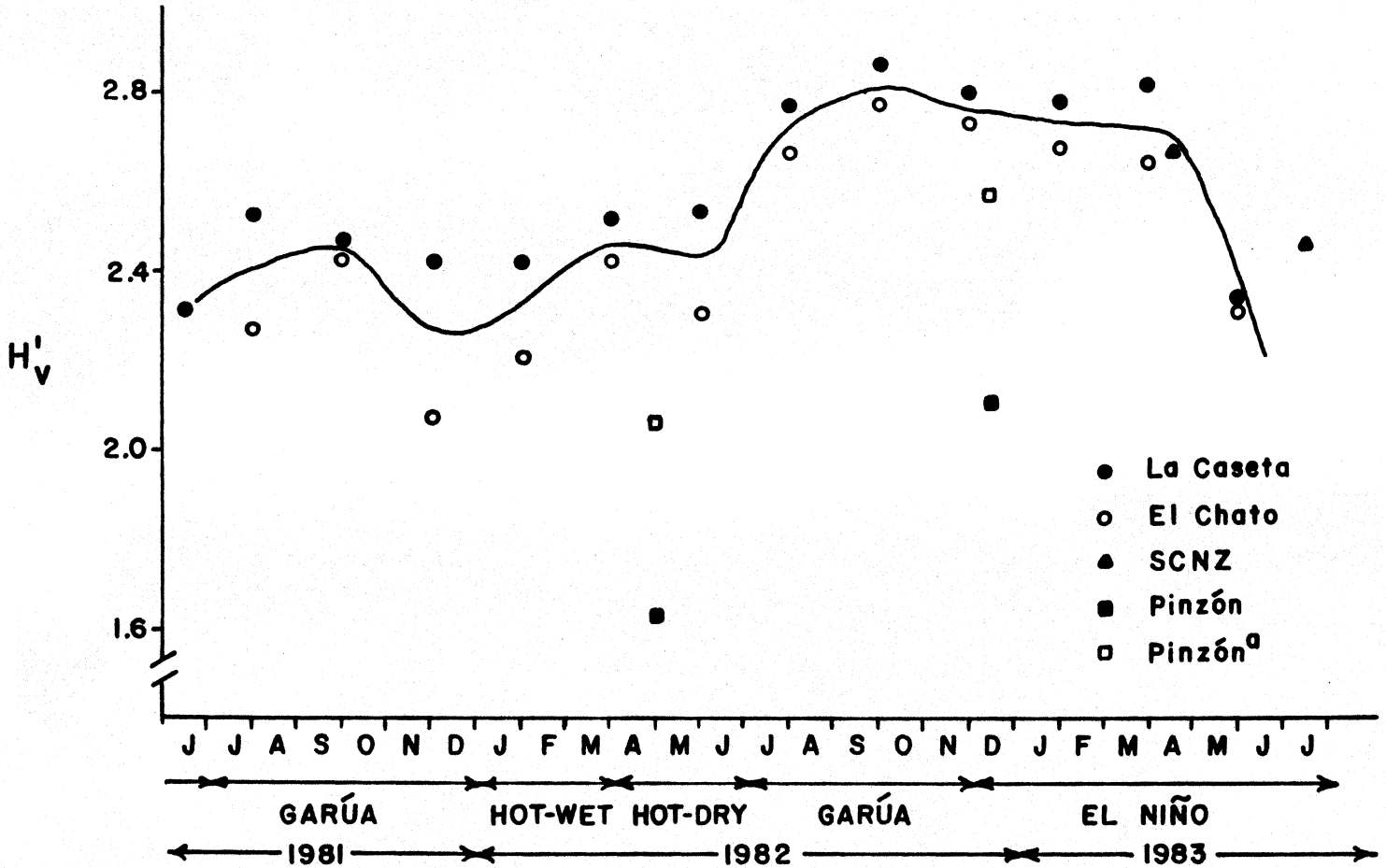

80
60
40
20
S_v
J J A S O N D J F M A M J J A S O N D J F M A M J J
GARÚA
HOT-WET
HOT-DRY
GARÚA
EL NIÑO
1981
1982
1983
La Caseta
El Chato
SCNZ
Pinzón

Fig. 3.7. Diversity of the available food (H'_v) at La Caseta, El Chato, the Santa Cruz Nesting Zone (SCNZ), and Pinzón over time. Measurements for Pinzón[a] exclude Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona (see text for explanation). Line drawn freehand for data from La Caseta and El Chato.


2.8
2.4
2.0
1.6
H'_v
La Caseta
El Chato
SCNZ
Pinzón
Pinzón[a]
J J A S O N D J F M A M J J A S O N D J F M A M J J
GARÚA
HOT-WET
HOT-DRY
GARÚA
EL NIÑO
1981
1982
1983

variable to enter the equation (full data set: $F_{1, 16}$ = 36.11, $P < .0001$, $R^2 = 0.69$, Fig. 3.8; subset of data: $F_{1, 14}$ = 29.32, $P < .0001$, $R^2 = 0.68$). H'_v showed a stronger relationship to total biomass for the full data set (Fig. 3.9), while precipitation was the only variable entering the equation for the subset excluding El Niño (Fig. 3.10). Although total biomass was a better predictor of S_v and H'_v, the major ultimate factor driving the change in these diversity indices over time was precipitation.

The distribution of J_v over time did not show the same pattern as the other indices (Fig. 3.11). No significant relationship was found between J_v and either total biomass or precipitation.

Lowlands: Santa Cruz Nesting Zone

At the onset of El Niño (December 1982), the adult tortoises inhabiting the upper regions of the Tortoise Reserve and the farmlands began a mass migration to lower elevations (Cayot 1985). In order to continue monitoring the adult population, a new study area was established in one of the several traditional nesting zones. This area was visited for 3-week periods in February/March, April, and July 1983. Males constituted the majority of tortoises in this study area also (Table 3.4). The increase in females in July may have resulted from additional females moving into the area due to the onset of the nesting season. Many of the same individuals, both males and females, remained in this area throughout El Niño.

Fig. 3.8. Relationship between species richness of the available food (S_v) and total available biomass at La Caseta and El Chato. Data from the Santa Cruz Nesting Zone (SCNZ) and Pinzón are plotted for comparison. Measurements for Pinzón[a] exclude Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona (see text for explanation).

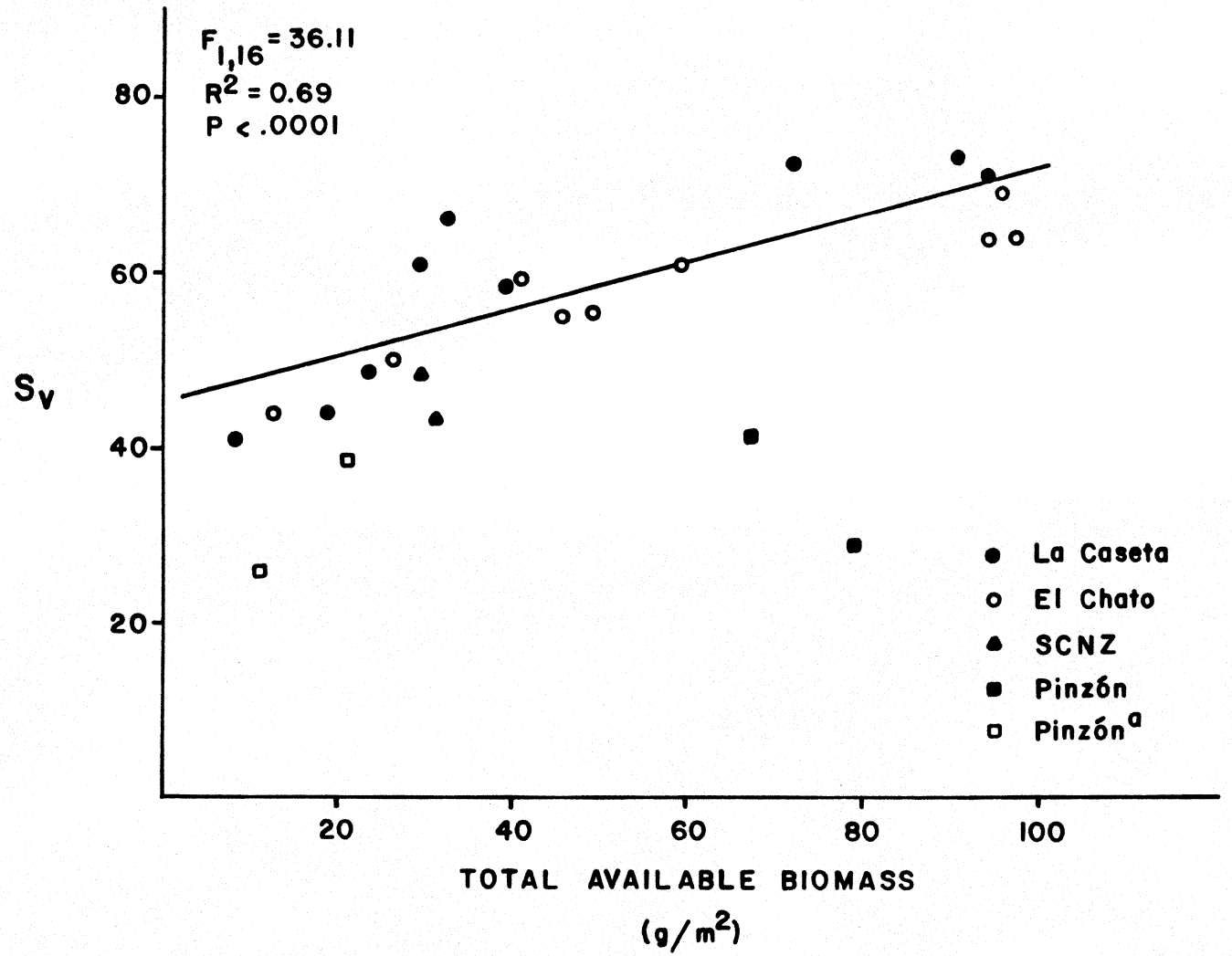

$F_{1,16} = 36.11$
$R^2 = 0.69$
$P < .0001$
80
60
40
20
S_V
20
40
60
80
100
TOTAL AVAILABLE BIOMASS
(g/m^2)
La Caseta
El Chato
SCNZ
Pinzón
Pinzón[a]

Fig. 3.9. Relationship between diversity of the available food (H'_y) and total available biomass at La Caseta and El Chato. Data from the Santa Cruz Nesting Zone (SCNZ) and Pinzón are plotted for comparison. Measurements for Pinzón[a] exclude Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona (see text for explanation).

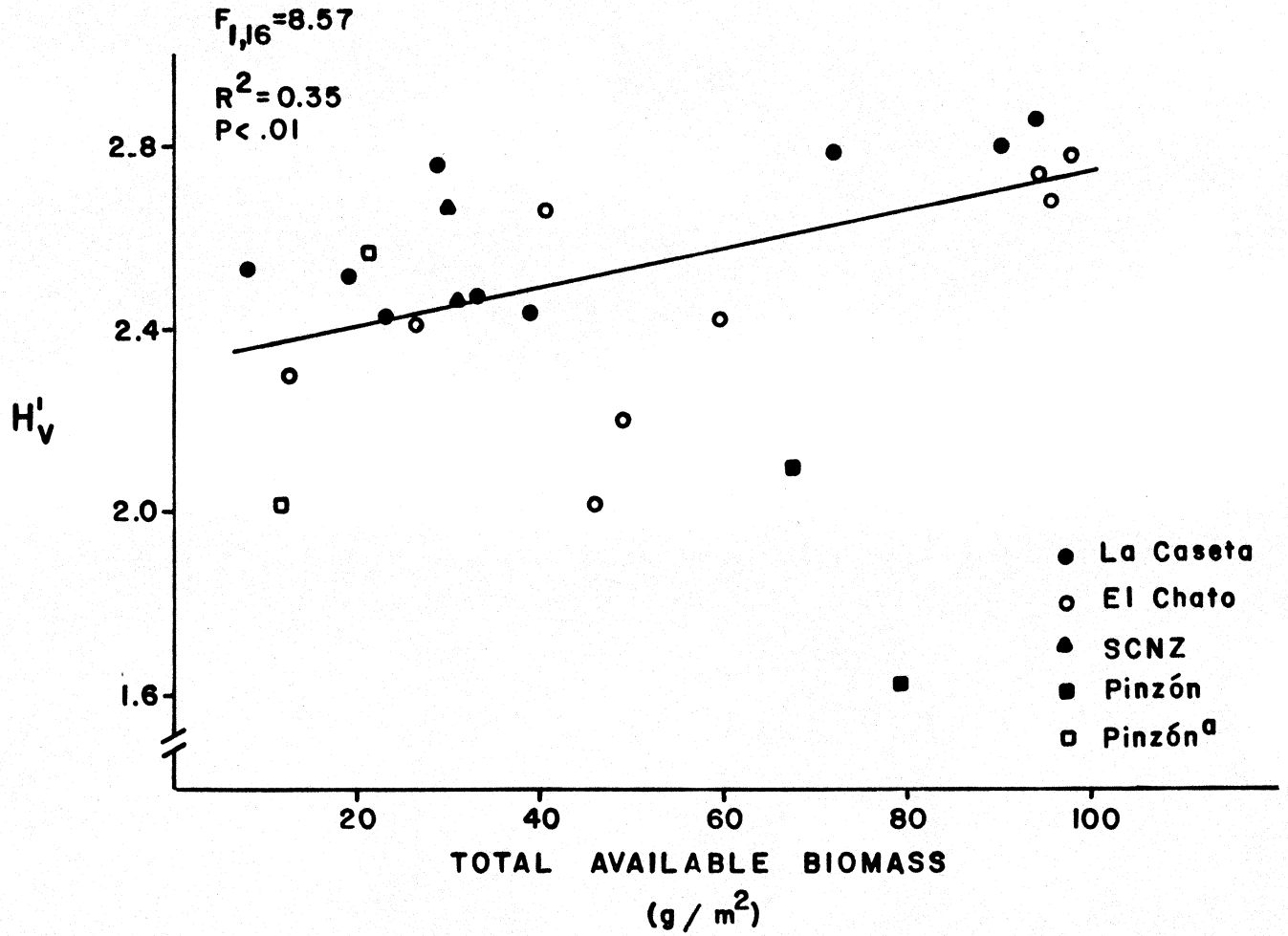

$F_{1,16}=8.57$
$R^2=0.35$
$P<.01$
2.8
2.4
2.0
1.6
H'_V
20
40
60
80
100
TOTAL AVAILABLE BIOMASS
(g/m^2)
La Caseta
El Chato
SCNZ
Pinzón
Pinzón[a]

Fig. 3.10. Relationship between diversity of the available food (H'_v) and precipitation, measured at La Caseta, for La Caseta and El Chato. Rainfall data reflect the period of time between sets of vegetation transects (range from 45 to 72 days). Data from El Niño, with its unusually high rainfall, were excluded from the analysis.

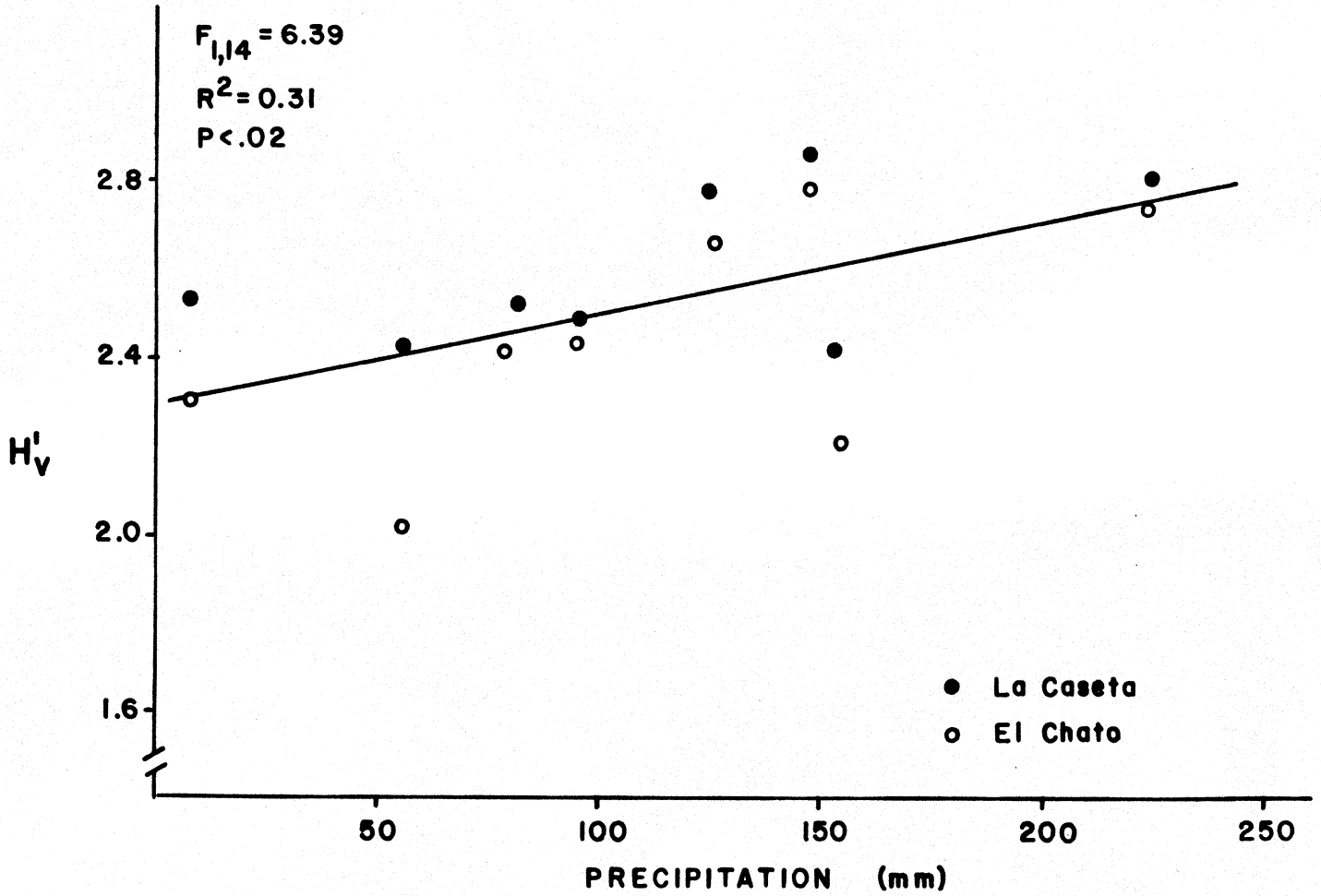

$F_{1,14} = 6.39$
$R^2 = 0.31$
$P < .02$
2.8
2.4
2.0
1.6
H'_V
50
100
150
200
250
PRECIPITATION (mm)
La Caseta
El Chato

Fig. 3.11. Species evenness of the available food (J_v) at La Caseta, El Chato, the Santa Cruz Nesting Zone (SCNZ), and Pinzón over time. Measurements for Pinzón[a] exclude Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona (see text for explanation). Line drawn freehand for data from La Caseta and El Chato. Half-open circles indicate data points common to both La Caseta and El Chato.

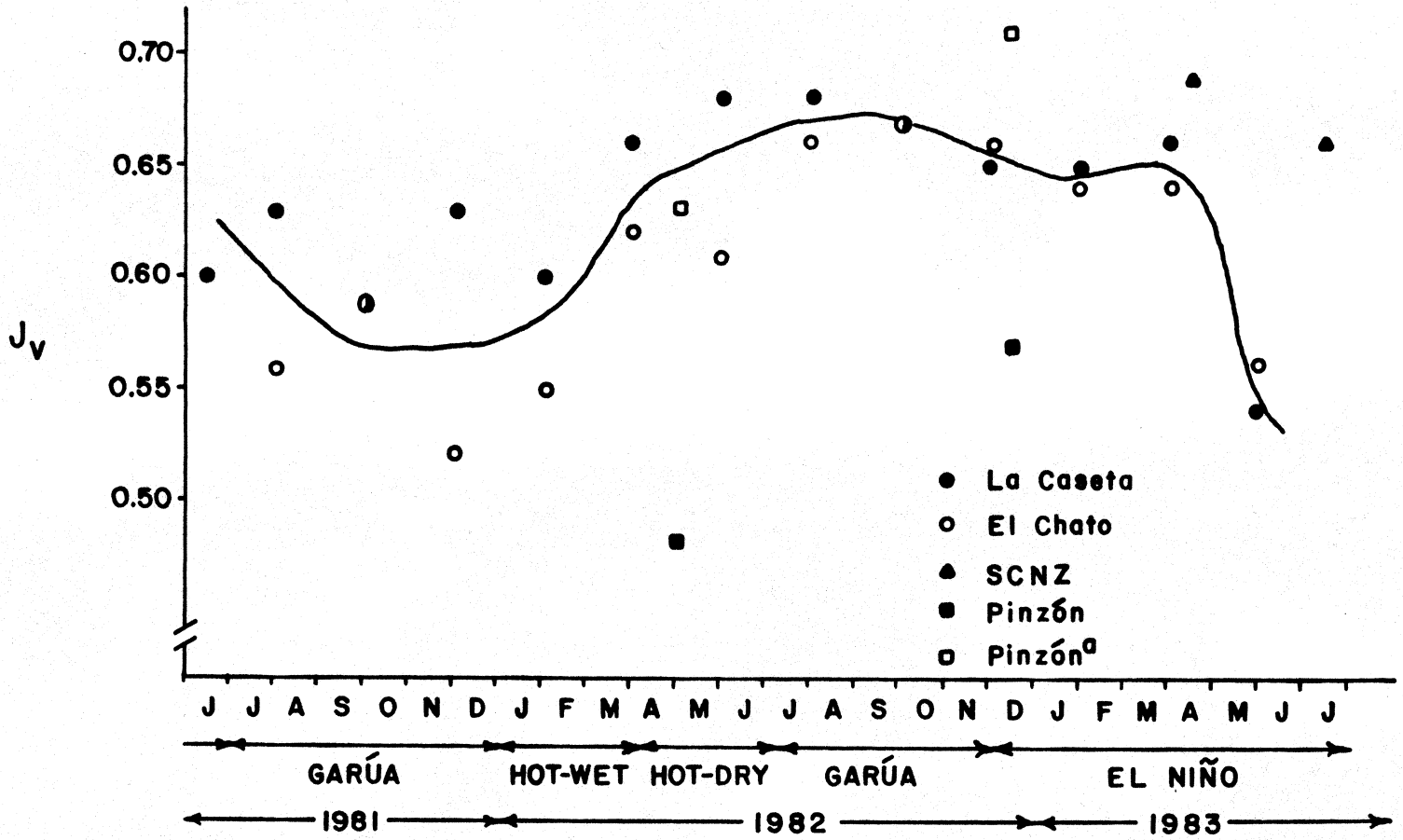

0.70
0.65
0.60
0.55
0.50
J_V
La Caseta
El Chato
SCNZ
Pinzón
Pinzón[a]
J J A S O N D J F M A M J J A S O N D J F M A M J J
GARÚA
HOT-WET
HOT-DRY
GARÚA
EL NIÑO
1981
1982
1983

Table 3.4. Estimated number of different tortoises (TOTAL) at the Santa Cruz Nesting Zone (SCNZ) during El Niño 1983, with precipitation and air temperatures corresponding to each trip. Tortoise numbers are based on a compilation of observations of marked tortoises (marked numbers were often difficult to distinguish) and of unmarked tortoises that were separated by sex and carapace measurements. Number of observations (OBS) when tortoise markings were recorded is given. Dates for weather data, collected at Manzanillos (coastal campsite below SCNZ), are given in parentheses.

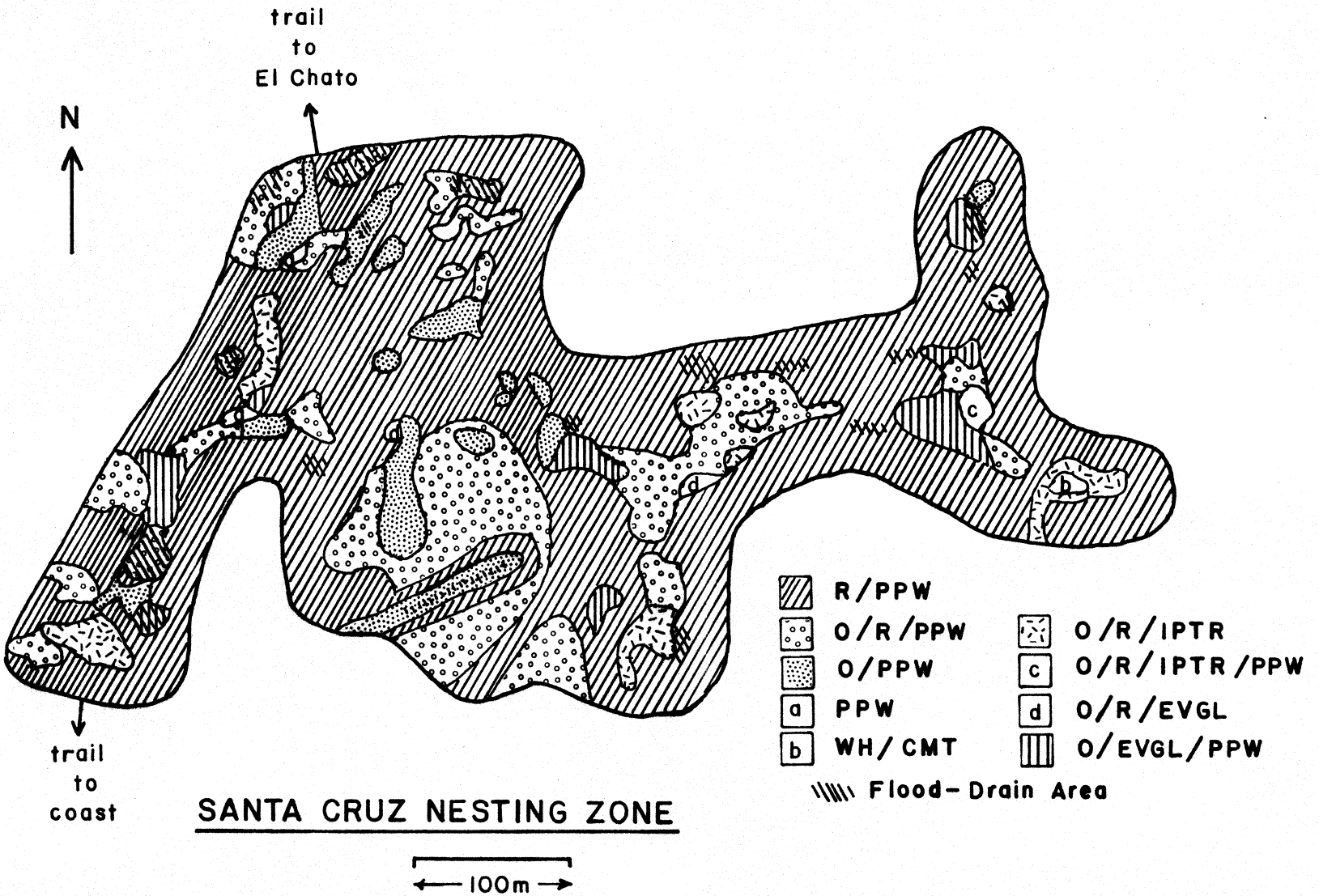
	TORTOISES					TEMP (C^{o})		
			SEX					
MONTH	OBS	TOTAL	M	F	?	$\bar{X}$ MIN	$\bar{X}$ MAX	PRECIPITATION (mm) (dates)
Feb/Mar	369	50	32	13	5	25.0	33.0	207.0 (2/23 - 3/7)
April	476	44	27	16	1	24.0	34.0	160.0 (4/7 - 4/21)
July	477	76	37	34	5	23.5	31.0	88.9 (7/12 - 7/23)

The Santa Cruz Nesting Zone study area (SCNZ) was located inland from Manzanillos at an elevation of 50-80 m, in the continuum between the Arid Zone and the Transition Zone (Wiggins and Porter 1971). In Laruelle's (1966) altitudinal zonation of soils, SCNZ lies in the center of the first zone which ranges from sea level to an elevation of 100-120 m. The soil of this zone is mostly restricted to lithosols, local superficial or interstitial material resting on or between lava blocks. The depth of this soil is never more than 5 cm. This zone also has isolated patches of deeper, reddish soils, which may reach a depth of 80 cm. These soils, always found in flat regions, were considered by Laruelle to be residual. These deeper soils are an important factor in determining the location of nesting zones, according to characteristics important in nesting as described by MacFarland et al. (1974a).

SCNZ was the smallest of the study areas and had the lowest diversity of habitat types (Fig. 3.12). A total of 61 plant species was recorded in the area during El Niño (Table 3.5). The most common tree species were Piscidia carthagenensis and Pisonia floribunda.

Introduced plants were nearly absent from SCNZ. It is more difficult for introduced species to invade the Arid Zone than the more humid highlands where soil development is greater (Haro 1975, Eliasson 1982). In addition, the nesting zones are far from developed areas. However, by July 1983, Momordica charantia was beginning to spread over much

Fig. 3.12. Santa Cruz Nesting Zone. Habitat type map of the study area during El Niño. Habitat types include various combinations of the following: R - Rock, O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea triloba, EVGL - Evolvulus glaber, WH - Water Hole, and CMT - Clerodendrum Thicket. Flood-drain areas filled with water after heavy precipitation, then drained within 2 to 3 days. Trails are indicated only where they exit the study area.



SANTA CRUZ NESTING ZONE

Table 3.5. Plant species encountered at the Santa Cruz Nesting Zone during El Niño 1983. Plant types include trees (T), shrubs (S), forbs (F), grasses and sedges (G), cactus (C), and other (O). Status includes endemic (E), indigenous (I), and introduced (INT). Species names, types, and status from Wiggins and Porter (1971) unless otherwise noted.

FAMILY SPECIES	TYPE	STATUS
Acanthaceae		
Blechum brownei	F	I
Tetramerium nervosum	F	I
Amaranthaceae		
Alternanthera halimifolia	F	I
A. sp.	S	I
Boraginaceae		
Cordia lutea	S	I
C. sp.	S	E
Heliotropium angiospermum	F	I
Tournefortia psilostachya	S	I
T. pubescens	S	E
Burseraceae		
Bursera graveolens	T	I
Cactaceae		
Opuntia echios	C	E
Commelinaceae		
Commelina diffusa	F	I
Compositae		
Ageratum conyzoides	F	I[a]
Bidens riparia	F	I
Blainvillea dichotoma	F	I
Convolvulaceae		
Dichondra repens	F	I
Evolvulus glaber	F	I
Ipomoea triloba	F	I
I. sp.	F	?
Merremia aegyptica	F	I
Stictocardia tiliifolia	F	I[b]

Table 3.5 continued.

FAMILY SPECIES	TYPE	STATUS
Cucurbitaceae		
Momordica charantia	F	INT[b,c,d,e]
Cyperaceae		
Cyperus brevifolius	G	I
C. confertus	G	I
Eleocharis sp.	G	I
Euphorbiaceae		
Acalypha sp.	F	E
Croton scouleri	S	E
Hippomane mancinella	T	I
Gramineae		
Leptochloa filiformis	G	I[a]
Panicum fasciculatum	G	I
Paspalum conjugatum	G	I[a]
Labiatae		
Salvia occidentalis	F	I
Leguminosae		
Acacia sp.	T	I
Cassia occidentalis	F	I
Desmodium canum	F	I[a]
D. procumbens	F	I
Erythrina velutina	T	I
Galactia striata	F	I
Piscidia carthagenensis	T	I
Loasaceae		
Mentzelia aspera	F	I
Malvaceae		
Bastardia viscosa	S	I
Sida hederifolia	F	I
S. spinosa	F	I
Myrtaceae		
Psidium galapageium	T	E

Table 3.5 continued.

FAMILY SPECIES	TYPE	STATUS
Nyctaginaceae		
Commicarpus tuberosus	F	I
Pisonia floribunda	T	E
Oxalidaceae		
Oxalis cornellii	F	I
Passifloraceae		
Passiflora colinvauxii	F	E
Plantaginaceae		
Plumbago scandens	F	I
Portulacaceae		
Portulaca oleracea	F	I[a]
Rubiaceae		
Borreria laevis	F	I[a,f]
Chiococca alba	S	I
Rutaceae		
Zanthoxylum fagara	S	I
Scrophulariaceae		
Mecardonia dianthera	F	I
Solanaceae		
Capsicum frutescens	S	INT[d,e]
Physalis galapagoënsis	F	E
Solanum nodiflorum	F	I[a]
Tiliaceae		
Corchorus orinocensis	F	I
Urticaceae		
Fleurya aestuans	F	I
Verbenaceae		
Clerodendrum molle	S	I
Lantana peduncularis	S	E

[a]Considered introduced to the islands (Porter 1983), but not believed so by author based on observed distributions.

[b]Status from Porter (1983).

Table 3.5 continued.

---

[c]Status from Eckhardt (1972).

[d]Status from Haro (1974).

[e]Status from Haro (1975).

[f]Status from Colinvaux and Schofield (1976).

of the area previously covered by the indigenous liana, Ipomoea triloba. A trail from the highland village of Santa Rosa (360 m) to the coast, that passes through both El Chato and SCNZ, is used by tortoises, as well as park guards and at times local residents with their horses and dogs. It is probable that any introduced species found in SCNZ was originally transported from higher elevations by way of this trail. Most of the introduced species are probably not evident in the Arid Zone except during periods of high rainfall such as El Niño.

The major impact of introduced mammals on the tortoise population of Santa Cruz occurs in the nesting zones and is due primarily to nest destruction and predation on hatchlings by pigs (MacFarland et al. 1974a). During this study, pigs were never seen in the study area. Burros, cats, and a single dog (Canis familiaris) were heard in the area. Although burros may be potential competitors for food, during El Niño the great abundance of food due to heavy precipitation made this potential affect negligible. Cats may prey on young tortoises (MacFarland et al. 1974a). Though feral dogs are believed to have been eradicated from the area, it is possible that individual dogs are at times left behind by pig hunters. Overall, the introduced mammals in SCNZ played a minor role in the lives and habitat of the giant tortoises during El Niño, and therefore had a negligible effect on the results of this study.

Although the climate of SCNZ is typical for that at low elevations in the archipelago, use of the area for this study was limited to El Niño months. Weather data were collected during each trip at the coastal camp at Manzanillos (Table 3.4). Flooding of the area occurred off and on throughout El Niño. Major flooding in May and June 1983, resulted in a dieback of much of the Ipomoea triloba that had been extremely abundant in the early months of El Niño.

Reeder and Riechert (1975) observed a decrease in percentage of canopy cover, as well as in species richness and equitability, with decreasing altitude in the Tortoise Reserve. In general, results from this study concurred with these observations. Sixty-one plant species were encountered at SCNZ during the study, while a total of 124 were found at La Caseta and El Chato (Table 3.2, 3.5). Total available biomass, a function of cover, was much lower at SCNZ than at either of the mid-elevation areas (Fig. 3.4). Species richness (S_v), determined from vegetation transects, was also lower at SCNZ (Fig. 3.6). However, species evenness (J_v) was higher at SCNZ (Fig. 3.11), and species diversity (H'_v) did not show a particular pattern in relation to the other areas (Fig. 3.7). The relationships between S_v and H'_v with total biomass were consistent with results reported for La Caseta and El Chato (Figs. 3.8, 3.9). Precipitation data were only available for each 3-week period and were not comparable with results from mid-elevation areas.

PINZÓN

The tortoise population on Pinzón consists of 120 native adults and approximately 200 repatriated tortoises ranging in age from 5-17 years. No natural reproduction of tortoises occurs on Pinzón due to the nearly 100% predation of hatchlings by the introduced black rat population (MacFarland et al. 1974a). Therefore, SPNG personnel collect eggs from this island annually and transport them to the Charles Darwin Research Station (CDRS), where incubation is maintained until hatching. The tortoises are then raised at the station for approximately 5 years, at which time they are no longer susceptible to predation and are returned to Pinzón.

The study area was located in the South Crater at an elevation of 280-300 m. Occasional visits were made to Las Tunas on the northeast slope, and to the outer southern slopes of the island. Although tortoises were common in the South Crater at the turn of the century (Heller 1903), all but one of the tortoises that currently occupy the area are repatriated tortoises, the majority of which are still too small to sex (Table 3.6). The oldest repatriated tortoises are now larger than the native adults. This population was studied intensively for 3-week periods in April/May and December 1982. A short trip was made to the area at the end of El Niño, in June 1983, and was reported on in Cayot (1985).

The slopes of Pinzón are densely covered with large lava blocks, with little soil development (Hamann 1981). Soil

Table 3.6. Number of different tortoises (TOTAL) encountered on Pinzón in 1982, with precipitation and air temperatures corresponding to each trip. Number of observations (OBS) when tortoise markings were recorded is given. Dates for weather data are given in parentheses.

	TORTOISES							
			SEX			TEMP (C^{o})		
MONTH	OBS	TOTAL	M	F	?	$\bar{X}$ MIN	$\bar{X}$ MAX	PRECIPITATION (mm) (dates)
Apr/May	848	85	18	9	58	22.0	30.0	6.1 (4/24 - 5/10)
December	905	70	17	9	44	23.0	28.0	302.2 (12/2 - 12/17)

development of the floor of the South Crater is more extensive, particularly in dry water holes, and may result from runoff from the higher elevations.

Hamann (1981) described the vegetation on Pinzón as predominantly xerophytic, with the plant cover lower and more thorny than at comparable sites elsewhere in the archipelago. Both Hamann (1981) and van der Werff (1978) found the vegetation of Pinzón little changed compared with the observations of Stewart (1915). This lack of change in the vegetation, unlike most of the larger islands, is primarily due to the absence of introduced plants and introduced grazers. No introduced plants were found in the South Crater study area. The only introduced mammal on Pinzón is the black rat. Although it is responsible for the absence of successful natural reproduction of tortoises (MacFarland et al. 1974a), it has little impact on the vegetation (Hamann 1981).

The South Crater on Pinzón was the largest of the four study areas. Except for dry water holes, habitat types were less well distinguished on Pinzón than on Santa Cruz (Fig. 3.13). A total of 48 plant species were seen in the study area (Table 3.7). The most common plant species in the South Crater include Prosopis juliflora, Alternanthera filifolia, Maytenus octogona, Croton scouleri, and Opuntia galapageia.

The climatic conditions on Pinzón are intermediate between the dry, low islands and the wetter, higher islands

Fig. 3.13. South Crater, Pinzón. Habitat type map of the study area. Habitat types include various combinations of the following: DWH/WH - Dry Water Hole/Water Hole, R - Rock, PR - Prosopis, CR - Croton, OP - Opuntia, MA - Maytenus, and Open. Rivers and flood ponds first appeared in December 1982, at the onset of El Niño. By June 1983, ponds covered much more of the valley floor than is indicated. Trails are indicated only where they exit the study area.

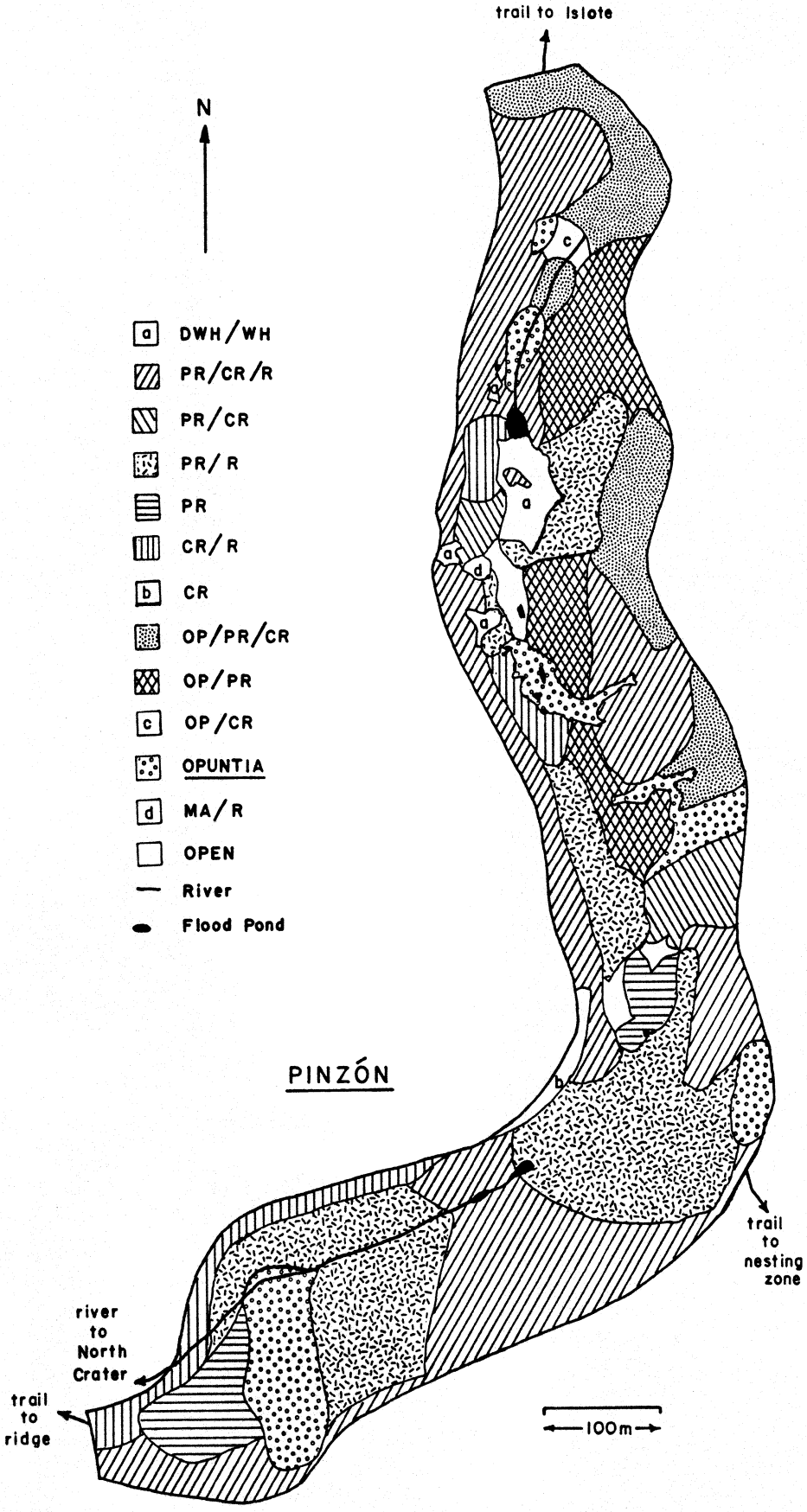

trail to Islote
N
a DWH/WH
PR/CR/R
PR/CR
PR/R
PR
CR/R
b CR
OP/PR/CR
OP/PR
c OP/CR
OPUNTIA
d MA/R
OPEN
River
Flood Pond
PINZÓN
trail to nesting zone
river to North Crater
trail to ridge
100m

Table 3.7. Plant species encountered in the South Crater of Pinzón during visits in April/May and December 1982, and June 1983. Plant types include shrubs (S), forbs (F), grasses and sedges (G), cactus (C), and other (O). Status includes endemic (E) and indigenous (I). Species names, types, and status from Wiggins and Porter (1971).

FAMILY SPECIES	TYPE	STATUS
Amaranthaceae		
Alternanthera echinocephala	S	I
A. filifolia	S	I
Basellaceae		
Anredera ramosa	F	I
Boraginaceae		
Cordia anderssonii	S	E
C. lutea	S	I
Heliotropium angiospermum	F	I
Tournefortia psilostachya	S	I
Bromeliaceae		
Tillandsia insularis	O	E
Cactaceae		
Opuntia galapageia	C	E
Celastraceae		
Maytenus octogona	S	I
Commelinaceae		
Commelina diffusa	F	I
Convolvulaceae		
Dichondra repens	F	I
Evolvulus glaber	F	I
Ipomoea triloba	F	I
Cyperaceae		
Cyperus confertus	G	I
C. elegans	G	E
Euphorbiaceae		
Croton scouleri	S	E

Table 3.7 continued.

FAMILY SPECIES	TYPE	STATUS
Gramineae		
Anthephora hermaphrodita	G	I[a]
Leptochloa filiformis	G	I[a]
Panicum fasciculatum	G	I
P. geminatum	G	I
Setaria setosa	G	I
Leguminosae		
Acacia macracantha	S	I
Galactia striata	F	I
Neptunia plena	F	I
Prosopis juliflora	S	I
Malvaceae		
Bastardia viscosa	S	I
Sida hederifolia	F	I
S. spinosa	F	I
Oxalidaceae		
Oxalis cornellii	F	I
Piperaceae		
Peperomia sp.	F	I
Plumbaginaceae		
Plumbago scandens	F	I
Polypodiaceae		
Polypodium tridens	O	E
Portulacaceae		
Portulaca oleracea	F	I[a]
Rubiaceae		
Chiococca alba	S	I
Rutaceae		
Zanthoxylum fagara	S	I
Scrophulariaceae		
Capraria peruviana	S	I

Table 3.7 continued.

FAMILY SPECIES	TYPE	STATUS
Simaroubaceae		
Castela galapageia	S	E
Solanaceae		
Grabowskia boerhaaviaefolia	S	I
Lycium minimum	S	E
Lycopersicon cheesmanii	F	E
Physalis pubescens	F	I
Solanum nodiflorum	F	I[a]
Urticaceae		
Fleurya aestuans	F	I
Verbenaceae		
Lantana peduncularis	S	E
Phyla strigulosa	F	I
Priva lappulacea	F	I
Viscaceae		
Phoradendron henslovii	O	E

[a]Considered introduced to the islands (Porter 1983) but not believed so by author, based on observed distributions.

(van der Werff 1983). No long-term climatological recordings have been made there. General observations indicate that the interior of South Crater receives very little rainfall annually (Hamann 1981). The south slopes and summit area are often bathed in fog and this sometimes moves into the South Crater on the southern slopes of its interior. Extremes in rainfall were represented in this study, while changes in temperature were less dramatic (Table 3.6).

Vegetation transects in the South Crater resulted in measurements of total available biomass unusually high for an arid region compared to the more mesic Santa Cruz upland sites (Fig. 3.4). This was due to a high density of shrubs within the range of feeding by tortoises. However, elimination of the biomass measurements for the three most abundant shrubs (Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona), none of which is among the preferred food items of tortoises, indicates that total tortoise-food biomass drops to levels lower than at any of the other study areas (Fig. 3.4).

Diversity of the vegetation, measured by S_V, H'_V, and J_V, was lower than at the other study areas, as expected for the smaller, arid island (Figs. 3.6, 3.7, 3.11). Compared with total available biomass, S_V and H'_V were much lower than would be predicted from the regressions for La Caseta and El Chato (Figs. 3.8, 3.9). This low vegetational diversity on Pinzón may also be due to the unexplained biological isolation of Pinzón, a central island, that is as great as that

of the islands in the periphery of the archipelago (Thornton 1971). However, when the three shrub species mentioned above were removed from the data, the diversity indices tended to follow the patterns set at the other study areas (Figs. 3.8, 3.9, 3.11).

DISCUSSION

The four study areas provided a good basis for comparison of results on tortoise behavior. Most important was the ability to examine differences between the dome-shaped tortoises on Santa Cruz and the saddle-backed tortoises on Pinzón. In addition, the four areas provided a substantial range of vegetation types. Hamann (1981) found that the correlations between the more common species in 48 plant communities, located throughout the islands, resulted in four major groupings of vegetation that could be placed along both an ecological and a geographical gradient. The major ecological gradient was from the more arid habitats to mainly humid habitats. The geographical gradient occurred from the more western and northern parts of the archipelago, with comparatively younger lava, to the central part of the archipelago, with predominantly older, more weathered lava. Three of those four groupings were represented by the four areas in this study. La Caseta and El Chato corresponded to the largest group, III, while SCNZ matched Hamann's group II, and Pinzón, his group I. The only group not represented in this study was group IV, the vegetation type found in the

more northern and western islands. Therefore, in addition to containing the two major morphological types of giant tortoise, the four study areas were representative of three out of four of the major vegetational alliances, described by Hamann (1981), in the islands.

CHAPTER FOUR - ACTIVITY PATTERNS

INTRODUCTION

Activity patterns of animals are often correlated with survival strategies, particularly in arid environments. Behavioral adaptations, exhibited in part by daily activity patterns and time budgets, combined with physiological adaptations provide the survival strategies of desert tortoises (*Gopherus agassizii*) in the southwestern United States (Nagy and Medica 1986). Thermoregulation is a major factor determining behavioral adaptations in arid environments. The choice of times for seasonal and daily activity appear to be the most critical behavioral choices in determining the body temperature of ectotherms (Stevenson 1985). The principal method by which many turtles regulate body temperature is by movement in and out of sun, shade, or water (Hutchison 1979). When their body temperature is near the upper or lower limits of the normal activity range, they usually do not feed (Mahmoud and Klicka 1979). Although the mass of giant tortoises is great enough to prevent rapid changes in body temperature due to thermal inertia, they are able to effect temperature regulation by a 'shot' of heat from the sun or cool from the shade (Mackay 1964), and their activity patterns should show some relationship to seasonal changes in ambient temperature.

Behavioral mechanisms of animals depend on temporal and spatial variability in the thermal environment. Although no

formal theory covers optimal times for feeding, a wide range of observations has indicated that climate will be overwhelmingly important in models of optimal feeding periods (Schoener 1971). Seasonality in prey availability, metabolic demands, and extra-foraging activities such as mating can also affect the allocation of time to different activities. A compilation of time budget data acquired in recent studies of warm-blooded animals has shown that the majority of daylight hours are spent resting (Herbers 1981). Ectotherms would be expected to rest for an even greater amount of time. Resting not only curtails energy expenditure, it serves as a buffer time to be utilized when needed (Herbers 1981). Therefore, changes in the amount of time allocated to resting may be closely related to seasonal changes, such as forage or water availability.

How an animal actually partitions the daylight hours to the various behaviors necessary for survival and reproduction should enhance its fitness. Knowledge of seasonal changes in daily activity patterns and time budgets of these tortoises can thus enhance our understanding of the life strategies of Galápagos tortoises.

Daily and seasonal activity patterns of terrestrial turtles, all of which are diurnal, are usually correlated with temperature and moisture (Auffenberg and Iverson 1979). Daily cycles for a single species may be unimodal in the cooler months when only midday temperatures are sufficiently warm for normal activity, and bimodal in the hottest, driest

part of the year when midday temperatures are too hot, forcing tortoises to seek shade. The highest overall peaks in activity of tortoises in xeric habitats generally occur during the rainy season.

The available information on daily activity patterns of Galápagos tortoises specify either a unimodal or a bimodal pattern of activity without attributing these patterns to seasonal environmental conditions. A unimodal pattern of activity, with initiation of activity occurring between 0800-0900h, generally continuous activity throughout the day, and an eventual cessation of activity between 1700-1800h has been reported as the typical daily activity pattern of Galápagos tortoises (Hendrickson 1965, Carpenter 1966, Rodhouse et al. 1975). Data for at least two of these reports were collected during the cool garúa season (Hendrickson 1965, Rodhouse et al. 1975). The bimodal pattern of activity, with tortoises becoming active both early in the morning and late in the afternoon, with a period of inactivity in the shade at midday, has also been reported as the normal condition for Galápagos tortoises (Beck 1903, Heller 1903, Black 1973, MacFarland and Reeder 1974). In addition, a single tortoise on Pinzón exhibited a bimodal activity pattern during a period in which other tortoises were generally inactive for most of the day (Rodhouse et al. 1975).

Fowler (1983) watched three to four tortoises on Volcán Alcedo, Isabela, for one to four days each, at three differ-

ent seasons (hot, garúa, and a transition period), and found no significant seasonal differences for the start of activity or the time at which an animal ceased activity for the day. This suggests that Galápagos tortoises do not show seasonal patterns. The only seasonal difference indicated in her study was a highly significant difference in the daily time budgets, with tortoises feeding and interacting more during the hot-rainy season, while during garúa season they spent more time resting and searching for water.

Giant tortoises on Aldabra seem to maintain a bimodal daily activity pattern year-round, with active periods limited to the early morning and late afternoon (Gaymer 1968, Grubb 1971, Swingland and Lessels 1979, Gibson and Hamilton 1983). However, on cool days, which are relatively infrequent on Aldabra, tortoises may remain active throughout the day (Gaymer 1968, Swingland and Frazier 1979, Swingland and Lessels 1979). As the dry season progresses, a lower proportion of tortoises feeds at any given time (Gibson and Hamilton 1983), with many tortoises remaining inactive for long periods of time, sometimes up to several weeks (Swingland and Lessels 1979).

Both the Galápagos Islands and the Aldabra atoll experience a rainy season and a dry season, with the highest peaks of activity by tortoises corresponding to the wet season (Fowler 1983, Gibson and Hamilton 1983), as reported for terrestrial turtles in general (Auffenberg and Iverson 1979). However, Aldabra does not have a cool season corre-

sponding to the garúa season in the Galápagos Islands. Therefore, although the bimodal daily activity pattern of tortoises is seen year-round on Aldabra, it would not necessarily be expected to occur year-round in the Galápagos. The conflicting reports of either a unimodal or a bimodal daily activity pattern for tortoises in the Galápagos suggest that there the seasonal changes may be sufficiently large to produce two different patterns of daily activity in the resident tortoise populations.

Definite seasonal patterns of activity related to reproduction, including breeding, nesting and its associated migrations, and hatching, have been noted on both the Galápagos (Carpenter 1966, Reeder and MacFarland 1978, Fowler 1983, Fowler de Neira and Roe 1984) and Aldabra (Bourn 1977, Bourn and Coe 1978, Swingland and Coe 1978, 1979). In general, breeding may occur throughout the year with a peak in breeding activity at the middle of the hot-rainy season. Nesting occurs throughout the dry (Aldabra) or cool-dry/garúa (Galápagos) season, with subsequent hatching near the onset of the following hot-rainy season.

RESULTS

Daily Activity Patterns

Instantaneous tortoise observations, along with corresponding hour and temperature data, were used to determine daily activity patterns of tortoises on a monthly basis from

June 1981 to January 1983, at La Caseta and El Chato, for each of the three trips to the Santa Cruz Nesting Zone (SCNZ) during El Niño 1983, and in April/May and December 1982, on Pinzón. A constant number of tortoises was observed per hour when possible after April 1982, while the number of tortoises observed for each activity varied considerably (Table 4.1).

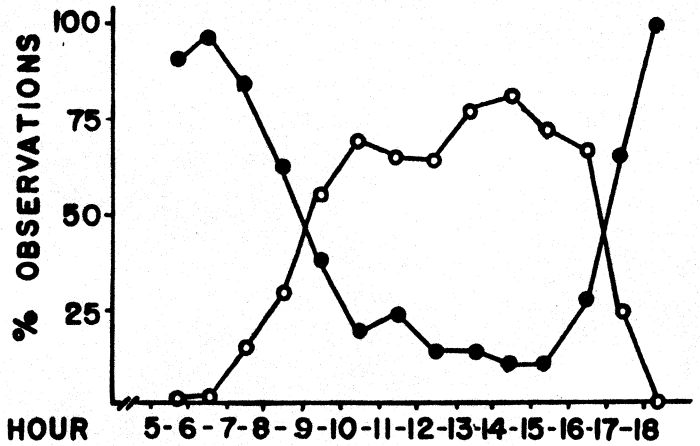
Graphical analyses of the percentage of observations per hour for resting and feeding, the two major activities of tortoises, show gradual seasonal shifts between a unimodal pattern of activity in the cool garúa season, and a bimodal pattern of activity in the hot-wet season (Fig. 4.1). Resting and feeding show opposing trends because feeding is the major active mode of tortoises and thus the near inverse of resting. During the hot and extremely dry period in May 1982, tortoises were nearly inactive with a single low peak of activity (note the dip in percent resting) occurring early in the day, corresponding to the initial peak of activity in the bimodal pattern of March 1982 (Fig. 4.1). The large decrease in tortoises resting early in the day in May was related primarily to an increase in tortoises traveling and interacting, both agonistically and mating, rather than in tortoises feeding. The last month of instantaneous observations at La Caseta and El Chato, January 1983, was the second month of El Niño, when daytime temperatures were high, and water and available food were abundant. The bimodal pattern which corresponds to the hot season was again evi-

Table 4.1. Number of instantaneous observations of tortoises in each of the six activity categories, by study area and month. Data from La Caseta and El Chato (CA/CH) were combined.

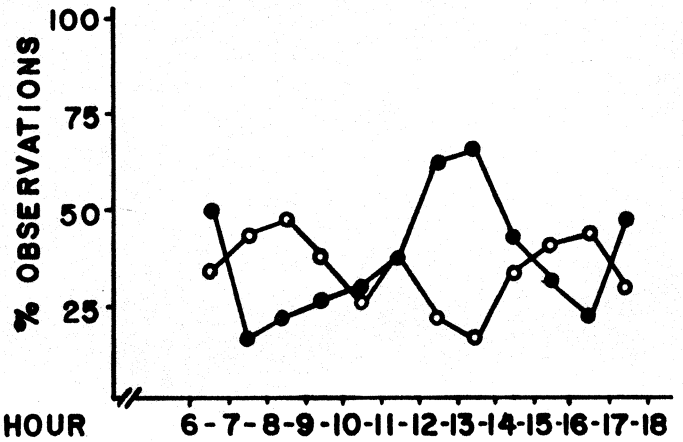
STUDY AREA	YEAR	MONTH	REST	FEED	TRAVEL	MATING	AGONISTIC INTERACT	DRINK	TOTAL
CA/CH	1981	Jun	151	126	26	24	10	4	341
		Jul	46	40	21	4	2	2	115
		Aug	49	18	8	6	0	1	82
		Sep	110	102	32	2	0	7	253
		Oct	87	169	24	2	2	8	292
		Nov	66	89	18	4	4	0	181
		Dec	239	225	56	12	0	26	558
	1982	Jan	184	195	81	38	11	28	537
		Feb	61	130	48	20	0	8	267
		Mar	196	199	102	40	16	6	559
		Apr	165	131	42	20	2	0	360
		May	411	39	51	28	18	0	547
		Jun	509	105	85	23	10	0	732
		Jul	341	239	45	10	2	25	662
		Aug	239	279	64	8	2	44	636
		Sep	277	326	57	0	0	9	669
		Oct	274	300	55	2	6	17	654
		Nov	338	265	26	4	2	18	653
		Dec	135	49	52	2	0	1	239
	1983	Jan	180	42	45	4	0	1	272
SCNZ[a]	1983	Feb/Mar	207	123	26	16	2	2	376
		Apr	273	169	16	20	2	3	483
		Jul	290	147	25	8	0	7	477
PINZÓN	1982	Apr/May	556	133	122	10	17	19	857
		Dec	551	259	84	4	2	9	909

[a]Santa Cruz Nesting Zone.

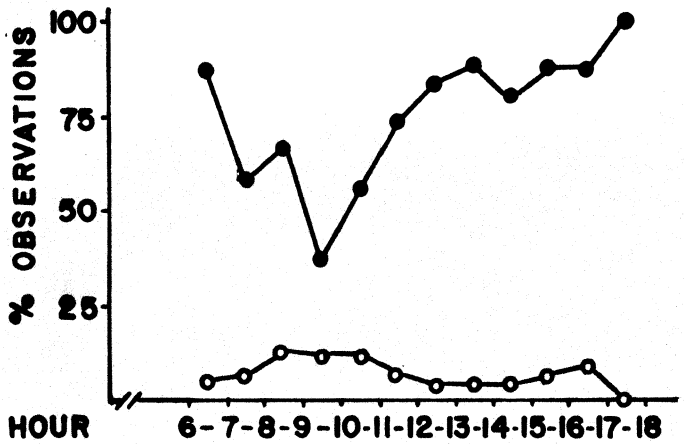
Fig. 4.1. Seasonal activity patterns for resting (●) and feeding (⊙) of giant tortoises at La Caseta and El Chato. Activities not shown include traveling, mating, agonistic interactions, and drinking. Observations began at 0530h and ended at 1830h in September 1982, and January 1983. Number of observations/hour (N) ranged from 45 to 57 for all hours in May and September 1982, except for 0530-0600h and 1800-1830h, when N = 20 to 23. In March 1982, N ranged from 12 to 72. In January 1983, N ranged from 20 to 25 for all hours except 0530-0600h and 1800-1830h, when N = 10.



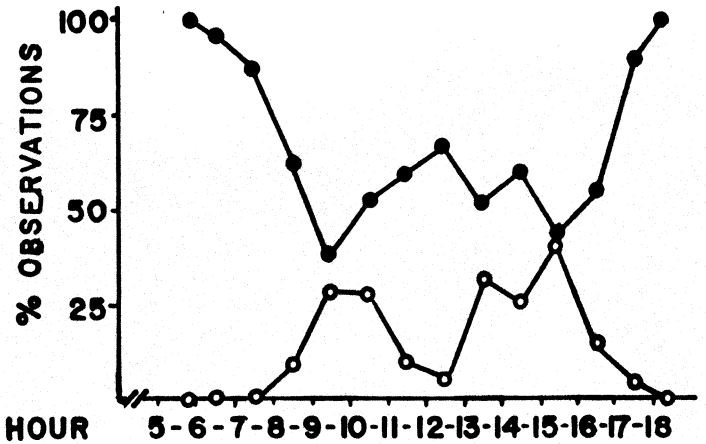
COOL-GARÚA, SEPTEMBER 1982



HOT-WET, MARCH 1982



HOT-DRY, MAY 1982



EL NIÑO, JANUARY 1983

dent, but the intensity of the peaks was lower (Fig. 4.1). The large number of animals migrating to lower elevations resulted in an increase in percent traveling, and reduced the number of tortoises actively feeding.

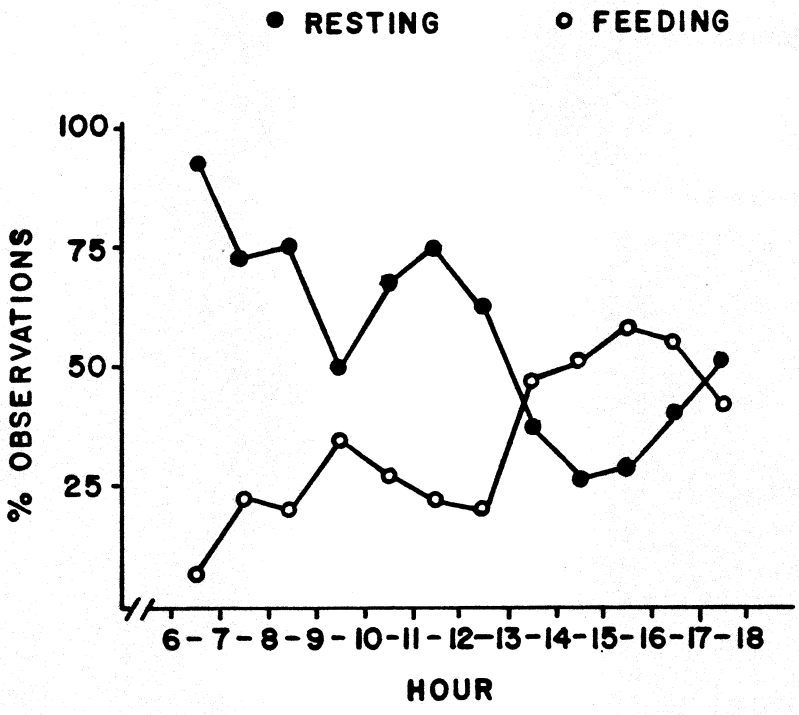
Activity of tortoises at SCNZ in April 1983, at the middle of El Niño, was bimodal as would be expected for the hot season, with the highest peak of activity in mid-afternoon (Fig. 4.2). Data at SCNZ for July 1983, a transition month at the cessation of El Niño rains, suggested the beginning of a shift from the bimodal toward the unimodal pattern of activity (Fig. 4.2).

Tortoises on Pinzón exhibited a bimodal pattern of activity in the hot-dry season (Fig. 4.3), similar to that at La Caseta and El Chato at the same period (Fig. 4.1), with the initial peak of activity being the largest. Data from December 1982, the transition month between the cool garúa season and El Niño, suggested a pattern in transition between the unimodal and bimodal patterns as would be expected for that time of year (Fig. 4.3).

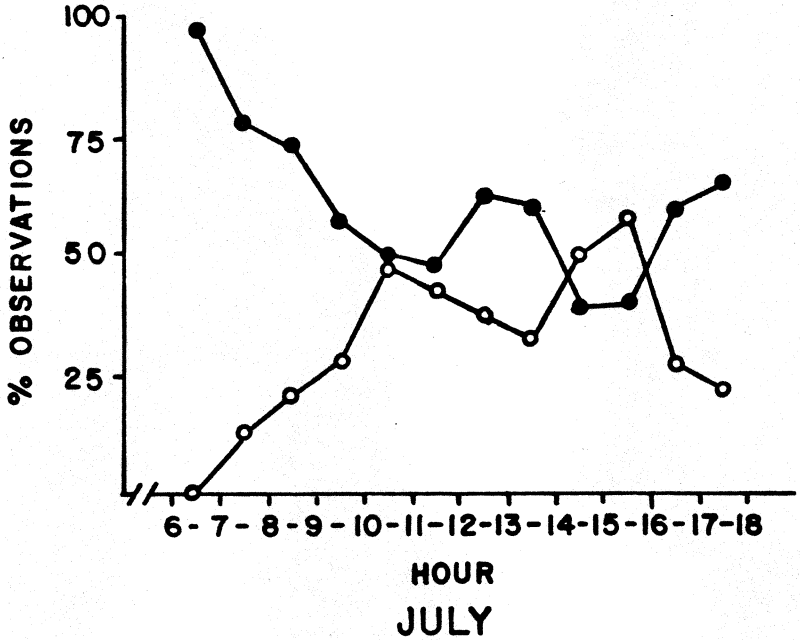
Graphs of percent activity versus temperature for the same months suggest the underlying reason for the activity patterns observed. Temperatures in September 1982, at La Caseta and El Chato, representative of the cool garúa season, never rose above 28 °C. This allowed tortoises to remain active throughout the day, and resulted in a unimodal pattern of activity (Fig. 4.4). Nighttime temperatures, however, reached a low of 16° C, resulting in low temperatures

Fig. 4.2. Activity patterns for resting and feeding of giant tortoises at the Santa Cruz Nesting Zone during El Niño 1983. Activities not shown include traveling, mating, agonistic interactions, and drinking. Number of observations/hour ranged from 38 to 41.

SANTA CRUZ NESTING ZONE



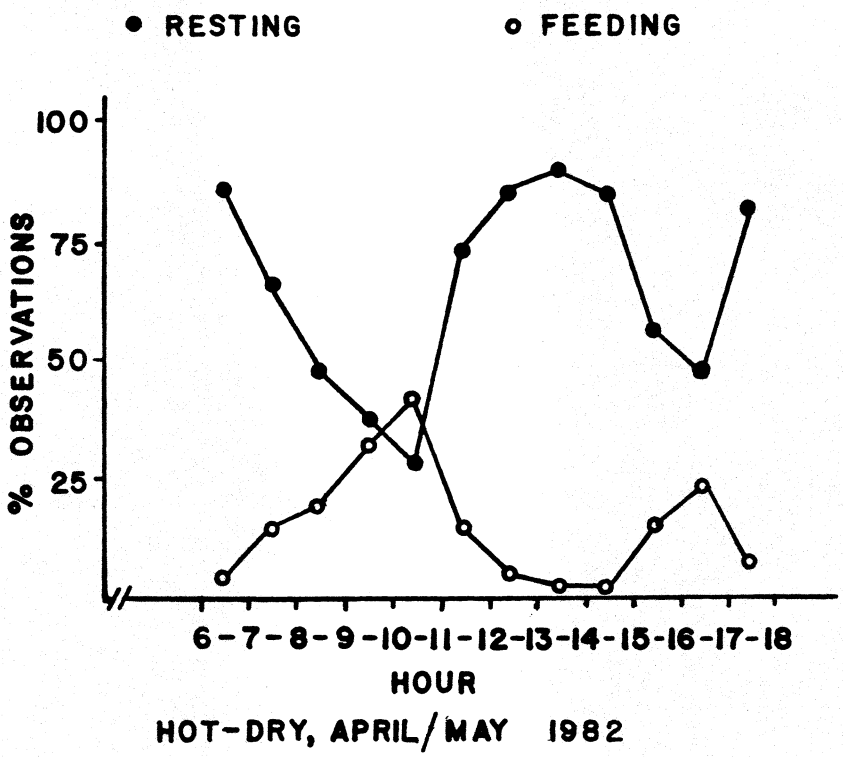
APRIL



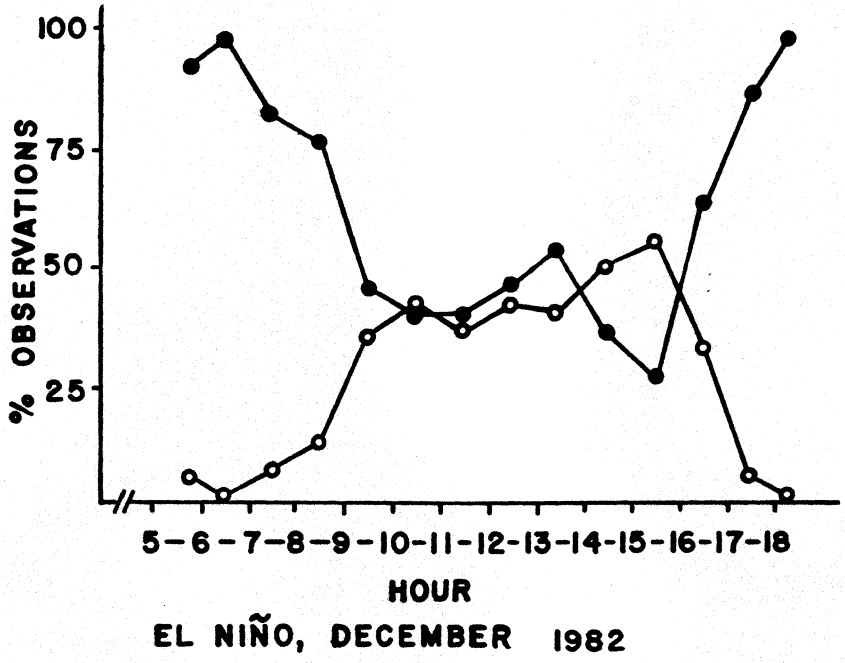
JULY

Fig. 4.3. Activity patterns for resting and feeding of giant tortoises on Pinzón. Activities not shown include traveling, mating, agonistic interactions, and drinking. Number of observations/hour (N) ranged from 64 to 74 for all hours except 0530-0600h and 1800-1830h, when N = 34 to 35.

PINZÓN

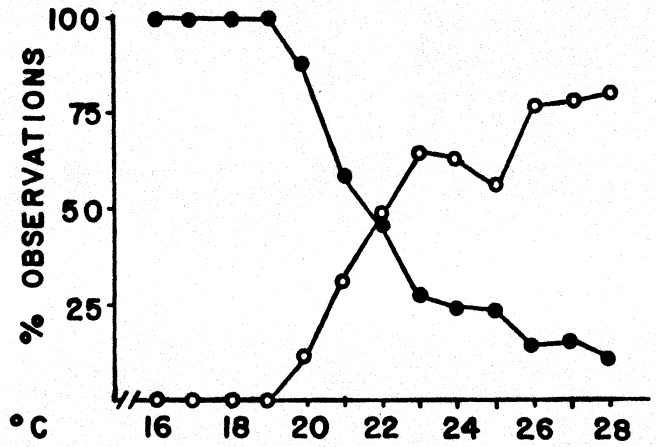


HOT-DRY, APRIL/MAY 1982

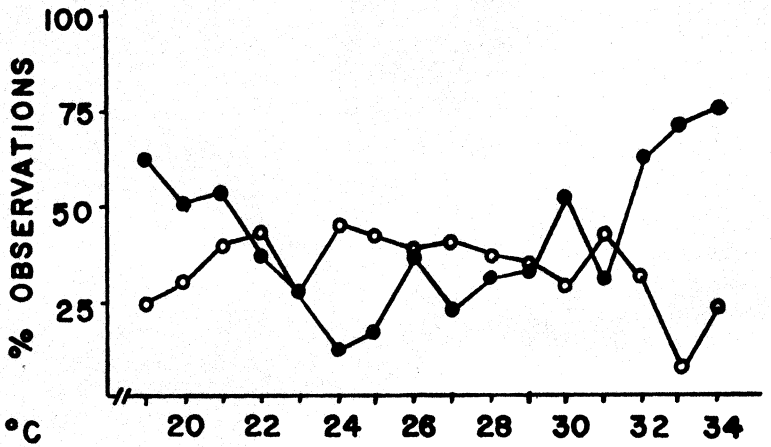


EL NIÑO, DECEMBER 1982

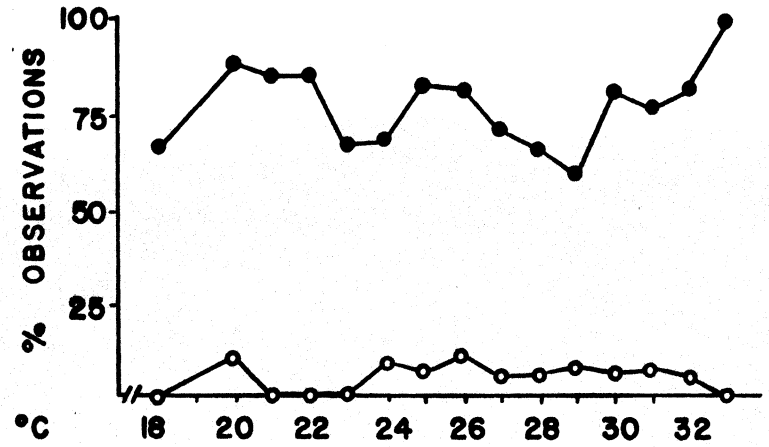
Fig. 4.4. Seasonal activity patterns, relative to ambient temperature adjacent to each animal, for resting (●) and feeding (○) of giant tortoises at La Caseta and El Chato. Activities not shown include traveling, mating, agonistic interactions, and drinking. Only those temperatures with N $\geq$ 3 are included. N ranged from 3 to 114.



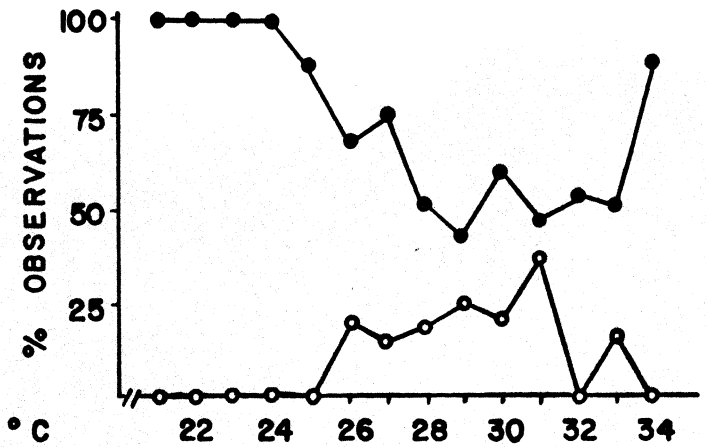
COOL - GARÚA, SEPTEMBER 1982



HOT - WET, MARCH 1982



HOT - DRY, MAY 1982



EL NIÑO, JANUARY 1983

in the early morning, inducing tortoises to sleep in. March 1982, representing the hot-wet season, had warmer nighttime temperatures and higher daytime temperatures, allowing tortoises to rise at daybreak, but requiring them to seek shade at midday (Fig. 4.4). As the temperature cooled late in the afternoon, tortoises became active again, creating a bimodal pattern of activity. In the hot-dry season, here represented by May 1982, tortoises were generally inactive, while at the onset of El Niño (January 1983), tortoises were active at mid-temperatures (Fig. 4.4).

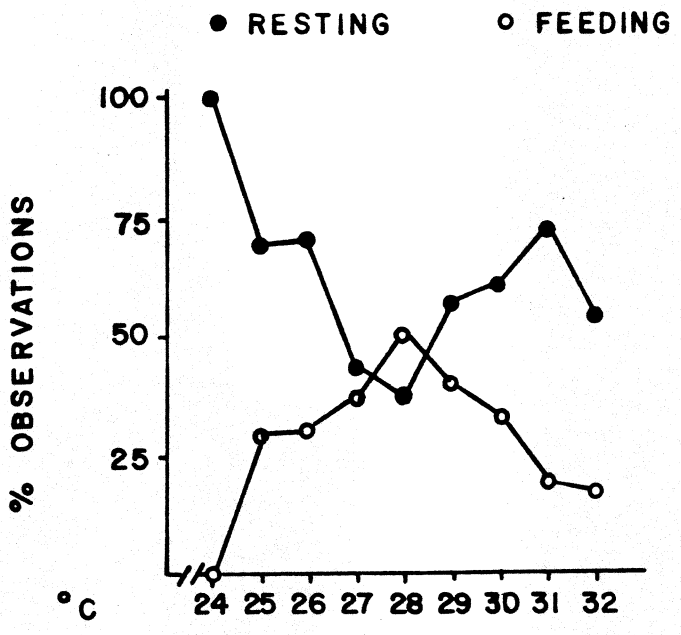
Tortoises at SCNZ, experiencing a narrower range of temperatures than at La Caseta and El Chato, showed the same general pattern for El Niño, with the peaks of activity at mid-temperatures (Fig. 4.5). Tortoises on Pinzón, also experiencing a narrow range of temperatures, showed peak activity at mid-temperatures (Fig. 4.6).

Preliminary statistical analyses to determine the overall importance of hour, temperature, and month on the percent of observations in each activity consisted of a general linear model with month, hour, and temperature entered as discrete variables. Analyses were done for each study area, and for each season at La Caseta and El Chato (Table 4.2). Resting and feeding were consistently correlated with at least one of the variables, while few significant relationships were found for the other activities.

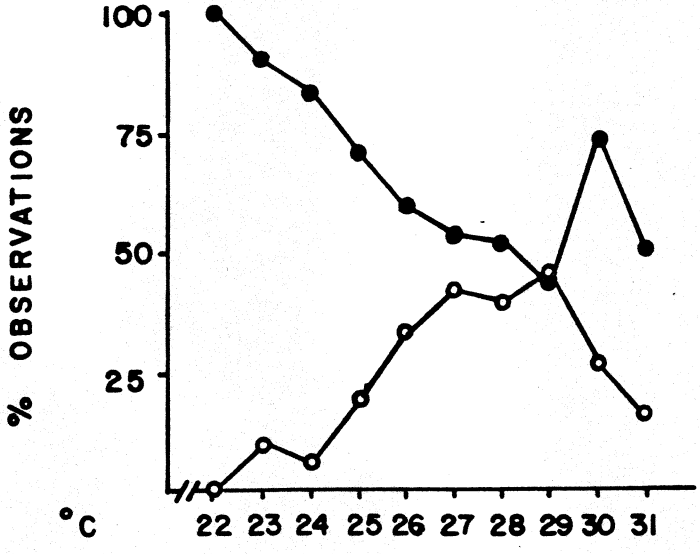
Separate stepwise regressions were completed with each activity as the dependent variable, while independent vari-

Fig. 4.5. Activity patterns, relative to ambient temperature adjacent to each animal, for resting and feeding of giant tortoises at the Santa Cruz Nesting Zone during El Niño 1983. Activities not shown include traveling, mating, agonistic interactions, and drinking. Only those temperatures with N $\geq$ 3 are included. N ranged from 3 to 99.

SANTA CRUZ NESTING ZONE



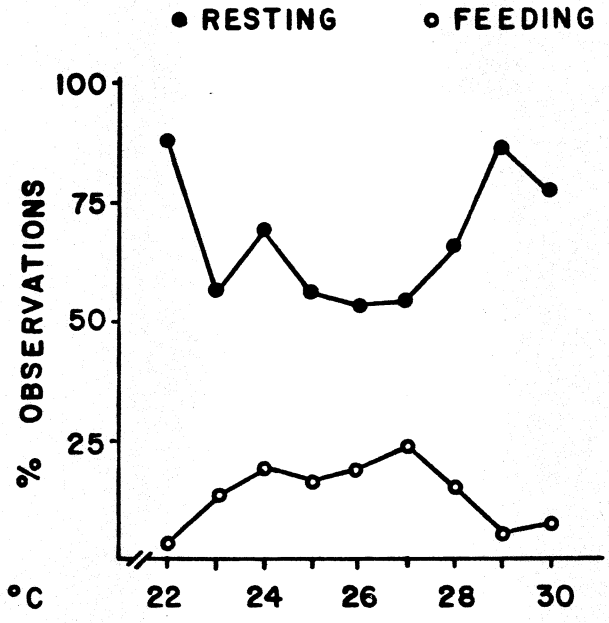
APRIL



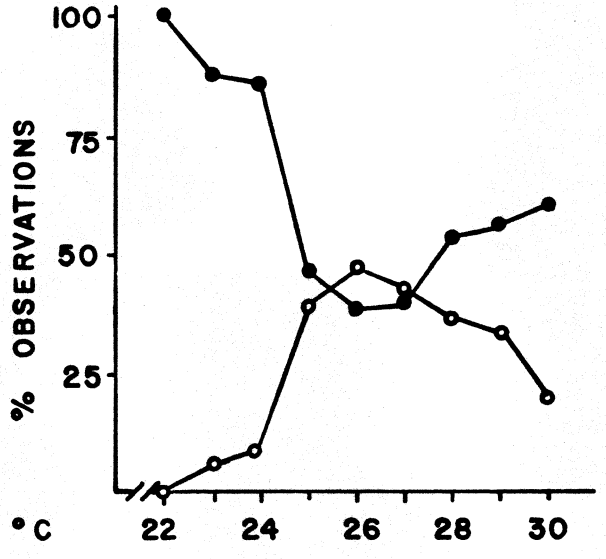
JULY

Fig. 4.6. Seasonal activity patterns, relative to ambient temperature adjacent to each animal, for resting and feeding of giant tortoises on Pinzón. Activities not shown include traveling, mating, agonistic interactions, and drinking. Only those temperatures with N $\geq$ 3 are included. N ranged from 18 to 216.

PINZÓN



HOT-DRY, APRIL/MAY 1982



EL NIÑO, DECEMBER 1982

Table 4.2. ANOVA results listing probabilities ($P \leq$), based on Type III sums of squares, for the significance of discrete variables in explaining proportion of time (arc sine square root) spent by tortoises in each of the six activity categories. Only those month-hour-temperature combinations with N>6 were used in the analyses. Final models include only those variables that were significant. Data for La Caseta and El Chato (CA/CH) were combined.

ACTIVITY	STUDY AREA	SEASON	HOUR	TEMP	HOUR x TEMP	MONTH	FINAL MODEL R^2	FINAL MODEL P
RESTING	CA/CH	All	.0001	.0001	NS	.0001	0.62	.0001
		Garúa81	NS	NS	NS	.005	0.26	.005
		HotWet82	NS	.03	NS	.01	0.34	.01
		HotDry82	.0001	NS	.03	.001	0.92	.0001
		Garúa82	.002	.0001	.01	.005	0.88	.0001
		Niño	.0001	NS	NS	NS	0.92	.0001
	SCNZ[a]	Niño	.0002	NS	NS	NS	0.39	.0002
	PINZÓN	All	.02	.002	NS	NS	0.53	.0001
FEEDING	CA/CH	All	.0001	.0001	NS	.0001	0.62	.0001
		Garúa81	NS	NS	NS	.0003	0.34	.0003
		HotWet82	NS	NS	NS	.03	0.09	.03
		HotDry82	.0001	NS	.03	.0002	0.90	.0002
		Garúa82	.0001	NS	NS	NS	0.73	.0001
		Niño	.0004	NS	NS	NS	0.87	.0004
	SCNZ[a]	Niño	.0001	NS	NS	NS	0.42	.0001
	PINZÓN	All	NS	.0001	NS	.001	0.41	.0001
TRAVEL	CA/CH	All	.0001	NS	NS	.0001	0.20	.0001
		Garúa81	NS	NS	NS	NS	-	NS
		HotWet82	NS	NS	NS	NS	-	NS
		HotDry82	.007	NS	NS	NS	0.26	.007
		Garúa82	NS	.0003	NS	.001	0.21	.0001
		Niño	NS	NS	NS	NS	-	NS
	SCNZ[a]	Niño	NS	NS	NS	NS	-	NS
	PINZÓN	All	NS	.006	NS	.005	0.26	.001

Table 4.2 continued.

ACTIVITY	STUDY AREA	SEASON	HOUR	TEMP	HOUR x TEMP	MONTH	FINAL MODEL R^2	FINAL MODEL P
MATING	CA/CH	All	NS	.04	NS	.0001	0.21	.0001
		Garúa81	.03	.03	.03	.001	0.97	.01
		HotWet82	NS	NS	NS	NS	-	NS
		HotDry82	NS	NS	NS	NS	-	NS
		Garúa82	NS	NS	NS	NS	-	NS
		Niño	NS	NS	NS	NS	-	NS
	SCNZ[a]	Niño	NS	NS	NS	NS	-	NS
	PINZÓN	All	NS	NS	NS	NS	-	NS
AGONISTIC INTERACT	CA/CH	All	NS	NS	NS	.005	0.08	.005
		Garúa81	NS	NS	NS	NS	-	NS
		HotWet82	NS	NS	NS	NS	-	NS
		HotDry82	NS	NS	NS	NS	-	NS
		Garúa82	NS	NS	NS	NS	-	NS
		Niño	NS	NS	NS	NS	-	NS
	SCNZ[a]	Niño	NS	NS	NS	NS	-	NS
	PINZÓN	All	NS	NS	NS	.02	0.06	.02
DRINKING	CA/CH	All	.02	NS	NS	.0001	0.19	.0001
		Garúa81	NS	NS	NS	NS	-	NS
		HotWet82	NS	.01	.01	NS	0.90	.01
		HotDry82	NS	NS	NS	NS	-	NS
		Garúa82	.05	NS	NS	.0004	0.18	.001
		Niño	NS	NS	NS	NS	-	NS
	SCNZ[a]	Niño	NS	NS	NS	NS	-	NS
	PINZÓN	All	.01	NS	NS	NS	0.27	.01

[a]Santa Cruz Nesting Zone.

ables included hour, air temperature, monthly precipitation (total precipitation measured monthly at La Caseta, and for each visit to SCNZ and Pinzón), total available food (g/m^2), water content of the food (%), and water content of the diet (%) (Table 4.3). All independent variables, excluding hour and temperature, were the same for a given month (Caseta/Chato), or trip (SCNZ and Pinzón), and were included in an attempt to determine why month was an important factor. Although several factors emerged as being significant, R^2s were generally low (Table 4.3). Results from stepwise regressions for El Niño at Caseta/Chato, and for Pinzón were omitted from the table. The little data at Caseta/Chato for El Niño produced no significant results. The only significant result for Pinzón was a negative relationship between time spent drinking and hour of the day ($R^2 = 0.06$, $P < .01$).

Correlations between each activity and the environmental parameters indicate the direction of each significant relationship appearing in the stepwise regression analyses (Table 4.4).

With all other variables controlled, time spent feeding increased with increasing total available food, water content of the food, and temperature (especially in the cool garúa season) (Table 4.4). Feeding time decreased with monthly precipitation for all Caseta/Chato data combined, while showing a positive relationship to precipitation in garúa season 1981, and the hot-dry season 1982. Given that

Table 4.3. Results of stepwise regressions of each activity[a] versus the following environmental parameters: hour, air temperature (TEMP, °C), monthly precipitation (PRECIP, mm)[b], total available food (FOOD, g/m^2), water content of the food (HOHFD)[a], and water content of the diet (HOHDT)[a]. Variables included in the final model were significant at $P \leq .05$*, .01**, .001***, and .0001****.

		LA CASETA/EL CHATO (Season)					SCNZ[c]
ACTIVITY	VARIABLE ORDER	All	Garúa81	HotWet82	HotDry82	Garúa82	El Niño
RESTING	1	HOHFD****	HOHFD***	HOHFD**	HOUR****	TEMP****	HOUR**
	2	PRECIP****			FOOD****	HOHDT****	TEMP*
	3	TEMP****				FOOD****	
	4	HOUR****					
	5	FOOD**					
	MODEL	$R^2 = 0.20$	$R^2 = 0.19$	$R^2 = 0.08$	$R^2 = 0.46$	$R^2 = 0.34$	$R^2 = 0.19$
		$P \leq .0001$	$P \leq .001$	$P \leq .01$	$P \leq .0001$	$P \leq .0001$	$P \leq .001$
FEEDING	1	HOHFD****	HOHFD***	HOHFD**	FOOD****	TEMP****	HOUR***
	2	PRECIP****	PRECIP**		HOUR****	PRECIP*	
	3	FOOD****	FOOD**		PRECIP*		
	4	TEMP****	TEMP*				
	MODEL	$R^2 = 0.24$	$R^2 = 0.36$	$R^2 = 0.08$	$R^2 = 0.36$	$R^2 = 0.38$	$R^2 = 0.15$
		$P \leq .0001$	$P \leq .001$	$P \leq .01$	$P \leq .0001$	$P \leq .0001$	$P \leq .001$

Table 4.3 continued.

ACTIVITY	VARIABLE ORDER	LA CASETA/EL CHATO (Season)					SCNZ[c]
		All	Garúa81	HotWet82	HotDry82	Garúa82	El Niño
TRAVELING	1	HOUR****	HOHDT*		HOUR****	PRECIP****	
	2	TEMP***				TEMP****	
	3	HOHFD****				HOUR*	
	4	HOHDT***					
	MODEL	R^2 = 0.08	R^2 = 0.08		R^2 = 0.15	R^2 = 0.13	
		P≤ .0001	P≤ .05	NS	P≤ .0001	P≤ .0001	NS
MATING	1	FOOD****	PRECIP***	TEMP*		FOOD***	HOUR*
	2	TEMP****	HOHDT**			TEMP*	
	3	HOUR*					
	MODEL	R^2 = 0.11	R^2 = 0.23	R^2 = 0.05		R^2 = 0.06	R^2 = 0.05
		P≤ .0001	P≤ .01	P≤ .05	NS	P≤ .002	P< .03
AGONISTIC INTERACTION	1	HOHFD**	HOHDT*	TEMP*	HOUR***	TEMP**	
	2				FOOD**		
	3				PRECIP*		
	MODEL	R^2 = 0.02	R^2 = 0.11	R^2 = 0.05	R^2 = 0.15	R^2 = 0.03	
		P≤ .01	P≤ .02	P≤ .05	P≤ .001	P≤ .01	NS

Table 4.3 continued.

ACTIVITY	VARIABLE ORDER	LA CASETA/EL CHATO (Season)					SCNZ[c]
		All	Garúa81	HotWet82	HotDry82	Garúa82	El Niño
DRINKING	1	HOHFD****	HOUR***			HOHDT**	
	2	PRECIP***					
	3	HOUR*					
	MODEL	R^2 = 0.10	R^2 = 0.21			R^2 = 0.05	
		$P \leq .0001$	$P \leq .001$	NS	NS	$P \leq .01$	NS

[a]Arc sine square root of the proportion.

[b]Precipitation per trip at the Santa Cruz Nesting Zone.

[c]Santa Cruz Nesting Zone.

Table 4.4. Significant correlation coefficients (models with only one independent variable) and partial correlation coefficients (models with greater than one independent variable) for tortoise activities with those environmental parameters significant in stepwise regressions (Table 4.3). Parameters include hour, air temperature (TEMP, °C), monthly precipitation (PRECIP, mm)[a], total available food (FOOD, g/m^2), water content of the food (HOHFD)[b], and water content of the diet (HOHDT)[b]. Significance levels at P≤ .05*, .01**.

		LA CASETA/EL CHATO (Season)					SCNZ[c]
ACTIVITY	VARIABLE	All	Garúa81	HotWet82	HotDry82	Garúa82	El Niño
RESTING	HOUR	+.15**			+.62**		-.30**
	TEMP	-.26**				-.57**	NS
	PRECIP	+.32**					
	FOOD	-.10*			-.39**	-.27**	
	HOHFD	-.35**	-.26**	-.28**			
	HOHDT					-.29**	
FEEDING	HOUR				-.44**		+.36**
	TEMP	+.20**	+.28*			+.49**	
	PRECIP	-.37**	+.29*		+.20*	NS	
	FOOD	+.24**	+.28*		+.47**		
	HOHFD	+.33**	+.34**	+.29**			
TRAVELING	HOUR	-.16**			-.38**	NS	
	TEMP	+.21**				+.27**	
	PRECIP					-.21**	
	HOHFD	+.12**					
	HOHDT	-.10*	NS				

Table 4.4 continued.

		LA CASETA/EL CHATO (Season)					SCNZ[c]
ACTIVITY	VARIABLE	All	Garúa81	HotWet82	HotDry82	Garúa82	El Niño
MATING	HOUR	NS					NS
	TEMP	+.09*		+.22*		NS	
	PRECIP		-.34**				
	FOOD	-.15**				-.15*	
	HOHDT		-.30**				
AGONISTIC INTERACTION	HOUR				-.31**		
	TEMP			-.22*		+.14*	
	PRECIP				-.22*		
	FOOD				-.25*		
	HOHFD	-.12**					
	HOHDT		NS				
DRINKING	HOUR	-.09*	-.27**				
	PRECIP	-.17**					
	HOHFD	+.27**					
	HOHDT					+.22**	

[a]Precipitation per trip at the Santa Cruz Nesting Zone.

[b]Arc sine square root of the proportion.

[c]Santa Cruz Nesting Zone.

both total available food and water content of the food increase with increasing precipitation, the overall negative relationship between time spent feeding and precipitation may seem paradoxical. However, at La Caseta and El Chato during the two months of highest precipitation at the onset of El Niño, tortoises spent most of their active time in migration rather than feeding. The negative relationship between hour and percent feeding in the hot-dry season 1982, at Caseta/Chato, in contrast to the positive relationship between hour and percent feeding during El Niño at SCNZ, reflects the difference between a relatively dry hot season (1982) and an extremely wet hot season (1983). At both times, daily activity patterns of tortoises tended to be bimodal. However, in the dry hot season of 1982, the highest peak in activity corresponded to the morning peak (Fig. 4.1), while in the wet hot season of 1983, the greatest peak in activity corresponded to the afternoon peak (Fig. 4.2).

The relationships between time spent resting and the environmental parameters were completely opposite to that of feeding, corresponding to the near inverse relationship between the two activities (Table 4.4).

In general, time spent traveling followed the same patterns as time feeding (Table 4.4). The negative relationship between traveling and water content of the diet does not follow the general pattern.

Mating and agonistic interactions were seasonal, with the highest concentration of either type of interaction

occurring during the hot season (January-June) regardless of precipitation or available food. This is most evident in the overall numbers of interactions observed (Table 4.1).

Tortoises concentrated their drinking in the early hours of the day (Table 4.4). The proportion of time spent drinking decreased with increasing precipitation, while increasing with water content of the food (Table 4.4). This also appears paradoxical, but may be explained by the fact that at very high levels of precipitation tortoises are probably satiated and thus seldom drink, while at the initiation of rainfall following a period of drought, tortoises tend to drink immediately and often. The onset of a rainy season coincides with increases in available food and water content of the food, while at high levels of precipitation these factors remain relatively constant.

Daily Time Budgets

Daily time budgets were obtained from observing focal animals for 2-day periods from dawn to dusk (Table 4.5). Focal animal observations were begun in April/May 1982, on Pinzón, and continued in all study areas for the duration of the study. Both males and females as well as smaller animals that were unsexable were observed. Tortoise size (curved width and curved length of the carapace) varied among locations and between sexes (Fig. 4.7). Comparisons of daily time budgets were done to determine differences among seasons and study areas, as well as among sizes and sexes of tortoises.

Table 4.5. List of focal animals (FA) observed, with dates of observation, specific animal characteristics, and environmental parameters. Tortoise measurements include the curved width (CW) and the curved length (CL) of the carapace (cm). Minimum (TMIN) and maximum (TMAX) air temperatures (°C), and precipitation (FAPRECIP) are for the 2-day period of observation only.

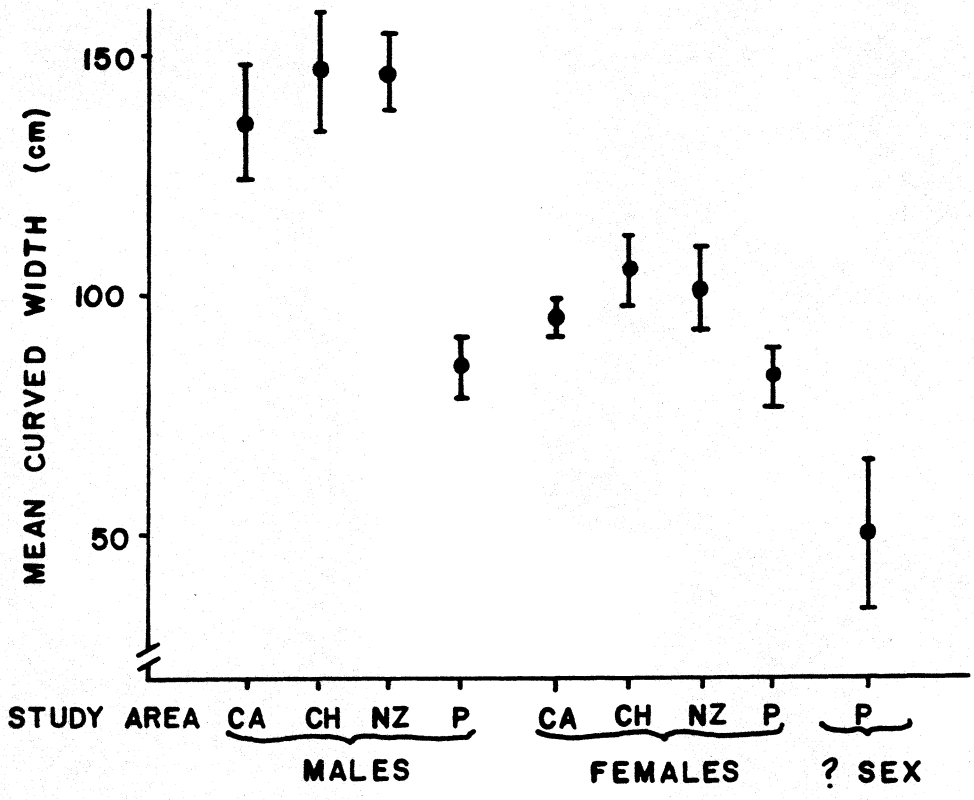
STUDY AREA	SEASON	FA No.	OBSERVATION DATES	SEX	CW	CL	TMIN	TMAX	FAPRECIP (mm)
CASETA	HotDry82	1	June 6-7	?	119	107	22.0	30.0	6.86
		2	June 8-9	M	134	122	21.0	31.5	2.54
	Garúa82	3	July 16-17	F	90	85	21.5	26.0	12.19
		6	July 24-25	M	158	139	20.0	26.5	0.51
		7	Aug. 15-16	M	129	114	19.0	26.5	5.84
		9	Aug. 27-28	F	97	85	21.5	26.0	10.16
		12	Aug. 28-29	F	95	92	21.0	28.5	6.35
		13	Sept. 18-19	M	125	117	21.0	28.0	6.35
		16	Oct. 11-12	M	138	124	20.5	28.0	0.0
		19	Nov. 5-6	F	96	89	21.0	29.5	6.60
	El Niño	22	Feb. 5-6	M	144	134	23.0	29.0	85.09
		27	Mar. 21-22	M	128	121	24.0	30.0	29.21
CHATO	Garúa82	4	July 19-20	M	148	144	21.0	25.0	7.62
		5	July 21-22	F	111	100	20.0	25.5	15.49
		14	Sept. 22-24[a]	M	148	128	20.0	24.0	12.70
		15	Sept. 24-25	M	123	106	20.0	27.0	3.81
		17	Oct. 21-22	F	97	89	21.5	31.0	7.62
		18	Oct. 23-24	F	103	93	19.5	31.0	0.51
		20	Nov. 8-9	F	108	96	22.0	28.0	12.70
		21	Nov. 10-11	M	151	145	21.5	27.5	12.70
	El Niño	23	Feb. 9-10	M	156	138	20.5	31.5	43.82
		32	May 23-24	M	157	145	23.0	35.0	50.80
SCNZ[b]	El Niño	24	Feb. 25-26	F	87	83	24.5	31.5	89.41
		25	Feb. 27-28	M	148	142	24.0	31.5	26.67
		26	Mar. 1-2	F	102	92	25.0	32.5	19.05
		29	Apr. 11-12	F	110	101	24.5	32.5	7.37
		30	Apr. 15-16	M	154	140	25.0	30.5	11.68

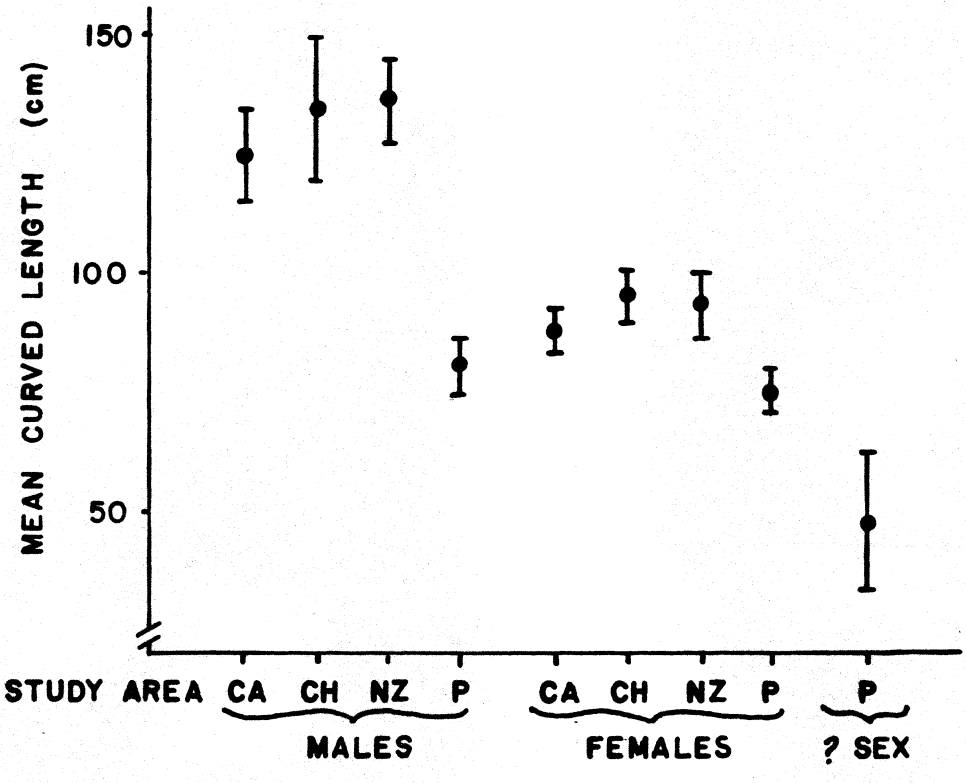
Table 4.5 continued.

STUDY AREA	SEASON	FA No.	OBSERVATION DATES	SEX	CW	CL	TMIN	TMAX	FAPRECIP (mm)
SCNZ[b]	El Niño	31	Apr. 17-18	F	103	89	24.5	33.0	39.12
		33	July 13-14	F	104	94	24.5	32.0	6.10
		34	July 17-18	M	139	127	23.0	30.0	11.18
PINZÓN	HotDry82	35	Apr. 25-26	?	58	56	22.5	33.5	0.0
		36	Apr. 27-28	F	88	75	22.5	31.0	1.27
		37	Apr. 29-30	M	93	86	22.0	31.0	1.52
		38	Apr. 29-30	M	89	81	22.0	31.0	1.52
		39	May 1-2	M	82	79	22.0	30.0	3.05
		40	May 3-4	F	88	81	22.5	31.0	0.0
		41	May 4-5	M	85	82	22.5	30.5	0.0
		42	May 6-7	F	83	77	22.0	30.5	0.0
		43	May 7-8	M	80	79	22.0	30.0	0.0
		44	May 8-9	F	78	72	22.5	29.5	0.0
	El Niño	45	Dec. 2-3	F	83	77	23.0	29.0	1.02
		46	Dec. 4-5	?	59	54	23.5	28.0	6.86
		47	Dec. 4-5	M	90	84	23.0	27.5	6.86
		48	Dec. 6-7	?	56	54	22.0	26.5	27.69
		49	Dec. 6-7	?	27	26	22.0	29.0	27.69
		50	Dec. 9-10	F	88	73	23.0	31.0	56.90
		51	Dec. 11-12	M	77	70	23.0	30.0	10.16
		52	Dec. 13-14	F	81	80	22.5	30.0	46.48
		53	Dec. 14-15	F	72	66	23.0	29.5	44.45

[a]Observation period from 1230h, September 22, to 1230h, September 24.
[b]Santa Cruz Nesting Zone.

Fig. 4.7. Mean carapace size of focal animals at La Caseta (CA), El Chato (CH), the Santa Cruz Nesting Zone (NZ), and Pinzón (P). Mean ± 1 standard deviation are indicated.


MEAN CURVED WIDTH (cm)
150
100
50
STUDY AREA
CA
CH
NZ
P
CA
CH
NZ
P
P
MALES
FEMALES
? SEX


MEAN CURVED LENGTH (cm)
150
100
50
STUDY AREA
CA
CH
NZ
P
CA
CH
NZ
P
P
MALES
FEMALES
? SEX

Giant tortoises are diurnal, attuned to the 24-hour circadian rhythm (Auffenberg and Iverson 1979). Due to the latitudinal position of the Galápagos Islands across the equator, and the resulting 12 and 1/2 hours of daylight year-round, one might expect tortoises to maintain a similar cycle of activity throughout the year. However, due to the fact that tortoises become less active during periods of stress (eg., drought conditions) and are able to sleep for days or weeks at a time (Swingland and Lessells 1979), cycle length may be dependent on environmental conditions with the length of a single cycle of activity for an individual tortoise varying from a period of 24 h to one of many days.

Day-to-day changes in time budgets of focal animals were examined by use of a paired t-test comparing the time budget of the first day of observation with that of the second day. Analyses were done for each activity separately, by study area, sex, and season (Table 4.6). Proportion of the day resting differed significantly between day 1 and day 2 only on Pinzón, in both the dry and the wet season when all animals were combined. Time spent feeding differed between day 1 and day 2 for females, as well as females and males together, in the cool garúa season 1982, at Caseta/Chato, and for males during El Niño at SCNZ. Traveling time differed only when all tortoises were considered together for the hot-dry season on Pinzón. Interaction (including both mating and agonistic interactions) showed a significant difference only in the cool garúa season 1982, at Caseta/Chato,

Table 4.6. Level of significance ($P \leq$) resulting from paired t-tests comparing time budgets of focal animals on the first day of observation with those on the second. Activities include resting (R), feeding (F), traveling (T), interacting (I, includes both mating and agonistic interactions), and drinking (D). Data from La Caseta and El Chato (CA/CH) were combined.

STUDY AREA	SEASON	SEX	N	R	F	T	I	D
CA/CH	HotDry82	All	2	-	-	-	-	-
	Garúa82	All	16	-	.05	-	.02	-
		M	8	-	-	-	-	-
		F	8	-	.004	-	-	-
	Niño	M	4	-	-	-	-	-
SCNZ[a]	Niño	All	8	-	-	-	-	-
		M	3	-	.05	-	-	-
		F	5	-	-	-	-	-
PINZÓN	HotDry82	All	10	.03	-	.05	-	-
		M	5	-	-	-	-	-
		F	4	-	-	-	-	-
	Niño	All	9	.01	-	-	-	-
		M	2	-	-	-	-	-
		F	4	-	-	-	-	-

[a]Santa Cruz Nesting Zone.

when all tortoises were considered together. Drinking, a very small proportion of the daily time budget, showed no significant differences between day 1 and day 2.

These results show few consistent differences, suggesting that, in general, a single cycle of activity for a tortoise was consistent with the 24-h day within the seasons examined. However, no focal animal studies were done at the most stressful time for tortoises, during the drought conditions present at La Caseta and El Chato in April/May 1982. At that time, many tortoises were observed sleeping in the same location and position for many days at a time. Therefore, under severe drought conditions the cycle of activity of an individual tortoise will probably extend well beyond the 24-h day. The fact that tortoises were observed active at some time nearly every day during the same period on Pinzón may relate to the availability of cactus, an extremely wet food, whereas, at La Caseta and El Chato, available foods were very low in water content.

In all further analyses of daily time budgets, proportion of day spent in each activity will be the mean of activity times for day 1 and day 2 for each tortoise.

Daily time budgets may differ by season, by location, or by sex of the tortoise. To determine to what extent these factors effect daily time budgets, general linear models were run for each activity with season, location, and sex included as discrete variables (Tables 4.7-4.11). Continuous independent variables included monthly precipitation

Table 4.7. Results of statistical analyses to determine which factors[a] were significantly related to the proportion of time spent resting (transformed to the arc sine square root, in radians). Mean % values indicated for Tukey's test and the t test below the transformed data. Variables included in the final models were significant at $P \leq .05$*, .01**, .001***, and .0001****.

STATISTICAL ANALYSIS	STUDY AREA[b]	N	SIGNIFICANT VARIABLES	R^2	REGRESSION EQUATION
ANOVA	ALL	49	SEASON***	0.26	
	CA/CH	22	FOOD*	0.24	REST = -0.002 FOOD + 1.06
	SCNZ	8		NS	
	PINZÓN	19	SEASON**	0.46	
STEPWISE REGRESSION	ALL	49	MOPRECIP**	0.12	REST = -0.0004 MOPRECIP + 1.01
	PINZÓN	19	TMAX**	0.34	REST = 0.05 TMAX - 0.55

TUKEY'S TEST - All Study Areas, df = 42, $P \leq .05$

SEASON	HotDry82	Garúa82	El Niño
N	12	16	21
MEAN	1.08	0.94	0.89
MEAN %	76.9	64.3	60.5

T TEST - PINZÓN, df = 17, $P \leq .002$

SEASON	HotDry82	El Niño
N	10	9
MEAN	1.08	0.90
MEAN %	77.4	61.7

[a] Significant factors included: season; total available food (FOOD, g/m^2); monthly precipitation (MOPRECIP, per trip at SCNZ[b] and Pinzón, mm); and average maximum air temperature (TMAX, °C, for the 2-day period).

[b] La Caseta and El Chato = CH/CH; Santa Cruz Nesting Zone = SCNZ.

Table 4.8. Results of statistical analyses to determine which factors[a] were significantly related to the proportion of time spent feeding (transformed to the arc sine square root, in radians). Mean % values indicated for Tukey's tests and the t test below the transformed data. Variables included in the final models were significant at $P \leq .05$*, .01**, .001***, and .0001****.

STATISTICAL ANALYSIS	STUDY AREA[b]	N	SIGNIFICANT VARIABLES	R^2	s_y^2	r_p
ANOVA	ALL	49	MODEL****	0.55		
			SEASON****			
			LOC*			
	CA/CH	22	MODEL**	0.56		
			SEASON**			
			FOOD**			
	SCNZ	8		NS		
	PINZÓN	19	SEASON****	0.60		
STEPWISE REGRESSION	ALL	49	MODEL***	0.27		
			MOPRECIP**		0.20	+.36
			FOOD*		0.07	+.30
		45	MODEL****	0.55		
			HOHFD****		0.35	+.66
			FOOD****		0.20	+.56
	CA/CH	22	FOOD***	0.43[c]		
	PINZÓN	19	MODEL***	0.56		
			TMAX**		0.37	-.61
			FAPRECIP*		0.19	+.55

TUKEY'S TEST - All Study Areas, df = 42, $P \leq .05$

SEASON	HotDry82	Garúa82	El Niño	
N	12	16	21	
MEAN	0.28	0.51	0.55	
MEAN %	8.7	24.6	27.4	
LOC	**Caseta**	**Pinzón**	**Chato**	**SCNZ[b]**
N	12	19	10	8
MEAN	0.39	0.41	0.57	0.58
MEAN %	16.0	18.0	29.4	30.8

Table 4.8 continued.

TUKEY'S TEST - Caseta/Chato, df = 19, P ≤ .05

SEASON	HotDry82	El Niño	Garúa82
N	2	4	16
MEAN	0.20	0.47	0.51
MEAN %	4.1	20.8	24.6

T TEST - Pinzón, df = 17, P ≤ .0001

SEASON	HotDry82	El Niño
N	10	9
MEAN	0.29	0.55
MEAN %	9.6	27.3

[a]Significant factors included: season; location (LOC); total available food (FOOD, g/m^2); monthly precipitation (MOPRECIP, mm, monthly at La Caseta and El Chato, per trip at SCNZ[b] and Pinzón); water content of the food (HOHFD, transformed to arc sine square root of the proportion, in radians); average maximum air temperature for the 2-day period (TMAX, °C); and precipitation during the 2 days of observation (FAPRECIP, mm).

[b]La Caseta and El Chato = CA/CH; Santa Cruz Nesting Zone = SCNZ.

[c]Regression equation: FEED = 0.003 FOOD + 0.27.

Table 4.9. Results of statistical analyses to determine which factors[a] were significantly related to the proportion of time spent traveling (transformed to the arc sine square root, in radians). Mean % values indicated for Tukey's test and the t test below the transformed data. Variables included in the final models were significant at P ≤ .05*, .01**, .001***, and .0001****. Also included are the results of Tukey's test for average distance traveled per day (m/day) in relation to location.

STATISTICAL ANALYSIS	STUDY AREA[b]	N	SIGNIFICANT VARIABLES	R^2	REGRESSION EQUATION
ANOVA	ALL	49	LOC****	0.36	
	CA/CH	22	LOC**	0.32	
	SCNZ	8	FAPRECIP*	0.50	TRAVEL = 0.0007 FAPRECIP + 0.19
	PINZÓN	19		NS	
STEPWISE REGRESSION	ALL	49	CW*	0.08	TRAVEL = -0.0007 CW + 0.36
	CA/CH	22		NS	

TUKEY'S TEST - All Study Areas, df = 42, P ≤ .05

LOC	Caseta	Pinzón	Chato	SCNZ[b]
N	12	19	10	8
MEAN	0.33	0.31	0.24	0.21
MEAN %	11.0	9.4	6.2	4.3

T TEST - Caseta/Chato, df = 20, P ≤ .01

LOC	Caseta	Chato
N	12	10
MEAN	0.33	0.24
MEAN %	11.0	6.2

TUKEY'S TEST - Average Distance/Day, df = 22, P ≤ .05

LOC	Caseta	Pinzón	Chato	SCNZ[b]
N	3	9	6	8
MEAN	243.33	166.94	128.83	57.56

[a]Significant factors included: location (LOC); precipitation during the 2 days of observation (FAPRECIP, mm); and curved width of the carapace (CW, cm).

[b]La Caseta and El Chato = CA/CH; Santa Cruz Nesting Zone = SCNZ.

Table 4.10. Results of statistical analyses to determine which factors[a] were significantly related to the proportion of time spent in interactions (transformed to the arc sine square root, in radians). Mean % values indicated for Tukey's test and the t test below the transformed data. Variables included in the final models were significant at P ≤ .05*, .01**, .001***, and .0001****.

STATISTICAL ANALYSIS	STUDY AREA[b]	N	SIGNIFICANT VARIABLES	R^2	s_y^2	r_p
ANOVA	ALL	49	MODEL*	0.13		
			TMAX*		0.07	+.30
			FAPRECIP*		0.08	NS
	CA/CH	22	SEASON****	0.64		
	SCNZ	8		NS		
	PINZÓN	19	SEASON*	0.25		
STEPWISE REGRESSION	CA/CH	22	MODEL**	0.36		
			FOOD**		0.14	-.55
			TMAX*		0.22	+.51
		18	HOHDT***	0.57[c]		
	PINZÓN	19		NS		

TUKEY'S TEST - Caseta/Chato, df = 15, P ≤ .05

SEASON	HotDry82	Garúa82	El Niño
N	2	16	4
MEAN	0.36	0.07	0.05
MEAN %	12.8	0.9	0.5

T TEST - Pinzón, df = 10.5[d], P ≤ .03

SEASON	HotDry82	El Niño
N	10	9
MEAN	0.15	0.04
MEAN %	3.5	0.3

[a] Significant factors included: average maximum air temperature for the 2-day period of observation (TMAX, °C); precipitation during the 2 days of observation (FAPRECIP, mm); season; total available food (FOOD, g/m^2); and water content of the diet (HOHDT, arc sine square root of the proportion, in radians).

[b] La Caseta and El Chato = CA/CH; Santa Cruz Nesting Zone = SCNZ.

[c] Regression equation: INTERACT = 1.2 HOHDT + 1.3.

[d] Variances were unequal.

Table 4.11. Results of statistical analysis to determine which factors[a] were significantly related to the proportion of time spent drinking (transformed to the arc sine square root, in radians). Mean % values indicated for Tukey's test below the transformed data. Variables included in the final models were significant at $P \leq .05$*, .01**, .001***, .0001****.

STATISTICAL ANALYSIS	STUDY AREA[b]	N	SIGNIFICANT VARIABLES	R^2	REGRESSION EQUATION
ANOVA	ALL	49	SEASON*	0.13	
	CA/CH	22		NS	
		18	HOHFD**	0.33	DRINK = 0.91 HOHFD - 0.83
	SCNZ	8		NS	
	PINZÓN	19		NS	
STEPWISE REGRESSION	ALL	49	TMAX**	0.13	DRINK = -0.01 TMAX + 0.4

TUKEY'S TEST - All Study Areas, df = 42, P = NS

SEASON	Garúa82	HotDry82	El Niño
N	16	12	21
MEAN	0.10	0.05	0.05
MEAN %	1.8	0.6	0.4

[a] Significant factors included: season; water content of the food (HOHFD, transformed to arc sine square root of the proportion, in radians); and the average maximum air temperature for the 2-day period (TMAX, °C).

[b] La Caseta and El Chato - CA/CH; Santa Cruz Nesting Zone = SCNZ.

(MOPRECIP, monthly at La Caseta and El Chato, per trip at SCNZ and Pinzón), precipitation during the 2 days of observation, minimum temperature (average minimum temperature recorded during the two days of observation), maximum temperature (average maximum temperature recorded during the two days of observation), total available food (FOOD, g/m^2), water content of the available food (HOHFD, %), water content of the diet (HOHDT, %), and curved width (cm) and curved length (cm) of the tortoise. HOHFD and HOHDT data were unavailable for the four tortoises observed at La Caseta and El Chato during El Niño.

For those study areas with results that included any of the discrete variables in the final model, a separate stepwise regression was run with all the continuous variables in an attempt to explain which of the factors, themselves dependent on season, location, and/or sex, had a significant effect on daily time budgets (Tables 4.7-4.11). Only two measurements of FOOD were done at SCNZ, thus FOOD was excluded from the analysis. For Pinzón, where only two seasons were included, MOPRECIP, FOOD, HOHFD, and HOHDT could not be included in the regression, each variable having only two levels.

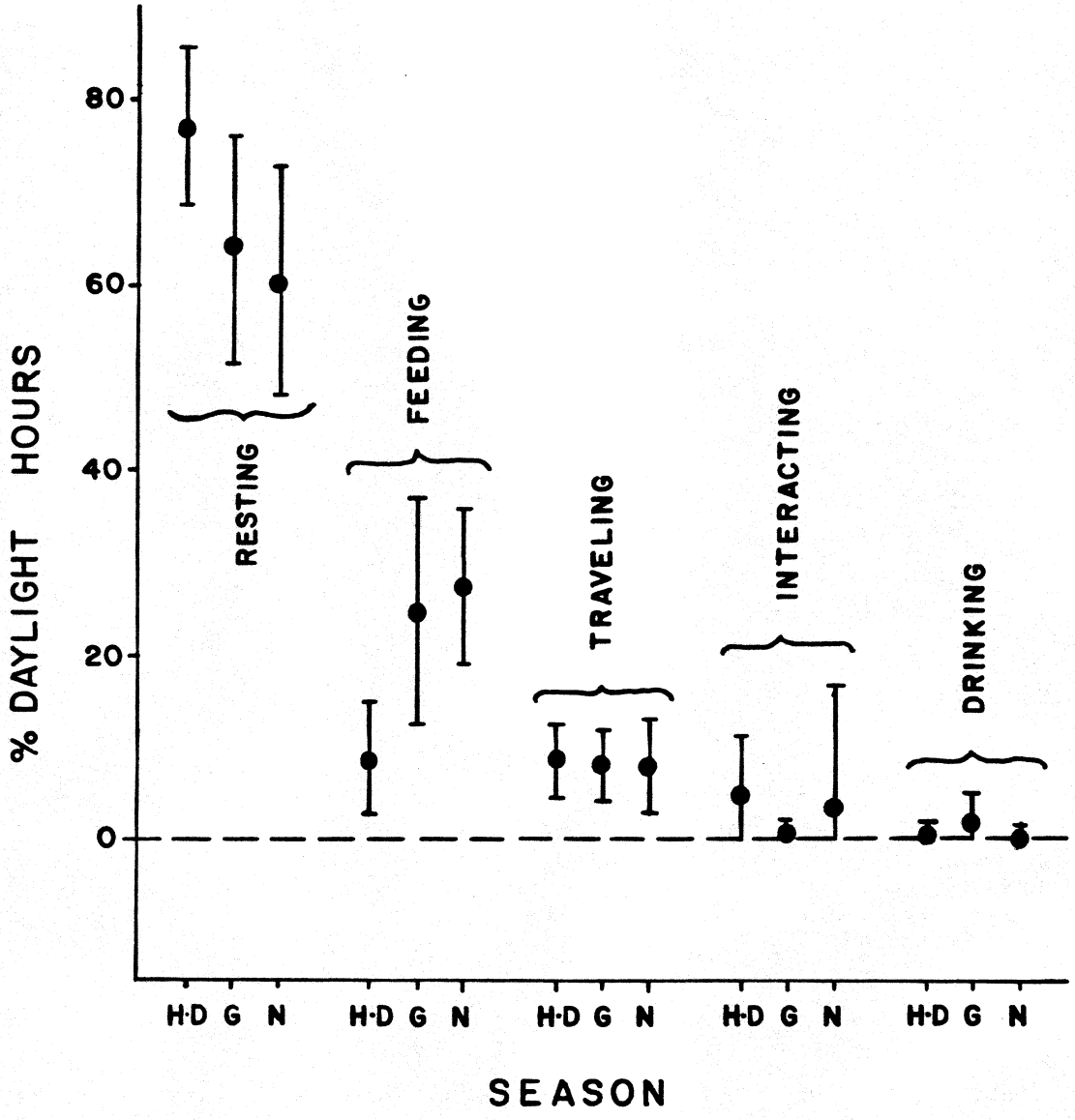
Secondary analyses were then run for those ANOVAs with significant discrete variables (Tables 4.7-4.11). For those variables with greater than two levels, Tukey's Studentized Range Test was used, while a t-test was used for those variables with only two levels.

Sex was never significantly related to the proportion of daylight hours spent in any of the five activities (Tables 4.7-4.11). Females and males, as well as the smaller unsexable tortoises, although the sample size for the latter was small, maintained the same basic daily time budgets. Therefore, any seasonal trends in time budgets should be observed in all animals.

Data from SCNZ included males and females in a single season at a single location. With no effect due to sex, it would be expected that activity times at SCNZ would show no significant relationship to any of the remaining variables. This held true for all activities except traveling, which did increase with higher levels of precipitation during the two days of focal animal observation (Table 4.9).

Season was the dominant factor affecting daily time budgets of tortoises (Tables 4.7-4.11, Fig. 4.8). It was found to be significant for at least one data set for every activity except traveling. Season was important in amount of time resting for all study areas combined, with tortoises resting less as monthly precipitation increased (Table 4.7). At Caseta/Chato, where observations were concentrated in garúa season 1982, season did not emerge as significant. However, resting time did decrease as the total available food increased. On Pinzón, where seasonal differences were most dramatic, season was again highly significant, with tortoises spending more time resting and less time feeding in the hot season compared to El Niño (Table 4.7, 4.8).

Fig. 4.8. Percent of the 12 1/2 hours of daylight that focal animals spent in each of the five activity categories, by season, with data from all study areas combined. N = 12, 16, and 21, for the Hot-Dry season 1982 (H·D), Garúa 1982 (G), and El Niño (N), respectively. Interacting included both mating and agonistic interactions.


% DAYLIGHT HOURS
80
60
40
20
0
RESTING
FEEDING
TRAVELING
INTERACTING
DRINKING
H·D G N
H·D G N
H·D G N
H·D G N
H·D G N
SEASON

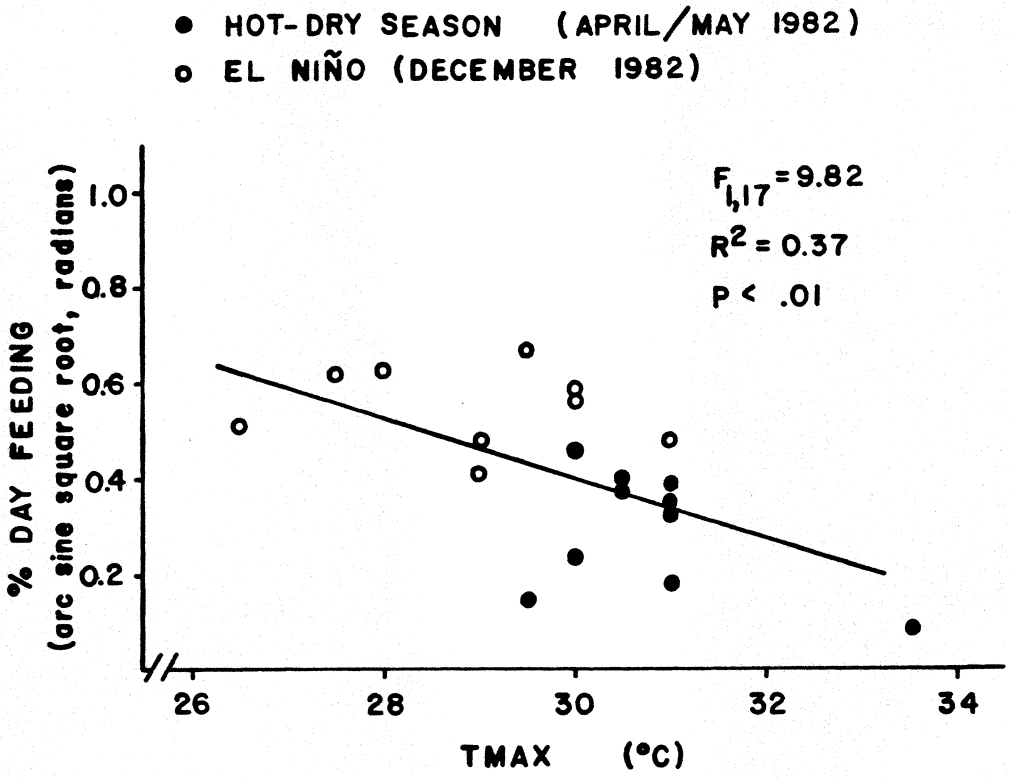
Both time spent resting and time spent feeding were significantly correlated to maximum temperature (Fig. 4.9).

Feeding was the activity most affected by season and the other variables measured (Table 4.8). For all study areas combined, amount of time spent feeding was significantly related to both season and location. Tortoises fed more as monthly precipitation and total available food increased (Fig. 4.10). When water content of the food was included in the regression (eliminating the four focal animals during El Niño at La Caseta and El Chato), it explained the greatest variance in the amount of time spent feeding (Fig. 4.10). At Caseta/Chato, and on Pinzón, amount of time spent feeding was related to season, with tortoises feeding more at higher levels of available food, ie., during the wet seasons.

Traveling was the only activity that had a strong site effect for all study areas combined and even between La Caseta and El Chato (Table 4.9). Tortoises traveled most at La Caseta and on Pinzón, and least at El Chato and SCNZ.

Estimated distance traveled, determined from maps drawn during the 2-day periods of observation for tortoises monitored beginning October 1982, was positively correlated to proportion of the day spent in travel (Fig. 4.11). Distance traveled, like time spent traveling, showed no significant relationship to sex or season (only included garúa 1982 and El Niño). Fowler (1983) also found no seasonal differences in distance traveled by tortoises on Volcán Alcedo. Distance traveled was related to location, similarly to percent

Fig. 4.9. Percent of daylight hours spent feeding and resting by focal animals on Pinzón, relative to average maximum air temperature (TMAX) experienced by each tortoise during the 2 days of observation. Percent of day feeding ranged from 1.3 to 38.7%. Percent of day resting ranged from 47.0 to 91.8%.


● HOT-DRY SEASON (APRIL/MAY 1982)
o EL NIÑO (DECEMBER 1982)
$F_{1,17} = 9.82$
$R^2 = 0.37$
$P < .01$
% DAY FEEDING
(arc sine square root, radians)
1.0
0.8
0.6
0.4
0.2
26
28
30
32
34
TMAX (°C)

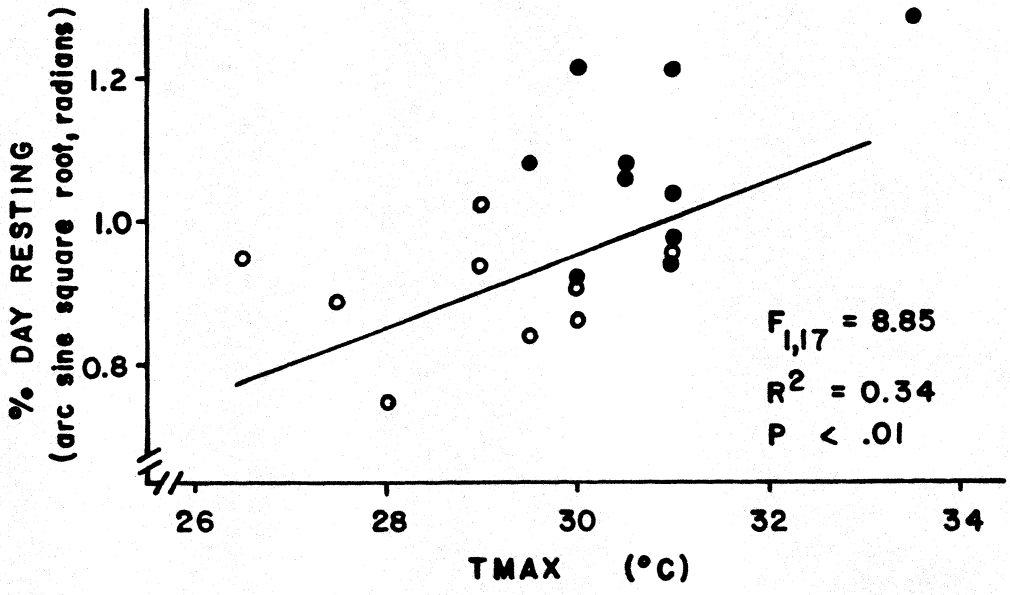
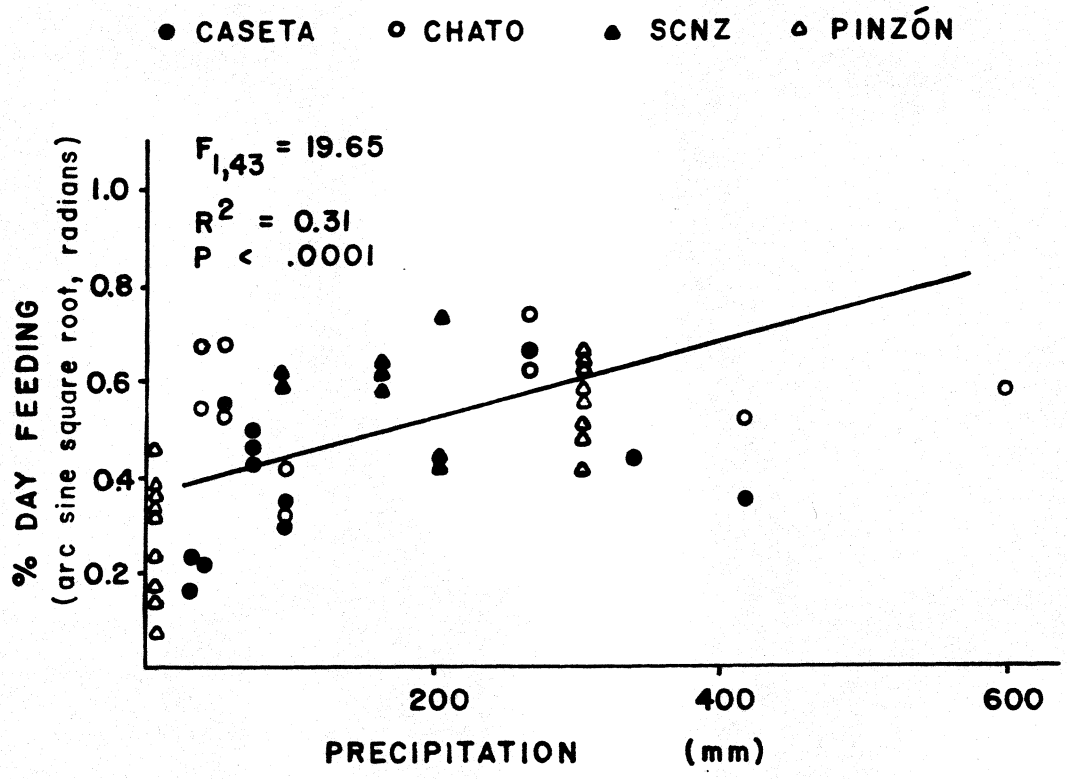

% DAY RESTING
(arc sine square root, radians)
1.2
1.0
0.8
$F_{1,17} = 8.85$
$R^2 = 0.34$
$P < .01$
26
28
30
32
34
TMAX (°C)

Fig. 4.10. Percent of daylight hours spent feeding by focal animals at all study areas relative to precipitation, and water content of the available food. Precipitation for La Caseta and El Chato are monthly totals recorded at La Caseta, while measurements for the Santa Cruz Nesting Zone (SCNZ) and Pinzón include totals for each visit (12-13 days each for SCNZ, and 16-17 days each for Pinzón). At low levels of precipitation (ie., Pinzón, April/May 1982) the effect of this discrepancy would be small. However, for all other data from SCNZ and Pinzón, data points should be shifted to the right. Percent of day feeding ranged from 1.3 to 45.3%.


● CASETA
○ CHATO
▲ SCNZ
△ PINZÓN
$F_{1,43}$ = 19.65
R^2 = 0.31
P < .0001
% DAY FEEDING
(arc sine square root, radians)
1.0
0.8
0.6
0.4
0.2
200
400
600
PRECIPITATION (mm)

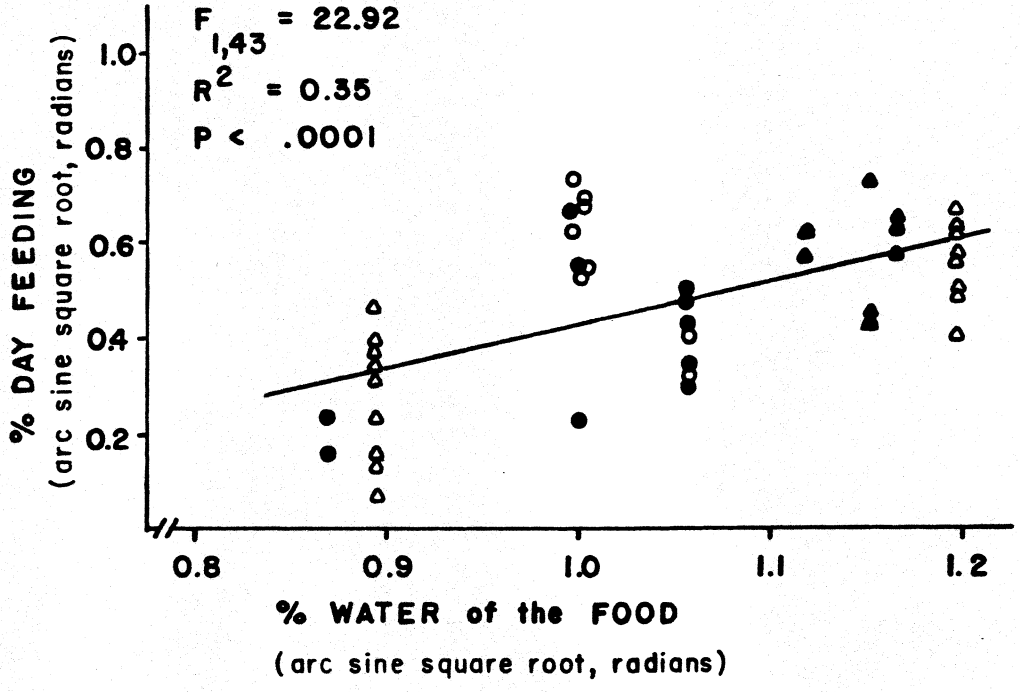
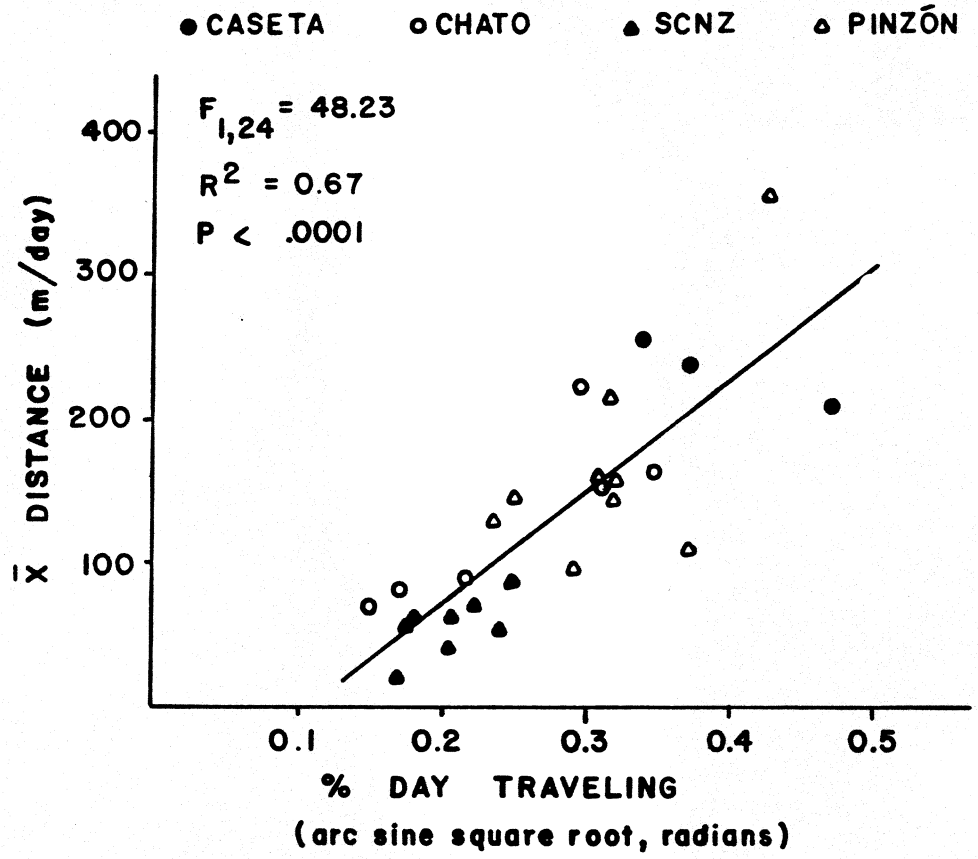
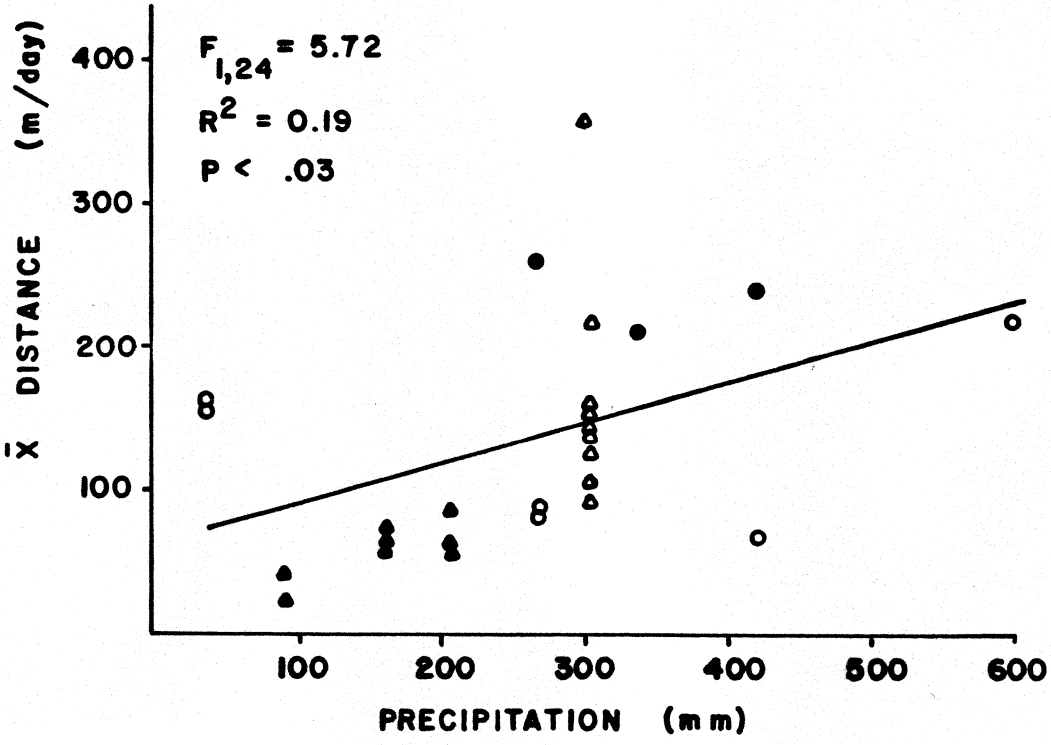

$F_{1,43}$ = 22.92
R^2 = 0.35
P < .0001
% DAY FEEDING
(arc sine square root, radians)
1.0
0.8
0.6
0.4
0.2
0.8
0.9
1.0
1.1
1.2
% WATER of the FOOD
(arc sine square root, radians)

Fig. 4.11. Average distance traveled per day by focal animals after October 1982, relative to the percent of daylight hours spent traveling and to precipitation. Precipitation for La Caseta and El Chato are monthly totals recorded at La Caseta, while measurements for the Santa Cruz Nesting Zone (SCNZ) and Pinzón include totals for each visit (12-13 days each for SCNZ, and 16-17 days each for Pinzón). Thus data for SCNZ and Pinzón should be shifted somewhat to the right. Percent of day traveling ranged from 2.7 to 20.8%.


● CASETA
○ CHATO
▲ SCNZ
△ PINZÓN
$F_{1,24}$ = 48.23
R^2 = 0.67
P < .0001
$\bar{X}$ DISTANCE (m/day)
400
300
200
100
0.1
0.2
0.3
0.4
0.5
% DAY TRAVELING
(arc sine square root, radians)


$F_{1,24}$ = 5.72
R^2 = 0.19
P < .03
$\bar{X}$ DISTANCE (m/day)
400
300
200
100
8
8
100
200
300
400
500
600
PRECIPITATION (mm)

of day traveling, with the greatest distance traveled at La Caseta, followed by Pinzón, El Chato, and SCNZ (Table 4.9). When compared to the same continuous independent variables, distance traveled was positively related to monthly precipitation (Fig. 4.11). Reeder and MacFarland (1978) found that home range, and presumably daily movements, increased dramatically during those hot seasons with little to no rain. However, distance data from this study did not include the hot-dry season.

Time spent in interactions with other tortoises, including both mating and agonistic interactions, increased with rising maximum temperatures (Table 4.10). However, 17 out of the 49 focal animals had no interactions during their 2-day period of observation. At Caseta/Chato, tortoises interacted most in the hot-dry season of 1982. During the hot El Niño of 1983, the density of tortoises was so low in these study areas due to the mass migration of tortoises to lower elevations (Cayot 1985) that any interaction between tortoises was unlikely.

Drinking showed a significant relationship to season with tortoises drinking most during the cool garúa season, and least in both the hot-dry season of 1982, and the hot El Niño of 1983 (Table 4.11). During the hot-dry season there was no water available to tortoises, while during El Niño, water was so abundant the tortoises were most likely satiated.

DISCUSSION

Daily activity patterns and time budgets of giant tortoises in the Galápagos Islands are strongly seasonal, and are correlated with temperature and moisture, as has been found for most terrestrial turtles (Auffenberg and Iverson 1979). Changes in daily activity patterns coincide with changes in temperature, with a bimodal pattern corresponding to the hot season, and a unimodal pattern corresponding to the cool season. Time budgets, which also vary seasonally, are more strongly related to precipitation than to temperature. Under extremely dry conditions with little available food, tortoises will spend little of the day in the active mode. The decrease in activity should curtail the majority of their energy expenditures, enabling them to live for a longer time on stored fat without additional food. They become more active, feeding for a greater portion of the day, with increasing precipitation, available food, and water content of the food.

In the Galápagos Islands, the bimodal pattern, although occurring in the hot season, is not as crucial to tortoise survival as it is on Aldabra. On Aldabra, feeding areas and shaded resting areas are generally separate and those tortoises that do not seek shade at midday on all but the coolest days are likely to die from overheating (Swingland and Frazier 1979, Coe and Swingland 1984). Shade, from trees, cactus, shrubs, or rocks, is much more dispersed in the Galápagos Islands, and tortoises may often feed in shaded

areas. The midday peaks in resting, although present and apparently due to high ambient temperatures, do not reach 100% in the Galápagos, as they do on Aldabra.

Study area had little effect on either activity patterns or time budgets of tortoises. The slightly greater levels of travel at La Caseta and on Pinzón may be related to the distribution of preferred habitats. At both El Chato and SCNZ, preferred areas are highly concentrated, while on Pinzón and at La Caseta, they are much more dispersed. In the latter two areas, tortoises may have to travel farther to reach preferred resting and feeding areas.

Although sex was not analysed as a factor in the instantaneous observations, it had no significant relationship to the time budgets of tortoises for any activity.

The ability of tortoises to store fat and to live for months without food or water was well known to whalers, who collected thousands of tortoises in the 1800's to supply their ships with fresh food for long periods of time at sea (Townsend 1925). Tortoise hunters often resorted to drinking the water in the pericardial sac, as well as the liquid in the bladder of the tortoise, to refresh themselves while traveling across the arid islands (Darwin 1860, Townsend 1925, Pritchard 1979a). This ability to store food and water, and to live for long periods of time without them, enables tortoises to change their behavior patterns to correlate with seasonal changes in temperature and precipitation, and the corresponding changes in both food and water

availability. Based on these studies on Santa Cruz and Pinzón, it is suggested that tortoises throughout the islands, regardless of sex, size (except perhaps the smallest, from hatching to 4-5 years old), or island, maintain the same general activity patterns and time budgets as each other, with seasonal changes consistent with changes in environmental conditions.

CHAPTER FIVE - FEEDING BEHAVIOR

INTRODUCTION

Animals with wide food preferences, and in many cases, greater tolerance for aridity, appear especially favored for establishment on oceanic islands (Carlquist 1974). The aridity and unpredictability of the climate in the Galápagos Islands require that animals maintain these characteristics to survive. This does not mean that herbivores on oceanic islands need be strict generalists, eating each species in proportion to its presence (Chew 1974), but rather that they be facultative strategists, having the ability to shift along the continuum from generalist to specialist depending on the current conditions (Glasser 1984). Herbivores living in arid regions are often generalized feeders, in that they feed on a wide range of species, plant types, and plant parts, but often show distinct seasonal changes in preference (Noy-Meir 1974). Most turtles are opportunistic with some species changing their food habits according to availability of food items in different seasons (Mahmoud and Klicka 1979), showing the strategy of flexible selectivity suggested by Noy-Meir (1974).

One hypothesis resulting from optimal foraging models is that animals should feed more selectively (ie., act as specialists) when food is abundant and should feed on all potential food items when food is very scarce (Ivlev 1961, MacArthur and Pianka 1966, Emlen 1966, 1968, Schoener 1971).

This conforms to Glasser's (1984) description of a facultative strategist. Schluter (1981), however, showed that in 15 studies of various species including fish, reptiles, birds, and mammals, only 4 showed an increase in diet breadth with diminishing food supplies, while 8 showed an increase in specialization. It may be that some facultative strategists perform in the opposite way from that proposed by Glasser (1984).

The diet of herbivores is generally made up of a variety of food items varying in quality. Large generalist herbivores should optimize the nutrient mix within a given food supply which is constrained by availability of foods only at rather low levels of availability (Westoby 1974). However, if a specific nutrient is limiting in the diet, the herbivore's diet may reflect preferences for food items with high levels of that nutrient, regardless of other quality characteristics. Although nitrogen has been noted as a major factor in determining food preferences (Sinclair 1975, White 1978, Mattson 1980), dietary habits of animals in arid ecosystems appear more often determined by water content of the food than by energy or protein content (Noy-Meir 1974). Desert tortoises in Utah obtain much of their water directly from their food or supplementally as metabolic water derived from food (Woodbury and Hardy 1948).

Galápagos tortoises have been considered not very selective in their feeding, eating almost any green vegetation they encounter (Slevin 1935, Hintz [1972?], Pritchard 1971,

1979a). The first quantitative study of their diet was done on Volcán Alcedo in 1980 (Fowler 1983, Fowler de Neira and Johnson 1985). Prior to that, the majority of descriptions of their diet consisted of general comments or lists of food items either seen eaten or found in their stomachs or feces (Table 5.1).

Cactus (primarily Opuntia, though not always so noted) and grasses were often named as the principal components of the tortoise diet (Table 5.1). The importance of cactus as a source of water in arid areas and in times of drought was also stressed (Darwin 1860, Hemsley 1895, Beck 1903, Heller 1903, Slevin 1935, Dawson 1966, Hendrickson 1966, Pritchard 1979a, Fritts 1983). Tortoises are known to obtain a great deal of fluid from their plant diet (Mahmoud and Klicka 1979). Cloudsley-Thompson (1971) suggested that all land tortoises can exist indefinitely on a vegetarian diet without free water.

After grasses and cactus, fruit was the most mentioned food item for Galápagos tortoises (Table 5.1). The small fruits of the endemic Psidium galapageium (known locally as guayavilla) were a large portion of the tortoise diet on Volcán Alcedo during garúa season (Fowler 1983, Fowler de Neira and Johnson 1985). Slevin (quoted in Van Denburgh 1914, and Fritts and Fritts 1982) thought that the fruits of Hippomane mancinella were preferred over cactus. Tortoises may spend up to 1 h feeding solely on this fruit (Rodhouse et al. 1975). However, Slevin also stated (Fritts and Fritts 1982):

Table 5.1. Food items of giant tortoises in the Galápagos Islands, as noted in the literature.

FOOD ITEM	REFERENCES
CACTUS	Darwin 1860, Baur 1889, Hemsley 1895, Beck 1903, Van Denburgh 1914, Townsend 1925, 1931, Snow 1964, Dawson 1966, Rodhouse et al. 1975, Fritts 1983
Cereus sp.[a]	Van Denburgh 1914
Opuntia spp.	Heller 1903, Slevin 1935, Carpenter 1966, Hendrickson 1966, MacFarland 1972, Pritchard 1979a, Fritts and Fritts 1982
GRASSES	Baur 1889, Heller 1903, Van Denburgh 1914, Townsend 1925, Brosset 1963, Snow 1964, Carpenter 1966, Hendrickson 1966, Hintz (1972?), Staedeli 1972, Black 1973, Rodhouse et al. 1975, Fritts and Fritts 1982, Fowler 1983, Fowler de Neira and Johnson 1985
FRUIT	
Psidium galapageium	Darwin 1860, Black 1973, Fowler 1983, Fowler de Neira and Johnson 1985
Hippomane mancinella	Stewart 1911, Van Denburgh 1914, Carpenter 1966, MacFarland 1972, Pritchard 1971, 1979a, Fritts and Fritts 1982
SHRUBS AND TREES	Darwin 1860, Baur 1889
Sida spp.[b]	Hintz (1972?), Rodhouse et al. 1975, Fowler 1983, Fowler de Neira and Johnson 1985
8 spp. (each noted by only one author)	Snow 1964, Carpenter 1966, Rodhouse et al. 1975
FORBS	Baur 1889
16 spp. (each noted by only one or two authors)	Snow 1964, Hintz (1972?), MacFarland 1972, Rodhouse el al. 1975
32 spp. - Alcedo	Fowler 1983
LICHEN[c]	Darwin 1860, Van Denburgh 1914, Slevin 1935, Rodhouse et al. 1975, Fritts and Fritts 1982
BROMELIAD - *Tillandsia insularis*	Snow 1964
FERNS - 3 spp.	Fowler 1983

Table 5.1 continued.

FOOD ITEM	REFERENCES
Sphagnum moss[d]	Rodhouse et al. 1975
LITTER - leaves	Rodhouse et al. 1975

[a] *Cereus* is now called *Brachycereus*; found in scat on Fernandina; only one tortoise ever found on Fernandina, in 1906.

[b] Predominant species is *Sida rhombifolia*; Rodhouse et al. (1975) refer to *S. hederifolia* as a shrub occurring alongside the trails; however, this description fits *S. rhombifolia* not *S. hederifolia*.

[c] In the original notes of Slevin (Van Denburgh 1914, Fritts and Fritts 1982), contents of several tortoise stomachs and one feeding observation, all on Pinzón, were lichens but were referred to as moss.

[d] Rodhouse et al. (1975) list *Sphagnum* moss as a food item, noting that it covered ponds in the lowlands of Santa Cruz. However, *Sphagnum* is only found at very high elevations in the islands (Wiggins and Porter 1971, Itow and Weber 1974). The food item mentioned was most likely *Azolla microphylla*, a floating fern commonly covering ponds in the Tortoise Reserve.

> "It appears to have somewhat of a poisonous nature and goes through the tortoise like a physic. The tortoises were full of this fruit and the intestines were much swollen and very thin, almost like a membrane . . . The only change noted from the fruit that passed through the tortoise was the change in color, having faded from green to a light yellow."

Other authors have commented that these fruits can pass through the gut virtually unaffected (Pritchard 1971, Rodhouse et al. 1975).

The only other food items mentioned by several authors were Sida spp. and lichens (Table 5.1). Sida spp. (predominantly Sida rhombifolia) were the most important food items in tortoise diets during the dry season and probably year-round on Volcán Alcedo (Fowler 1983, Fowler de Neira and Johnson 1985). Lichens were mentioned primarily in association with tortoises on Pinzón (Van Denburgh 1914, Rodhouse et al. 1975, Fritts and Fritts 1982).

Several forbs, shrubs, and a tree species were also listed as food items. However, none of these was considered a major component of the tortoise diet. In addition, a bromeliad (Tillandsia) and a probable fern (see footnote 3, Table 5.1) were mentioned as food items.

Only two species were noted as avoided by tortoises, Cryptocarpus sp. (Carpenter 1966), and Maytenus octogona (Pritchard 1979a). However, Rodhouse et al. (1975) included M. octogona in a list of species eaten on Pinzón.

Gilberto Moncayo, a tortoise hunter in the islands prior to the establishment of the National Park, stated in an interview with Carpenter (1966) that he had seen tortoises

feeding on the dried skin of a goat as well as on rotting goat carcasses. Rodhouse et al. (1975) noted that tortoises had no interest in goat carcasses. Galápagos tortoises have been known to eat meat in captive situations (Loveridge 1945), but no other records of this behavior in the wild are known. Aldabra tortoises, on the other hand, are known to eat various animals, including dead tortoises (Gaymer 1968, Grubb 1971, Bourn and Coe 1979).

Although the various accounts of the diet of Galápagos tortoises are predominantly anecdotal, the compilation of reports produces a consistent description of tortoise food habits. Based on the available literature, tortoises appear to eat a wide variety of food items, both in terms of food types (eg., cactus, grass, fruit, etc.), and the number of species within food types. Grasses and cactus appear to be the principal components of their diet. Fowler (1983, Fowler de Neira and Johnson 1985), working in the highlands of Volcán Alcedo where cactus is generally unavailable, found that grasses and Sida spp. were the year-round staples of the tortoise diet. Both of the major fruits in the Galápagos, Psidium galapageium and Hippomane mancinella, appear to be highly preferred. In addition to these major foods, tortoises eat a wide variety of food items, avoiding few.

This study examines the feeding behavior of Galápagos tortoises in relation to seasonal changes in climate and food availability. The feeding ecology of dome-shaped tor-

toises on Santa Cruz and saddle-backed tortoises on Pinzón were compared. The primary hypothesis for the evolution of the saddle-backed morphology is related to differences in food availability and the resulting feeding behavior of tortoises between the lower arid islands and the higher humid islands (Snow 1966, Pritchard 1979a, Fritts 1983, 1984). Presented here are the first quantitative measurements of food abundance for tortoises in the islands. The occurrence of a hot, extremely dry period during the study, both on Pinzón and Santa Cruz, is of particular importance in this respect, as it is proposed that the selective advantage of an increased vertical feeding range for tortoises on the lower arid islands would be accentuated during dry periods (Fritts 1983).

RESULTS

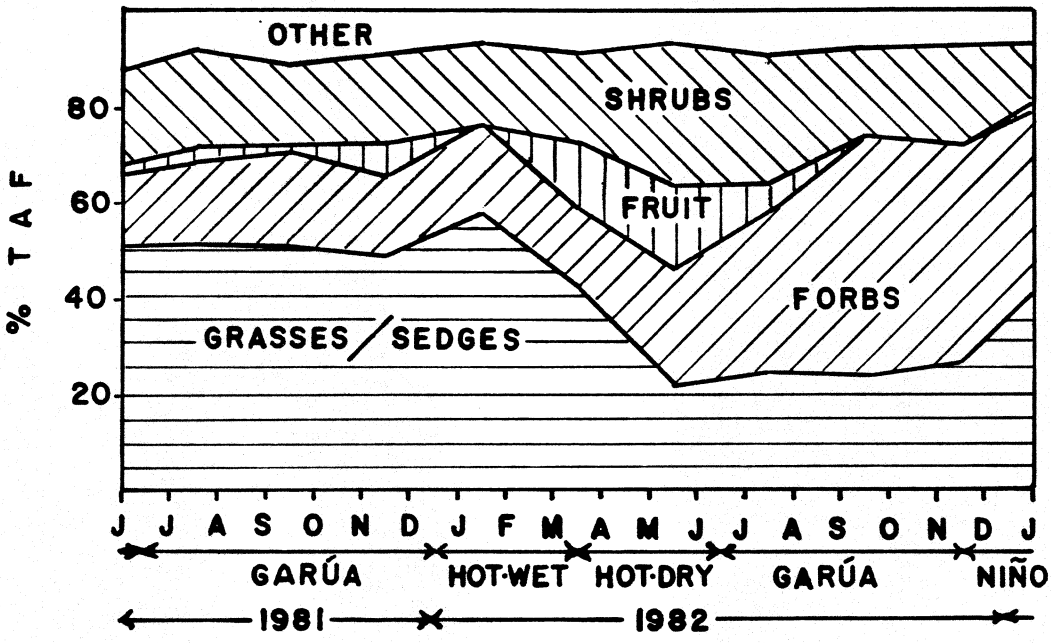
Food Habits

Tortoises obtained their food from a wide variety of species and food types. Graphical analysis of the percent diet by food type, based on instantaneous observations of feeding tortoises, as opposed to available food shows selectivity on the part of tortoises, as well as seasonal changes in the importance of different food types (Figs. 5.1-5.4). The most obvious differences between diet and food availability are the huge increase in percent fruit in the diet whenever there is a slight increase in availability, at both

Fig. 5.1. Available food, determined bi-monthly, and tortoise diet, determined monthly, at La Caseta, by food type. Although shrubs were abundant in the food supply, they were rare in the diet and are included in 'other' in the diet. Months with less than 50 feeding observations include July and August 1981, December 1982, and January 1983.

LA CASETA

TOTAL AVAILABLE FOOD



DIET

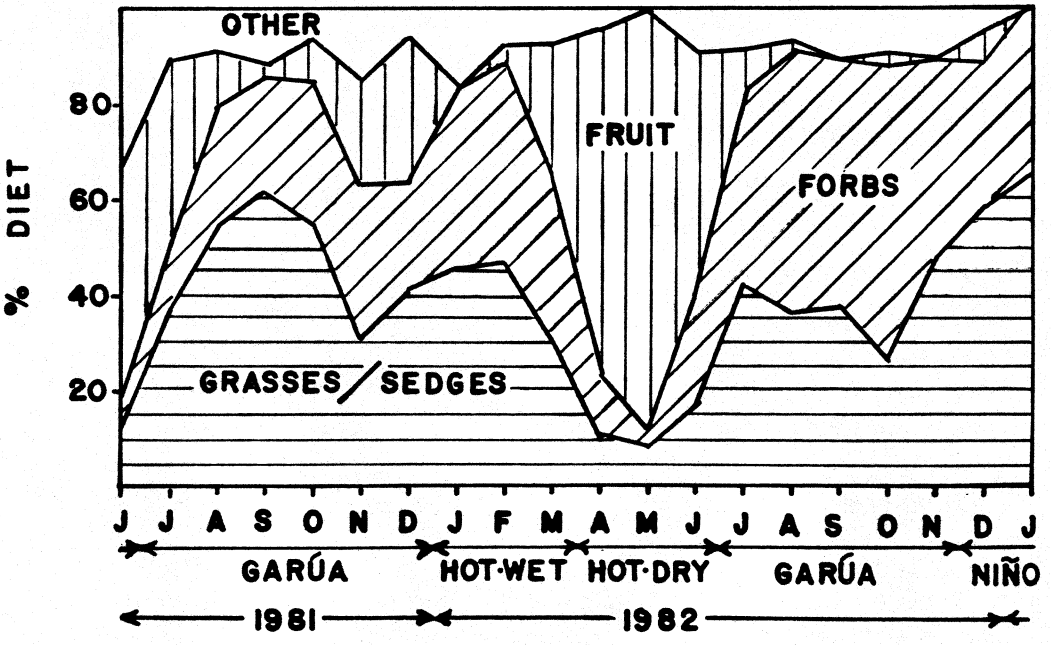
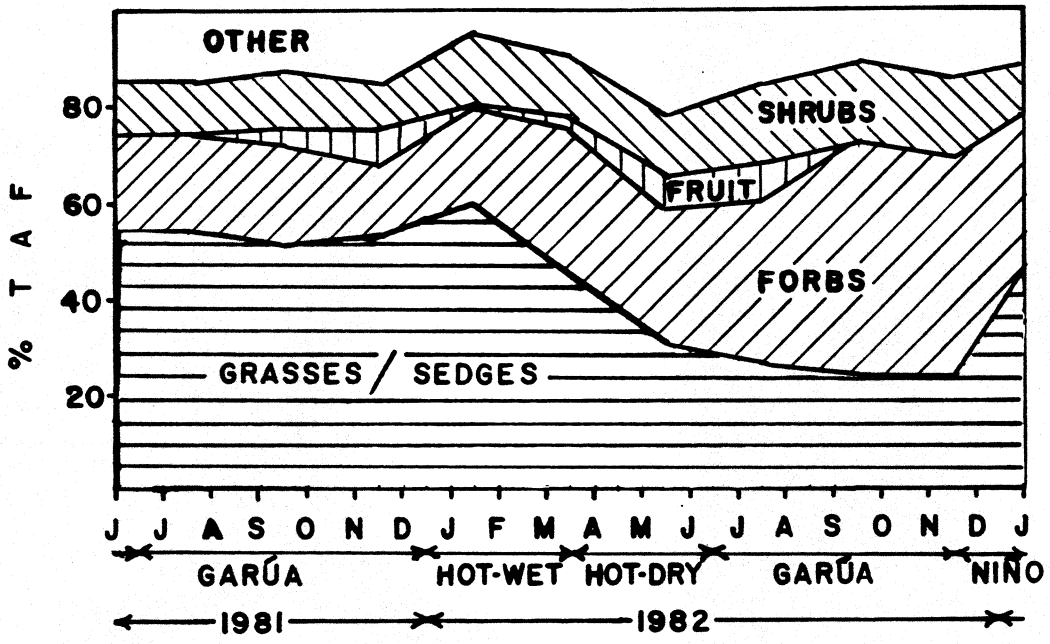


Fig. 5.2. Available food, determined bi-monthly, and tortoise diet, determined monthly, at El Chato, by food type. Although shrubs were abundant in the food supply, they were rare in the diet and are included in 'other' in the diet. Months with less than 50 feeding observations include June through September 1981, May and December 1982, and January 1983.

EL CHATO

TOTAL AVAILABLE FOOD



DIET

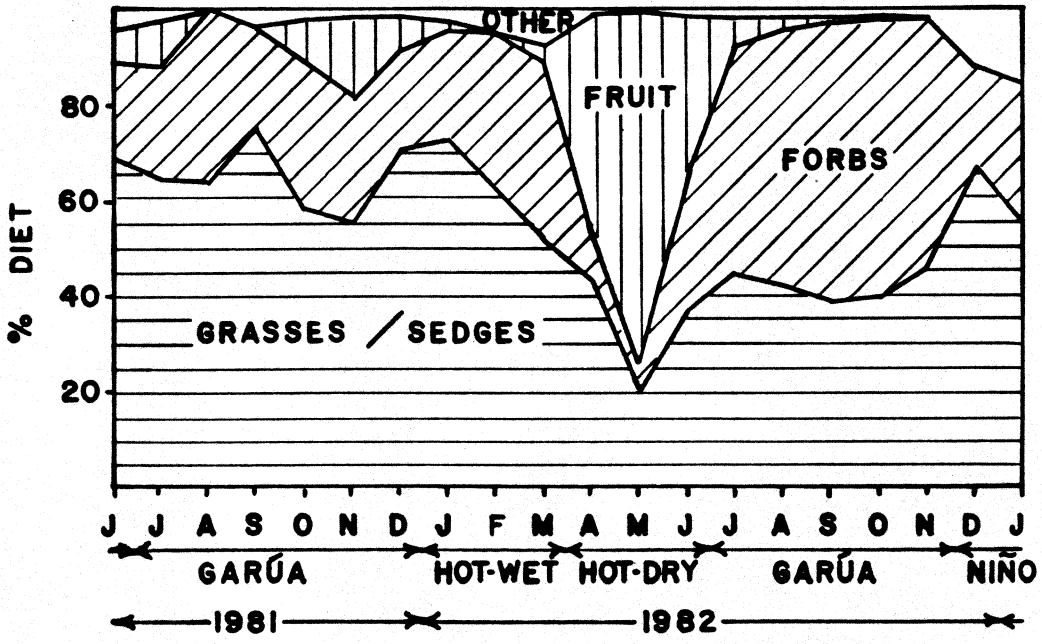


Fig. 5.3. Available food and tortoise diet at the Santa Cruz Nesting Zone during El Niño 1983, by food type. Available food was not measured in March, and April's values were used.

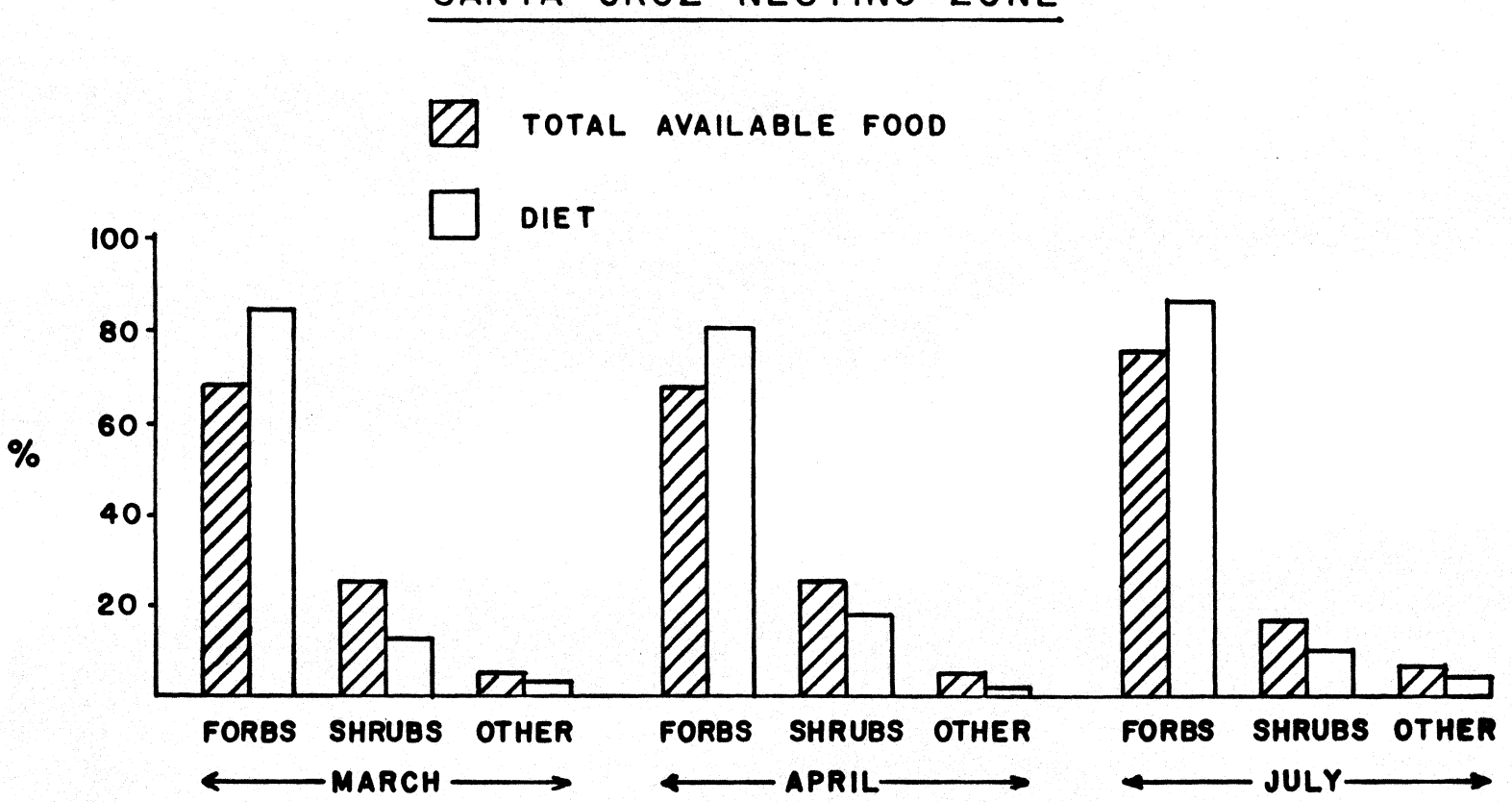
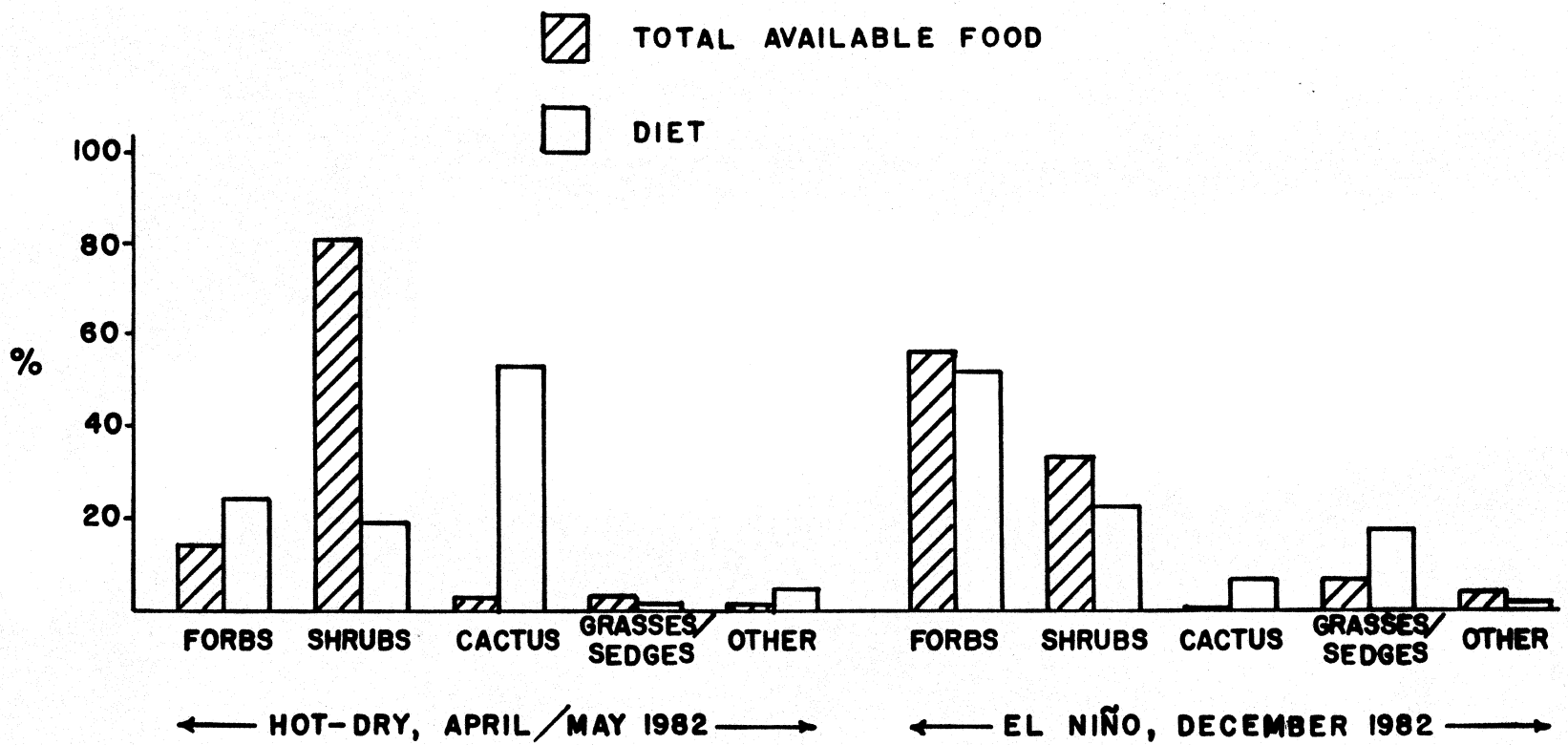

SANTA CRUZ NESTING ZONE
TOTAL AVAILABLE FOOD
DIET
100
80
60
40
20
%
FORBS
SHRUBS
OTHER
FORBS
SHRUBS
OTHER
FORBS
SHRUBS
OTHER
MARCH
APRIL
JULY

Fig. 5.4. Available food and tortoise diet on Pinzón in 1982, by food type. Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona were excluded from the total available food. When they are included, shrubs constitute 92.8% and 78.5% of the available food in the hot-dry season, and at the onset of El Niño, respectively.

PINZÓN


TOTAL AVAILABLE FOOD
DIET
100
80
60
40
20
%
FORBS
SHRUBS
CACTUS
GRASSES/SEDGES
OTHER
FORBS
SHRUBS
CACTUS
GRASSES/SEDGES
OTHER
HOT-DRY, APRIL/MAY 1982
EL NIÑO, DECEMBER 1982

La Caseta and El Chato, and the amount of cactus in the diet on Pinzón.

Specific food items eaten changed seasonally, along with food availability (Tables 5.2-5.5). Significant food items, determined on a monthly basis, included items that had greater than 3% frequency of observation and occurred in at least two observations. Of the 38 and 31 food items that were significant at La Caseta and El Chato respectively, 26 were significant in both areas. On the average, significant food items made up more than 80% of the diet, but never more than 67% of the available food, and always less than 45% of the total number of food items eaten (Table 5.6).

Few items were significant more than 50% of the time, with Paspalum conjugatum, the dominant grass in the Caseta/Chato region, the only food item that was significant in all 20 months at the two study areas. Along with P. conjugatum, only the seasonally abundant fruits at La Caseta and El Chato, Hippomane mancinella and Psidium galapageium, ever constituted more than 50% of the diet. No individual food items were ever that large a proportion of the diet at SCNZ or on Pinzón. Less than 10 food items per study area made up greater than 5% of the diet each, averaged over all months in which they were significant, but those that did were distributed across food types (Table 5.7). Extremely abundant but non-preferred or avoided food items could be significant due to their overwhelming abundance (eg., Alternanthera filifolia and Prosopis juliflora on Pinzón).

Table 5.2. Seasonal averages by food item of % of tortoise diet (%D) and % of total available food (%TAF) at La Caseta. The number of months a food item was significant (NSIG), and its maximum %D for a single month (MAX) are given. Only those food items that constituted at least 1% of the diet for any month or at least 1% TAF for any season are included. However, totals by food type include all items eaten or available. Significant food items that on the average were preferred (*) or avoided (**) are indicated.

			GARÚA 81		HOT-WET 82		HOT-DRY 82		GARÚA 82		EL NIÑO	
FOOD ITEM	NSIG	MAX	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF
FORBS[a]			24.65	17.63	37.80	18.15	12.90	20.60	49.84	43.79	33.90	38.80
*Ageratum conyzoides**	2	5.1	-	0.9	-	0.1	-	-	1.9	6.7	-	0.9
A. conyzoides - sprouts*	2	5.4	-	-	-	-	-	-	2.0	0.2	-	-
*Alternanthera halimifolia**	1	1.6	1.2	0.5	0.4	0.8	0.3	0.2	0.4	0.2	-	0.4
Apium sp.*	1	2.0	-	-	-	-	-	-	0.7	0.1	-	-
*Astrephia chaerophylloides**	2	3.2	-	-	-	-	-	-	1.2	-	-	-
*Blechum brownei**	3	10.1	0.6	3.1	0.7	2.0	0.6	3.4	0.6	0.7	5.0	6.6
*Borreria laevis**	1	1.4	0.2	0.1	-	0.1	-	-	0.6	0.2	-	0.3
*Cassia occidentalis**	2	4.2	0.8	0.7	1.8	0.4	0.6	0.2	0.9	2.2	-	0.9
*Commelina diffusa**	2	2.7	0.6	0.03	0.7	-	-	-	0.8	0.1	1.8	0.2
*Desmodium canum***	18	25.0	6.8	7.4	14.7	9.5	5.7	14.4	18.4	21.2	20.2	19.0
*Dichondra repens**	10	13.1	3.1	1.4	6.4	2.0	0.3	0.2	4.6	4.8	1.5	0.9
*Enydra maritima**	3	8.2	3.9	-	-	-	0.4	-	0.6	-	-	0.7
Fleurya aestuans	0	1.2	-	-	-	-	-	-	0.4	0.03	-	0.1
*Galactia striata**	4	3.8	0.3	0.3	2.3	0.4	1.2	0.4	1.3	0.4	-	0.2
Ipomoea spp.	0	2.1	0.05	-	-	-	-	-	0.5	0.1	-	0.1

Table 5.2 continued.

FOOD ITEM	NSIG	MAX	GARÚA 81		HOT-WET 82		HOT-DRY 82		GARÚA 82		EL NIÑO	
			%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF
FORBS cont.												
*Justicia galapagana**	11	5.4	1.1	1.3	3.5	1.3	0.9	1.2	2.3	1.5	1.5	4.6
*Ludwigia leptocarpa**	2	3.3	1.1	-	0.2	-	-	-	-	-	-	-
Mecardonia dianthera	0	8.3	1.4	-	0.4	-	-	-	0.3	0.1	-	0.1
*Momordica charantia**	6	4.5	-	0.2	1.5	0.2	1.2	0.4	2.5	1.0	1.5	0.6
Passiflora colinvauxii	0	1.3	0.1	-	0.5	0.05	0.4	-	0.2	0.2	-	-
Phyla strigulosa	0	1.5	-	-	0.5	-	0.3	-	0.6	0.1	-	-
*Phyllanthus caroliniensis**	4	2.6	0.1	-	1.3	0.1	-	-	1.4	1.2	1.2	-
*Pilea baurii**	4	5.5	0.4	0.2	-	-	-	-	3.3	0.3	-	0.1
Polygonum opelousanum	0	1.3	0.2	-	-	-	-	-	-	-	-	-
*Sida hederifolia**	3	3.3	0.6	0.3	1.8	0.3	0.3	-	0.8	0.2	-	0.2
*Sida spinosa**	3	4.8	1.7	0.2	0.7	0.2	0.5	-	1.0	0.3	1.2	0.2
*Solanum nodiflorum**	2	2.3	0.3	-	-	-	-	-	1.1	0.2	-	0.4
Stictocardia tiliifolia	0	-	-	0.6	-	0.5	-	0.2	-	1.3	-	1.9
S. tiliifolia-cotyledon*	1	1.8	-	-	-	-	-	-	0.5	-	-	-
GRASSES/SEDGES[a]			46.20	50.90	41.70	50.00	12.50	32.40	38.64	25.13	61.50	40.50
*Cyperus brevifolius**	2	12.1	-	-	0.4	-	-	-	0.2	0.03	10.2	0.7
Cyperus ligularis	0	1.5	0.2	-	-	-	-	-	-	-	-	-
Cyperus spp.	0	1.8	-	-	-	-	-	-	0.2	-	0.9	-
*Digitaria horizontalis**	4	12.1	0.8	-	0.5	-	-	-	0.6	0.1	6.0	0.5

Table 5.2 continued.

FOOD ITEM	NSIG	MAX	GARÚA 81 %D	GARÚA 81 %TAF	HOT-WET 82 %D	HOT-WET 82 %TAF	HOT-DRY 82 %D	HOT-DRY 82 %TAF	GARÚA 82 %D	GARÚA 82 %TAF	EL NIÑO %D	EL NIÑO %TAF
GRASSES/SEDGES cont.												
Eleocharis spp.	0	1.2	-	-	-	-	-	-	0.1	0.1	0.6	-
*Elusine indica**	1	2.6	0.5	-	0.3	-	0.3	-	0.2	-	-	-
*Ichnanthus nemorosus**	1	4.1	-	1.6	0.9	1.3	0.6	0.4	0.9	0.5	-	0.6
Panicum dichotomiflorum	0	1.0	0.2	-	-	-	0.3	-	0.1	-	-	-
*Paspalum conjugatum**	20	54.2	39.1	35.4	29.7	28.8	7.1	14.4	23.3	12.8	22.0	9.5
*Paspalum distichum**	1	3.5	0.2	-	0.4	-	1.2	-	0.6	-	-	-
*Rhynchospora nervosa**	7	5.4	1.2	3.3	1.6	2.8	0.7	1.0	2.3	3.3	3.8	6.8
*Scleria pterota***	5	4.9	0.7	7.2	1.9	11.4	0.4	12.6	2.8	6.6	4.6	21.4
*Stenotaphrum secundatum**	14	16.1	3.1	3.4	5.6	5.7	1.9	4.0	7.2	1.7	13.4	0.8
SHRUBS			4.0	18.6	4.6	17.45	1.3	23.8	7.8	20.9	1.8	12.4
Chiococca alba	0	1.4	0.1	2.9	0.3	3.0	0.4	5.6	0.5	3.7	-	1.7
Psychotria rufipes	0	0.9	-	7.7	0.5	5.4	-	6.6	0.2	7.4	-	3.9
*Sida rhombifolia**	13	9.4	3.7	0.9	3.6	1.4	0.6	2.1	6.8	0.8	1.8	1.0
Zanthoxylum fagara	0	1.5	0.1	6.2	0.2	6.4	0.3	8.3	0.1	7.1	-	3.6
FRUIT			19.4	3.7	9.9	7.0	70.6	15.6	2.3	2.0	3.6	1.4
Citrus spp. (lemon)*	1	14.8	0.3	-	0.3	-	5.3	-	-	-	-	-
*Hippomane mancinella**	8	73.2	8.4	0.9	9.6	7.0	32.4	12.4	-	-	3.6	0.4
*Psidium galapageium**	6	63.0	10.7	2.8	-	-	32.9	3.2	1.9	2.0	-	1.0

Table 5.2 continued.

FOOD ITEM	NSIG	MAX	GARÚA 81 %D	GARÚA 81 %TAF	HOT-WET 82 %D	HOT-WET 82 %TAF	HOT-DRY 82 %D	HOT-DRY 82 %TAF	GARÚA 82 %D	GARÚA 82 %TAF	EL NIÑO %D	EL NIÑO %TAF
FERNS			4.8	2.9	3.1	2.3	0.8	1.6	0.6	3.2	-	2.5
Asplenium auritum	0	1.0	-	0.6	0.3	0.2	-	-	0.1	0.6	-	0.1
*Azolla microphylla**	4	23.0	3.4	-	0.6	-	-	-	-	-	-	-
Polypodium spp.	0	2.4	-	0.3	-	0.4	0.8	-	0.1	1.0	-	0.5
*Thelypteris tetragona**	1	3.0	1.4	1.3	2.2	1.5	-	1.6	0.3	0.7	-	1.3
TREES (leaves)			-	0.5	0.5	0.4	0.4	0.2	0.2	1.5	-	0.9
Psidium galapageium	0	1.1	-	0.5	0.5	0.4	0.4	0.2	-	0.5	-	0.1
BROMELIAD												
*Tillandsia insularis**	3	3.8	0.7	-	1.5	-	1.9	-	0.1	-	-	-
MOSS	0	-	-	6.0	-	4.2	-	5.7	-	3.3	-	3.3
LITTER - grass[b]	0	1.1	-	NM	-	NM	0.4	NM	-	NM	-	NM
Litter - leaves[b,c]	0	2.3	-	NM	0.8[d]	NM	-	NM	0.2	NM	-	NM

[a]Flowers and seeds were often eaten along with vegetative parts when available, but were seldom selected separately.

[b]NM = not measured.

[c]Included *Hippomane mancinella* and *Psidium galapageium*.

[d]All leaves were wet with rain.

Table 5.3. Seasonal averages by food item of % of tortoise diet (%D) and % of total available food (%TAF) at El Chato. The number of months a food item was significant (NSIG), and its maximum %D for a single month (MAX) are given. Only those food items that constituted at least 1% of the diet for any month or at least 1% TAF for any season are included. However, totals by food type include all items eaten or available. Significant food items that on the average were preferred (*) or avoided (**) are indicated.

			GARÚA 81		HOT-WET 82		HOT-WET 82		GARÚA 82		EL NIÑO	
FOOD ITEM	NSIG	MAX	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF
FORBS[a]			26.03	18.38	30.40	24.90	15.00	29.10	53.50	41.99	25.00	31.50
Ageratum conyzoides**	3	4.2	-	2.4	-	0.3	-	0.2	1.6	8.3	-	2.4
A. conyzoides - sprouts*	1	2.2	-	-	-	-	-	-	0.6	0.3	-	-
Alternanthera halimifolia	0	1.8	-	0.6	-	0.8	-	0.4	0.1	0.4	0.9	0.3
Blechum brownei*	7	9.3	1.0	3.7	0.8	5.0	0.8	6.8	1.6	1.5	1.6	6.9
Borreria laevis*	8	4.4	1.2	0.6	1.9	1.0	0.2	0.6	2.4	0.7	2.1	0.4
Cassia occidentalis*	1	1.6	0.3	0.6	0.5	0.8	0.5	0.5	0.5	1.4	-	0.9
Commelina diffusa*	1	2.4	0.6	0.03	-	-	-	-	0.9	0.1	1.8	0.1
Desmodium canum	17	22.5	7.0	6.2	17.6	12.4	7.8	17.7	17.2	18.3	7.6	15.6
Dichondra repens*	13	19.1	4.9	1.5	4.5	1.4	1.7	0.6	13.5	5.4	4.4	0.9
Galactia striata	0	1.2	0.1	0.4	0.3	0.5	-	0.4	0.9	0.6	-	0.1
Justicia galapagana*	6	3.9	1.0	0.4	1.6	0.5	-	0.3	1.6	0.9	1.6	1.2
Ludwigia peploides*	1	5.6	3.4	0.03	-	-	-	-	-	-	-	-
Momordica charantia*	4	2.6	0.6	0.4	0.6	0.2	0.1	0.1	1.2	0.7	-	0.7
Passiflora colinvauxii	0	3.6	-	0.1	0.1	-	-	-	0.1	-	1.8	-
Phyla strigulosa*	5	7.2	0.1	0.1	0.4	0.6	2.7	1.0	3.8	0.5	-	-
Phyllanthus caroliniensis*	1	1.9	0.1	0.1	-	-	-	-	0.8	0.2	-	-

Table 5.3 continued.

FOOD ITEM	NSIG	MAX	GARÚA 81		HOT-WET 82		HOT-DRY 82		GARÚA 82		EL NIÑO	
			%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF
FORBS cont.												
*Pilea baurii***	2	4.5	0.1	-	-	-	-	-	1.5	0.2	-	-
Polygonum opelousanum	0	1.2	-	-	-	-	-	-	0.3	-	-	-
*Sida hederifolia**	3	5.5	2.0	0.2	0.6	0.2	0.5	0.2	1.1	0.3	0.4	-
*Sida spinosa**	5	5.3	2.9	0.03	0.9	0.05	0.5	-	1.6	0.2	0.9	0.2
*Solanum nodiflorum**	2	3.0	0.2	-	-	-	-	-	0.9	0.2	1.5	0.3
Stictocardia tiliifolia	0	1.1	0.2	0.3	0.4	0.4	-	0.1	0.1	0.9	-	1.0
Unknown-14	0	1.0	0.2	-	-	-	-	-	-	-	-	-
GRASSES/SEDGES[a]			64.50	53.30	62.60	53.30	34.20	38.80	42.60	25.66	61.70	47.00
*Cyperus brevifolius**	2	12.7	-	0.1	-	-	-	-	0.2	0.3	12.3	1.0
Cyperus spp.*	1	1.6	-	-	-	-	-	-	0.9	-	-	-
Eleocharis spp.*	2	3.5	0.1	0.1	0.3	0.05	-	-	1.0	0.4	-	2.3
Eleusine indica	0	1.0	0.2	-	0.3	-	-	-	-	-	-	-
Ichnanthus nemorosus	0	1.8	-	0.2	0.1	0.05	0.6	-	0.2	0.03	-	0.1
Panicum dichotomiflorum	0	2.0	0.7	-	1.1	0.2	-	-	0.2	-	-	-
*Panicum laxum**	1	8.6	1.0	0.3	-	0.1	-	-	0.2	0.03	-	-
*Paspalum conjugatum**	20	71.0	56.9	41.1	52.9	38.8	30.8	22.6	27.6	15.2	37.6	17.3
*Paspalum distichum**	2	4.7	0.9	-	0.2	0.1	-	0.3	0.8	-	-	-
*Rhynchospora nervosa**	9	6.6	1.3	1.7	1.3	1.0	0.6	0.5	4.3	1.4	2.4	2.5
*Scleria pterota***	5	5.3	0.3	8.4	0.9	9.7	1.1	12.9	3.3	7.5	2.4	22.2
*Stenotaphrum secundatum**	13	9.2	2.2	1.4	5.3	3.2	1.1	2.2	3.7	0.8	7.0	0.8

Table 5.3 continued.

FOOD ITEM	NSIG	MAX	GARÚA 81		HOT-WET 82		HOT-DRY 82		GARÚA 82		EL NIÑO	
			%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF
SHRUBS			1.3	10.83	2.9	13.6	0.4	12.3	1.54	17.3	2.8	10.9
Cassia picta	0	0.7	0.03	0.6	-	1.4	-	0.7	0.2	1.2	-	1.1
Chiococca alba	0	0.7	-	0.5	-	0.6	0.2	1.0	-	1.1	-	1.0
Clerodendrum molle	0	0.5	-	0.5	-	0.8	-	0.4	0.2	2.0	-	1.5
Croton scouleri	0	1.2	-	0.03	-	0.2	-	0.2	0.2	0.1	0.6	0.1
Psychotria rufipes	0	0.7	-	5.0	0.3	5.3	-	3.8	0.02	6.1	-	3.6
*Sida rhombifolia**	2	2.7	1.1	0.2	2.3	0.2	0.2	0.2	0.8	0.2	2.2	0.3
Tournefortia rufo-sericea	0	-	-	0.6	-	1.2	-	1.4	-	0.8	-	0.5
Zanthoxylum fagara	0	0.9	-	3.4	0.3	3.9	-	4.6	0.1	5.8	-	2.8
FRUIT			6.8	4.0	1.2	1.0	49.9	4.2	1.9	2.8	-	0.1
*Hippomane mancinella**	5	66.7	0.8	0.1	1.2	1.0	40.6	4.2	0.1	-	-	0.1
Passiflora incarnata	0	3.7	0.6	-	-	-	-	-	0.1	-	-	-
*Psidium galapageium**	5	21.2	5.4	3.9	-	-	9.3	-	1.6	2.8	-	-
FERNS			0.5	1.1	1.3	1.25	0.3	1.8	0.3	2.16	10.0	1.5
*Azolla microphylla**	2	14.5	0.3	-	-	-	-	-	-	-	10.0	-
Polypodium spp.	0	-	-	0.5	-	0.2	-	-	-	1.3	-	0.4
*Thelypteris tetragona**	1	4.0	0.2	4.0	1.3	1.0	0.3	1.8	0.3	0.8	-	0.8
TREES (leaves)			-	0.16	0.4	0.6	-	0.8	0.1	0.5	-	2.0
Citrus spp.	0	1.0	-	-	0.3	-	-	-	-	-	-	-
Psidium galapageium	0	0.2	-	0.03	0.1	0.2	-	0.1	-	0.1	-	1.5

Table 5.3 continued.

FOOD ITEM	NSIG	MAX	GARÚA 81		HOT-WET 82		HOT-DRY 82		GARÚA 82		EL NIÑO	
			%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF	%D	%TAF
MOSS	0	0.7	-	12.2	-	5.4	0.2	13.2	-	9.5	-	5.2
LITTER - leaves[b]	0	1.4	-	NM	0.5	NM	-	NM	-	NM	-	NM
WATER-NYMPH												
Naja guadalupense	0	1.2	-	-	-	-	-	-	-	-	0.6	1.6
GOAT HORNS	0	1.4	0.2	-	-	-	-	-	-	-	-	-

[a]Flowers and seeds were often eaten along with vegetative parts when available, but were seldom selected separately.

[b]*Hippomane mancinella* leaves; all were wet with rain; NM = not measured.

Table 5.4. Seasonal averages by food item of % of tortoise diet (%D) and % of total available food (%TAF) at the Santa Cruz Nesting Zone. The number of trips a food item was significant (NSIG), and its maximum %D for a single trip (MAX) are given. Only those food items that constituted at least 1% of the diet for any trip or at least 1% TAF for any season are included. However, totals by food type include all items eaten or available. Significant food items that on the average were preferred (*) or avoided (**) are indicated.

			EL NIÑO		JULY 83[a]	
FOOD ITEM	NSIG	MAX	%D	%TAF	%D	%TAF
CACTUS			1.5	-	2.0	-
Opuntia echios - pad*	1	2.5	1.2	-	2.0	-
FORBS[b]			82.45	68.60	86.60	76.60
*Alternanthera halimifolia**	2	13.9	3.8	8.8	13.9	10.2
*Bidens riparia**	1	4.4	2.6	0.8	-	0.2
*Blainvillea dichotroma**	2	3.7	2.6	2.0	-	-
*Blechum brownei***	1	5.1	0.6	1.6	5.1	12.4
*Commicarpus tuberosus***	1	2.4	0.6	5.6	2.4	4.1
*Corchorus orinocensis**	1	2.0	1.3	0.2	-	-
*Desmodium procumbens**	1	2.5	1.4	0.4	1.0	0.3
*Evolvulus glaber***	3	6.2	5.2	9.4	6.2	1.9
Galactia striata	0	1.0	0.5	0.8	-	0.1
Heliotropium angiospermum	0	0.3	0.2	2.0	0.2	2.7
*Ipomoea triloba**	3	45.2	37.3	9.4	1.7	0.3
Mentzelia aspera	0	1.5	1.2	0.2	0.7	-
*Oxalis cornellii**	2	3.9	3.8	1.0	0.3	-
*Physalis galapagensis**	1	6.6	4.2	0.4	-	-
Plumbago scandens	0	0.3	0.2	5.9	-	9.5
Salvia occidentalis	0	1.0	0.3	0.8	1.0	1.0
*Sida hederifolia***	2	9.1	1.6	4.3	9.1	5.5
*Sida spinosa**	3	19.0	10.4	6.8	19.0	3.7
*Tetramerium nervosum***	3	25.0	4.0	8.0	25.0	24.7

Table 5.4 continued.

FOOD ITEM	NSIG	MAX	EL NIÑO %D	EL NIÑO %TAF	JULY 83[a] %D	JULY 83[a] %TAF
GRASSES/SEDGES			1.0	0.9	1.4	-
Eleocharis spp.	0	1.2	0.8	-	-	-
SHRUBS			15.1	25.6	10.0	17.0
*Bastardia viscosa***	3	17.6	14.6	21.0	8.8	7.9
Chiococca alba	0	-	-	0.2	-	1.8
Clerodendrum molle	0	-	-	-	-	1.1
Croton scouleri	0	-	-	0.2	-	1.0
Lantana peduncularis	0	0.3	0.1	1.2	0.3	0.3
Tournefortia psylostachya	0	0.6	0.4	2.8	0.6	4.9
TREES (leaves)			-	4.8	-	6.4
Pisonia floribunda	0	-	-	4.7	-	5.8

[a]Although July 1983 was at the very end of El Niño rains, it is separated here because many species, abundant in earlier months, were much reduced due to huge levels of rainfall and subsequent flooding in May and June.

[b]Flowers and seeds were often eaten along with vegetative parts when available, but were seldom selected separately.

Table 5.5. Seasonal averages by food item of % of tortoise diet (%D) and % of total available food (%TAF) on Pinzón. The number of trips that a food item was significant (NSIG), and its maximum %D for a single trip (MAX) are given. Only those food items that constituted at least 1% of the diet or at least 1% TAF for any trip are included. However, totals by food type include all items eaten or available. Significant food items that on the average were preferred (*) or avoided (**) are indicated.

			HOT-DRY 82		EL NIÑO	
FOOD ITEM	NSIG	MAX	%D	%TAF	%D	%TAF
CACTUS			52.8	0.2	6.6	-
Opuntia galapageia - fruit*	1	3.2	3.2	-	1.5	-
O. galapageia - pads*	2	46.1	46.1	0.2	5.1	-
O. galapageia - spineballs	0	1.9	1.9	-	-	-
FORBS[a]			23.2	1.2	52.6	16.8
Anredera ramosa	0	1.9	-	-	1.9	2.5
*Commelina diffusa**	2	19.5	6.5	0.4	19.5	5.0
Evolvulus glaber	0	1.2	1.2	0.1	0.4	0.3
*Phyla strigulosa**	1	3.5	3.5	0.1	0.8	-
*Portulaca oleracea**	2	27.5	11.2	0.6	27.5	7.8
Sida spinosa	0	1.1	-	-	1.1	0.1
GRASSES/SEDGES[a]			0.8	0.2	16.6	2.1
*Cyperus elegans**	1	5.8	-	-	5.8	0.2
*Panicum fasciculatum**	1	2.6	-	-	2.6	0.6
Panicum geminatum	0	1.7	-	-	1.7	-
*Setaria setosa**	1	6.5	0.8	0.2	6.5	1.0
SHRUBS[a]			15.0	92.8	23.5	78.5
*Alternanthera filifolia***	1	5.4	5.4	38.6	1.7	38.8
Bastardia viscosa	0	1.8	1.8	0.3	1.7	0.7
Castela galapageia	0	-	-	1.9	-	0.5
Cordia lutea	0	2.3	-	0.2	2.3	0.4
*Croton scouleri**[b]	1	4.1	0.8	1.3	4.1	3.3
*Lantana peduncularis**	1	11.2	0.8	0.2	11.2	0.8

Table 5.5 continued.

FOOD ITEM	NSIG	MAX	HOT-DRY 82 %D	HOT-DRY 82 %TAF	EL NINO %D	EL NINO %TAF
SHRUBS cont.						
Maytenus octogona	0	-	-	23.3	-	15.4
*Prosopis juliflora***	1	3.5	1.1	23.9	0.4	14.6
*Zanthoxylum fagara**[b]	1	5.1	5.1	2.5	1.9	2.5
SEED POD (with seeds)						
Prosopis juliflora	0	1.6	1.6	-	-	1.0
LICHEN**	1	2.8	2.8	5.1	-	1.3
LITTER - leaves[c]	0	4.0	4.0	NM	-	NM

[a]Flowers and seeds were often eaten along with vegetative parts when available, but were seldom selected separately.

[b]Preferred when *Alternanthera filifolia*, *Maytenus octogona*, and *Prosopis juliflora* are included in TAF; avoided when they are excluded from TAF.

[c]Includes *Prosopis julifora* and *Croton scouleri*; NM = not measured.

Table 5.6. Averages with standard deviations of % of tortoise diet (%DIET), % of the total number of food items in the diet (%FOOD ITEMS), and % of total biomass of available food (%TAF) contributed by significant food items, determined on a monthly basis.

		%DIET		%FOOD ITEMS		%TAF	
STUDY AREA	No. MONTHS	$\bar{X}$	SD	$\bar{X}$	SD	$\bar{X}$	SD
CASETA	20	84.49	7.02	40.69	11.65	51.60	9.42
CHATO	20	86.86	4.40	40.04	12.26	52.98	10.58
SCNZ[a]	3	91.47	3.41	43.98	14.73	67.03	6.44
PINZÓN	2	84.80	3.54	40.35	9.92	45.30	37.19

[a]Santa Cruz Nesting Zone.

Table 5.7. Number of food items that on the average (averaged over months in which each item was significant) constituted greater than 5% of the tortoise diet.

	NUMBER OF FOOD ITEMS							
STUDY AREA	TOTAL	FORB	GRASS	SEDGE	SHRUB	FRUIT	FERN	CACTUS
CASETA	9	2	2	1	-	3	1	-
CHATO	9	3	2	1	-	2	1	-
CASETA/CHATO - in common	7	2	1	1	-	2	1	-
SCNZ[a]	9	8	-	-	1	-	-	-
PINZÓN	8	2	1	1	3	-	-	1

[a]Santa Cruz Nesting Zone.

The highly preferred fruits of Hippomane mancinella were often consumed one after another with no other food items mixed in. In January 1982, when the fruits first reappeared in the environment, tortoises were feeding on them off the ground and directly off low, hanging branches, before the fruits were noticed by human observers. This marked preference would be strange if it is true that the fruits, which are poisonous to other animals, pass through the tortoise gut unaffected (Pritchard 1971, Rodhouse et al. 1975). To examine this, six fresh scats of 100% H. mancinella fruits, with from 50-100 fruits each, were collected. The amount of flesh removed from the nut-like core during digestion was noted for each fruit. Although the scats varied considerably, the majority of flesh was removed. The average percentage of fruits in a scat with all of the flesh removed was 56.7% ± 21.0, while 14.2% ± 4.8 had between 50-99% of flesh removed, and 19.0% ± 13.7 had between 0-50% of the flesh removed. Only 10.2% ± 10.0 had none of the flesh removed.

Non-significant foods included abundant species that tortoises avoided, and rare species that tortoises either avoided or seldom located. Many of the rare foods eaten (constituting between 0.05 and 1.0% of the total available food) were never 1% or more of the diet (Table 5.8, 5.9). Rare food items not eaten at one study area were often eaten at another, leaving few items never consumed by tortoises.

Table 5.8. Food items eaten at La Caseta and El Chato that never constituted 1% or more of the diet and were never more than 1% of the available food.

FOOD TYPE	LA CASETA	EL CHATO
FORBS	Acalypha sp.	Apium sp.
	Crotolaria incana	Astrephia chaerophylloides
	Heliotropium indicum	Cissus sicyoides
	Hippomane mancinella -cotyledon	Desmodium limense
	Ludwigia peploides	Enydra maritima
	Oxalis corniculata	Fleurya aestuans
	Peperomia sp.	Ipomoea sp.
	Physalis pubescens[a]	Mecardonia dianthera
	Plantago major	Oxalis corniculata
	Sclerothrix fasciculata	Phaseolus mollus
	Synedrella nodiflora	Stictocardia tiliifolia - cotyledon
	Teucrium vesicarium[a]	Teucrium vesicarium
GRASSES/SEDGES	Panicum geminatum	Panicum geminatum
	Panicum laxum	
SHRUBS	Cassia picta[a]	Tournefortia psylostachya
	Clerodendrum molle	
	Croton scouleri	
FRUIT	Citrus sp. (orange)	Citrus sp. (lemon)
	Passiflora incarnata	
FERNS	Doryopteris pedata	Asplenium autritum[a]
	Trachypteris pinnata[a]	Doryopteris pedata[a]
TREES (leaves)	Hippomane mancinella	Scalesia pedunculata
	Pisonia floribunda[a]	
	Scalesia pedunculata[b]	
FUNGI	Unknown species	

[a]Only seen eaten by focal animals (not part of % diet).

[b]Always young plant whose top was within reach of tortoise.

Table 5.9. Food items eaten at the Santa Cruz Nesting Zone (SCNZ) or Pinzón that never constituted 1% or more of the diet and were never more than 1% TAF.

FOOD TYPE	SCNZ	PINZÓN
CACTUS	Opuntia echios - young	Opuntia galapageia - root
		O. galapageia - young
FORBS	Acalypha sp.	Galactia striata
	Ageratum conyzoides	Heliotropium angiospermum[a]
	Cassia occidentalis	Ipomoea triloba
	Dichondra repens	Neptunia plena
	Fleurya aestuans[a]	Oxalis cornellii
	Merremia aegyptica	Sida hederifolia[a]
	Portulaca oleracea	
GRASSES/SEDGES	Cyperus brevifolius	Leptochloa filiformis[a]
	Cyperus sp.	
	Paspalum conjugatum	
SHRUBS	Cordia sp.	Acacia macracantha[a]
		Alternanthera echinocephala
		Chiococca alba[a]
MUSHROOM		Unknown species
LIVERWORT	Unknown species[a]	

[a]Only seen eaten by focal animals (not part of % diet).

Feeding by focal animals showed breadth of diet of individual tortoises during 2-day periods, and specific food items on which tortoises concentrated. Neither bite counts nor number of minutes feeding on specific food items were done for focal animals because it was not always possible to see the head of the tortoise. Instead, food items were mentioned in the notes when possible. This did not result in a quantitative analysis of diet, but did produce a minimum number of food items eaten in a day. Consistency of mentioning food items in the notes was determined by regression, comparing the total number of times specific food items were mentioned against the total number of minutes spent feeding in a day. A strong relationship would suggest that food items could be ranked in importance in the daily diet based on the number of times they were mentioned. Regressions for all study areas were highly significant (Caseta/Chato: $F_{1,43} = 117.27$, $R^2 = 0.73$, $P < .0001$; SCNZ: $F_{1,14} = 9.84$, $R^2 = 0.41$, $P < .007$; Pinzon: $F_{1,36} = 109.23$, $R^2 = 0.75$, $P < .0001$).

The number of food items eaten by focal animals per day changed seasonally, ranging from 0 (on Pinzón and at La Caseta during the hot-dry season) to 27 (at La Caseta and El Chato during the cool garúa season) (Tables 5.10-5.12). Thirty-seven food items were consumed by more than 3 of the 22 focal animals at Caseta/Chato (Table 5.13), while 13 and 16 were eaten by only 2 and 1 focal animals, respectively. Only 5 items were eaten by more than 50% of the focal ani-

Table 5.10. Number of food items eaten by focal animals during each day at La Caseta or El Chato. TOTAL indicates the number of different items in the 2-day period.

SEASON	FA No.	NUMBER OF FOOD ITEMS DAY 1	DAY 2	TOTAL
HOT-DRY 82	1	4	0	4
	2	1	5	5
$\bar{X}$		2.5		4.5
SD		2.4		0.7
GARÚA 82	3	5	2	6
	4	10	3	10
	5	10	2	11
	6	10	9	16
	7	5	10	11
	9	10	6	12
	12	11	3	12
	13	10	14	16
	14	15	18	22
	15	15	8	17
	16	3	8	7
	17	10	17	19
	18	20	9	22
	19	27	16	30
	20	13	12	17
	21	15	27	29
$\bar{X}$		11.0		16.1
SD		6.3		7.1
EL NIÑO	22	10	4	11
	23	4	5	5
	27	8	5	8
	32	8	8	11
$\bar{X}$		6.5		8.8
SD		2.3		2.9

Table 5.11. Number of food items eaten by focal animals during each day at the Santa Cruz Nesting Zone. TOTAL indicates the number of different items in the 2-day period.

MONTH	FA No.	NUMBER OF FOOD ITEMS		
		DAY 1	DAY 2	TOTAL
February 83	24	7	5	8
	25	3	7	7
March 83	26	4	4	6
April 83	29	7	10	12
	30	6	9	11
	31	8	8	11
July 83	33	6	8	10
	34	6	6	9
$\overline{X}$		6.5		9.2
SD		1.9		2.1

Table 5.12. Number of food items eaten by focal animals (FA) during each day on Pinzón. TOTAL indicates the number of different items in the 2-day period.

MONTH	FA No.	NUMBER OF FOOD ITEMS DAY 1	DAY 2	TOTAL
April 82	35	0	2	2
	36	0	1	1
	37	6	10	12
	38	5	10	12
May 82	39	9	8	11
	40	6	5	8
	41	13	13	15
	42	11	10	15
	43	1	9	9
	44	1	8	9
$\bar{X}$		6.6		9.4
SD		4.7		4.8
December 82	45	12	10	14
	46	10	16	19
	47	6	9	10
	48	10	9	13
	49	17	15	21
	50	14	10	14
	51	12	9	13
	52	9	9	11
	53	5	9	9
$\bar{X}$		10.6		13.8
SD		3.2		4.0

Table 5.13. Food items eaten by more than two focal animals at La Caseta and El Chato, including the number of focal animals (possible total of 22) eating each item (No. FAs), the average number of times the item was mentioned per day (AVE/DAY), and the maximum number of times the item was mentioned per day (MAX/DAY). Food types include forbs (F), grasses and sedges (G), shrubs (S), fruit (FR), ferns (FE), and tree leaves (T).

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
F	*Acalypha* sp.	3	10.8	20
F	*Ageratum conyzoides*	7	2	3
F	*Alternanthera halimifolia*	5	2.1	6
F	*Blechum brownei*	10	3.1	8
F	*Borreria laevis*	6	2.4	4
F	*Cassia occidentalis*	3	3.7	5
F	*Commelina diffusa*	3	3.8	8
S	*Croton scouleri*	4	2.8	6
G	*Cyperus brevifolius*	4	5	12
F	*Desmodium canum*	20	16	69
F	*Dichondra repens*	13	8	21
G	*Eleocharis* spp.	6	2	2
F	*Enydra maritima*	3	4	8
F	*Fleurya aestuans*	3	2	3
F	*Galactia striata*	8	3	13
FR	*Hippomane mancinella* - fruit	3	15	46
F	*Justicia galapagana*	13	8	56
F	*Momordica charantia*	7	2	4
G	*Paspalum conjugatum*	19	17	48
F	*Passiflora colinvauxii*	6	3	6
F	*Phyla strigulosa*	5	1	2
F	*Phyllanthus caroliniensis*[a]	5	9	33
F	*Pilea baurii*	9	19	78
FE	*Polypodium* spp.	3	6	14
FR	*Psidium galapageium* - fruit	6	7	18
G	*Rhynchospora nervosa*	11	2	6

Table 5.13 continued.

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
T	Scalesia pedunculata - young	4	2	5
G	Scleria pterota	12	4	9
F	Sida hederifolia	4	4	7
S	Sida rhombifolia	8	6	29
F	Sida spinosa	7	3	6
F	Solanum nodiflorum	11	5	15
G	Stenotaphrum secundatum	10	11	96
F	Stictocardia tiliifolia	4	1	2
FE	Thelypteris tetragona	4	1	1
S	Zanthoxylum fagara	6	2	4
	MOSS	3	1	1

[a]Much was consumed by FA 19, and most of it was bare stems without leaves.

mals, while 9 received more than 20 mentions maximum per day (Table 5.13). Twenty-five food items were eaten by focal animals at SCNZ, with only 6 items eaten by more than 50% of the tortoises (Table 5.14). Seven items received more than 20 mentions maximum per day.

Food habits of focal animals on Pinzón were different for the two seasons. The ten focal animals followed during the hot-dry season ate a total of 30 separate food items, although 15 of these were each eaten by only one animal, and only 7 items were eaten by more than half the focal animals (Table 5.15). Alternanthera filifolia, generally an avoided species (Table 5.5), was the only food item to receive greater than 20 mentions maximum on a single day. However, the number of times that Opuntia galapageia pads were mentioned may be unrealistically low because they were often only mentioned when a tortoise began feeding on a pad and again when the pad was finished, a span of time ranging from a few minutes to a half hour. Thirty-six food items, only 6 more than during the dry season, were eaten by the nine focal animals during the wet season (Table 5.16). However, only 8 of these were eaten by a single individual, while 11 were eaten by more than half of the focal animals. In addition, 6 items were mentioned more than 20 times in a day.

Selectivity and Diversity of Diet

Dietary diversity depends upon both the diversity of the available food and the selectivity of the herbivore while

Table 5.14. Food items eaten by focal animals at the Santa Cruz Nesting Zone, including the number of focal animals (possible total of 8) eating each item (No. FAs), the average number of times the item was mentioned per day (AVE/DAY), and the maximum number of times the item was mentioned per day (MAX/DAY). Food types include forbs (F), grasses and sedges (G), shrubs (S), fruit (FR), and cactus (C).

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
F	*Alternanthera halimifolia*	5	8	24
S	*Bastardia viscosa*	8	9	31
F	*Bidens riparia*	5	2	3
F	*Blechum brownei*	3	2	4
F	*Blainvillea dichotroma*	4	3	7
F	*Commicarpus tuberosus*	3	1	1
F	*Corchorus orinocensis*	3	1	1
F	*Evolvulus glaber*	5	10	33
F	*Fleurya aestuans*	1	1	1
F	*Ipomoea triloba*[a]	6	32	77
F	*Mentzelia aspera*	4	4	9
C	*Opuntia echios* - pad	1	1	1
F	*Oxalis cornellii*	4	6	17
G	*Panicum fasciculatum*	1	46	51[b]
F	*Physalis galapagensis*	3	2	3
F	*Portulaca oleracea*	1	14	20[b]
FR	*Psidium galapageium* - fruit	1	3	3
F	*Salvia occidentalis*	1	1	1
F	*Sida spinosa*	4	9	37
F	*Tetramerium nervosum*	6	10	32
S	*Tournefortia psylostachya*	2	2	2
G	sedge	1	1	1
	LIVERWORT	1	10	10[b]
	LITTER - leaves	1	7	7[b]
	SOIL (wet)	1	6	6[b]

[a]The two animals not eating *I. triloba* were in July 1983, when it was no longer abundant.

[b]All eaten by a single female, FA 33.

Table 5.15. Food items eaten by focal animals in the hot-dry season 1982, on Pinzón, including the number of focal animals (possible total of 10) eating each item (No. FAs), the average number of times the item was mentioned per day (AVE/DAY), and the maximum number of times the item was mentioned per day (MAX/DAY). Food types include cactus (C), forbs (F), grasses (G), shrubs (S), ferns (FE), and bromeliads (B).

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
S	*Alternanthera filifolia*	5	8	25
F	*Anredera ramosa*	1	1	1
S	*Bastardia viscosa*	8	4	9
S	*Capraria peruviana*	1	1	1
S	*Chiococca alba*	1	1	1
F	*Commelina diffusa*	3	1	1
S	*Cordia lutea*	1	1	1
S	*Croton scouleri*	8	4	11
F	*Galactia striata*	1	1	1
F	*Heliotropium angiospermum*	1	1	1
S	*Lantana peduncularis*	2	2	2
F	*Neptunia plena*	3	2	3
C	*Opuntia galapageia* - bark	1	1	1
C	*O. galapageia* - fruit	6	2	4
O	*O. galapageia* - pads	9	4	9
G	*Panicum fasciculatum*	1	1	1
F	*Peperomia* sp.	1	1	1
F	*Portulaca oleracea*	4	5	17
S	*Prosopis juliflora*	7	2	7
	P. juliflora - seed pods	1	4	5
G	*Setaria setosa*	4	2	3
B	*Tillandsia insularis*	1	1	1
S	*Zanthoxylum fagara*	8	4	9

Table 5.15 continued.

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
FE	fern	1	1	1
G	grass	4	1	2
	LICHEN	4	2	4
	ROOT	1	2	2
	LITTER - grass	1	4	4
	- leaves (dry)	6	4	12
	- leaves (wet)	1	6	6

Table 5.16. Food items eaten by focal animals at the onset of El Niño, December 1982, on Pinzón, including the number of focal animals (possible total of 9) eating each item (No. FAs), the average number of times the item was mentioned per day (AVE/DAY), and the maximum number of times the item was mentioned per day (MAX/DAY). Food types include cactus (C), forbs (F), grasses and sedges (G), and shrubs (S).

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
S	*Acacia macracantha*	1	3	3
S	*Alternanthera echinocephala*	3	3	5
S	*Alternanthera filifolia*	7	9	31
F	*Anredera ramosa*	3	4	7
S	*Bastardia viscosa*	7	4	9
F	*Commelina diffusa*	7	14	33
S	*Cordia andersonii*	1	1	1
S	*Cordia lutea*	6	5	14
S	*Croton scouleri*	8	13	43
G	*Cyperus elegans*	2	3	5
F	*Evolvulus glaber*	1	6	9
F	*Galactia striata*	4	1	2
F	*Heliotropium angiospermum*	4	1	2
F	*Ipomoea triloba*	1	4	5
S	*Lantana peduncularis*	9	23	68
G	*Leptochloa filiformis*	1	17	17
C	*Opuntia galapageia* - fruit	2	7	11
C	*O. galapageia* - pads	5	5	8
F	*Oxalis cornellii*	2	2	3
G	*Panicum fasciculatum*	3	7	17
G	*Panicum geminatum*	2	4	7
F	*Phyla strigulosa*	1	4	4
F	*Portulaca oleracea*	9	15	57
S	*Prosopis juliflora*	2	2	4
	P. juliflora - seed pods	2	4	9
G	*Setaria setosa*	9	11	41
F	*Sida hederifolia*	1	1	1

Table 5.16 continued.

FOOD TYPE	FOOD ITEM	No. FAs	AVE/DAY	MAX/DAY
F	*Sida spinosa*	1	4	4
S	*Zanthoxylum fagara*	6	3	5
G	grass	6	4	11
	LICHEN	3	2	3
	FUNGI	2	3	4
	LITTER - leaves (dry)	1	2	2
	- leaves (wet)	2	2	3
	SNAIL SHELLS	1	2	2
	SOIL	1	2	2

feeding (McNaughton 1985a). Richness of the diet (S_d = number of food items) should be a subset of the richness of the vegetation, while overall diet diversity ($H'_d = -\Sigma[p_i \ln p_i]$, where p_i = proportion of food item i in the diet) and evenness of the diet ($J_d = H'_d / \ln S_d$) may have a more complex relationship with characteristics of the available food, and the subsequent selectivity of the tortoise.

Initial stepwise regressions of diet diversity indices for all study areas, and for La Caseta and El Chato alone, including all months with data collection, resulted in log N, where N equals the total number of feeding observations per month, as the primary significant variable in 50% of the equations. To avoid the dominance of N on the diet diversity indices, only those months with a minimum of 50 feeding observations were included in all further analyses in this section. By eliminating those months with fewer feeding observations (range 7 to 38/month), log N was no longer significant in the majority of the regressions.

Analyses of Pinzón data in this section were based on total available biomass excluding the three highly avoided species, Alternanthera filifolia, Maytenus octogona, and Prosopis juliflora (see Study Areas chapter for further explanation).

Feeding selectivity of tortoises varied seasonally with the highest levels of selectivity during the hot-dry season 1982, when conditions were harsh and food was scarce, while the lowest levels of selectivity occurred in the hot seasons

that had ample to abundant rainfall (Table 5.17). Although selectivity did not show a significant linear relationship with precipitation, there was a significant negative Spearman's rank correlation between selectivity and precipitation (all study areas: $r_s = -0.44$, $df = 31$, $P < .01$; Caseta/Chato: $r_s = -0.38$, $df = 26$, $P < .04$), suggesting that tortoises specialize more when food is scarce.

When all study areas were included, richness of the diet was positively related to the total biomass of available food and overall diversity of the vegetation (Fig. 5.5), while being negatively related to feeding selectivity of tortoises (Table 5.18). At Caseta/Chato, S_d was a positive function of the richness of the vegetation, and still showed a significant positive relationship to log N (Table 5.18). The number of items in the tortoise diet was consistently less than that of the available food supply for all study areas ($t = 21.24$, $df = 34$, $P < .0001$), with a mean difference of 31 items (many of which were relatively rare) at Caseta/Chato, 23 at SCNZ, and 12 on Pinzón.

Diversity of the diet increased with increasing diversity of the vegetation (Fig. 5.6), but was negatively affected by increases in feeding selectivity of tortoises (Table 5.18). H'_d was significantly less than H'_v at all study areas ($t = 5.66$, $df = 34$, $P < .0001$), with a mean difference of 0.34 at Caseta/Chato, 0.49 at SCNZ, and 0.16 on Pinzón.

Evenness of the diet was a positive function of diversity of the vegetation (Table 5.18). Unlike the other two

Table 5.17. Mean feeding selectivity (SEL)[1] for food items of tortoises in different seasons at the four study areas. Only those months with a minimum of 50 feeding observations were included. For seasonal differences $F_{4,25} = 16.97$, $P \leq .0001$; for study area differences $F_{3,25} = 3.07$, $P \leq .05$; interaction term was not significant. Numbers for all study areas combined followed by different letters are significantly different at $P \leq .05$. Tukey's range test showed no differences among study areas.

	STUDY AREA				
SEASON	LA CASETA	EL CHATO	SCNZ[2]	PINZÓN	ALL
			Selectivity[a]		
Hot-Wet 82	0.385 ± 0.02	0.348 ± 0.03			0.366[a]
El Niño			0.416 ± 0.10	0.357	0.415[ab]
Garúa 81	0.453 ± 0.04	0.388 ± 0.02			0.425[ab]
Garúa 82	0.477 ± 0.03	0.457 ± 0.05			0.467[b]
Hot-Dry 82	0.657 ± 0.10	0.682 ± 0.24		0.715	0.628[c]

[1] Calculated as in McNaughton (1978) as $SEL = \Sigma |p_s - p_c|/2$, where p_s was proportion of the stand and p_c was proportion of the diet. SEL ranges from 0 when consumption is proportional to abundance to near 1 when consumption is the inverse of abundance.

[2] Santa Cruz Nesting Zone.

Fig. 5.5. Richness of the diet (S_d) in relation to total available food and vegetation diversity (H'_y) at all study areas (SCNZ = Santa Cruz Nesting Zone).

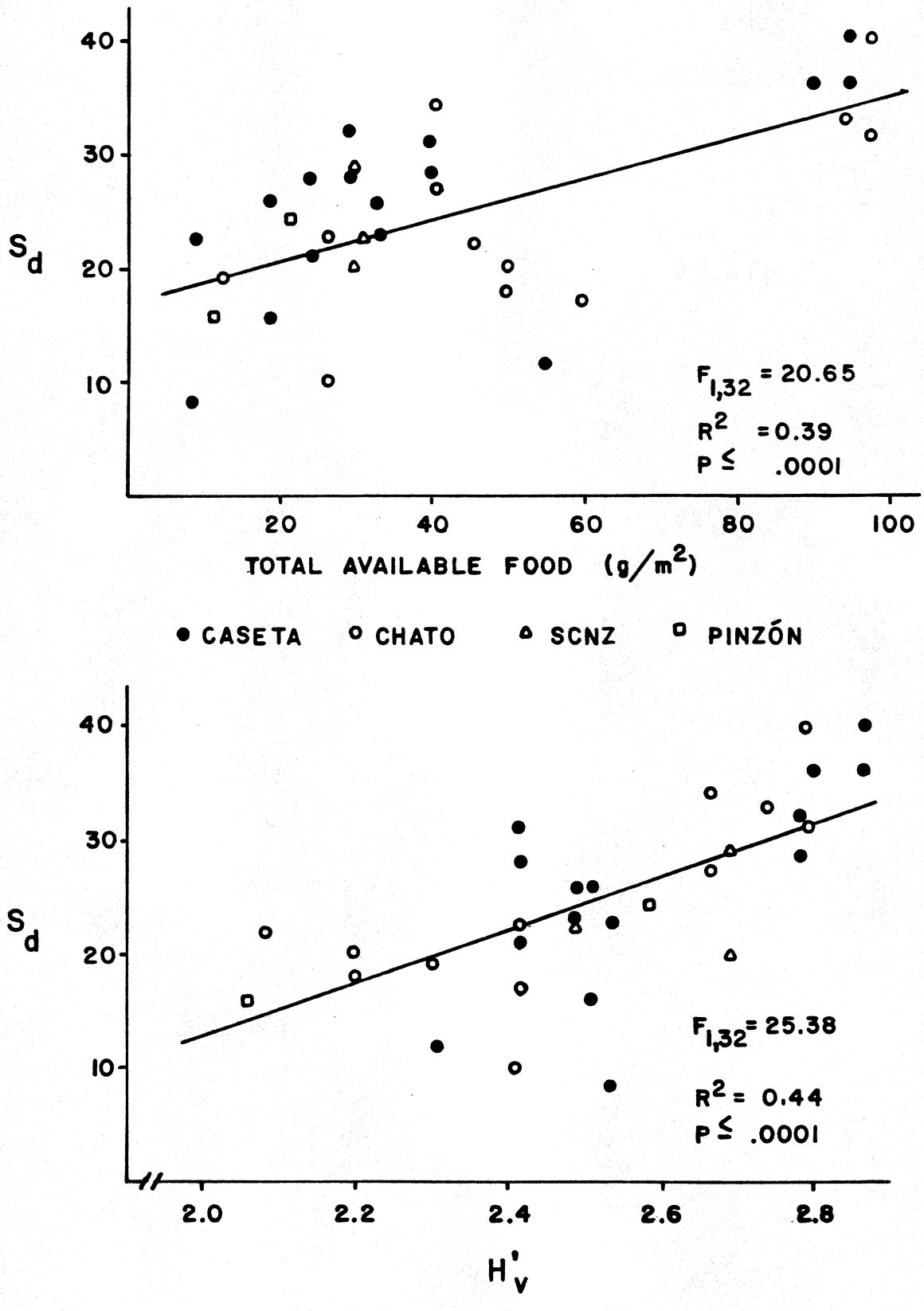

40
30
20
10
S_d
20
40
60
80
100
TOTAL AVAILABLE FOOD (g/m^2)
$F_{1,32} = 20.65$
$R^2 = 0.39$
$P \leq .0001$
● CASETA
○ CHATO
△ SCNZ
□ PINZÓN
40
30
20
10
S_d
2.0
2.2
2.4
2.6
2.8
H'_v
$F_{1,32} = 25.38$
$R^2 = 0.44$
$P \leq .0001$

Table 5.18. Results from stepwise regressions of diet diversity indices[a]. Independent variables included number of feeding observations/month (N), log N, precipitation, total available food (TAF, g/m^2), vegetation diversity indices[b], and selectivity[c] (SEL, arc sine square root). Number of months in each regression was 34 for all study areas, and 29 for Caseta/Chato. Results list explained variance and partial correlations (r_p) at $P \leq .05$*, .01**, .001***, and .0001****. The correlation coefficient rather than r_p is given in results for species evenness (J_d) where only one variable entered the equation.

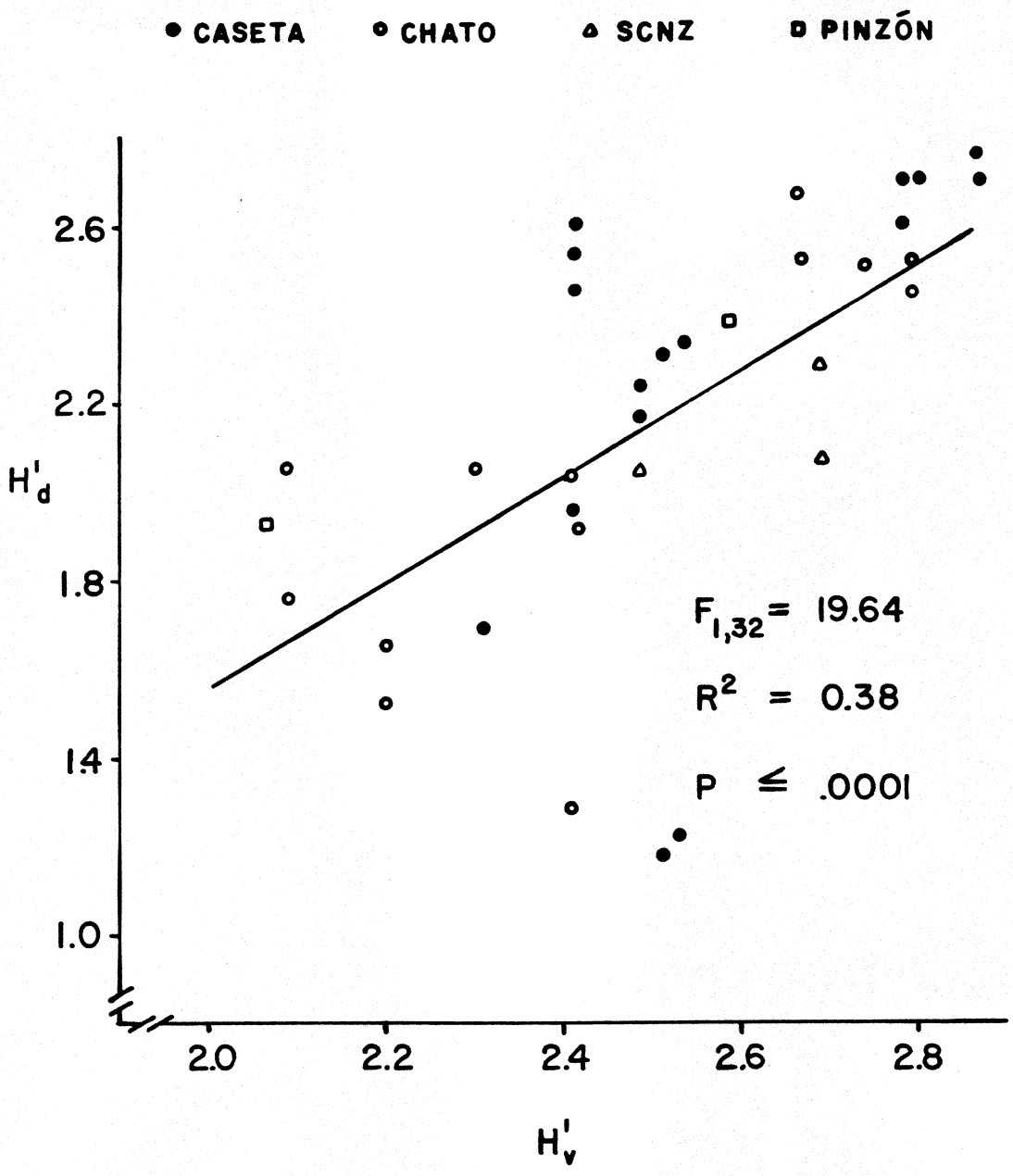
		ALL STUDY AREAS		CASETA/CHATO	
INDEX[a]	SIGNIFICANT VARIABLES	VARIANCE EXPLAINED	r_p	VARIANCE EXPLAINED	r_p
S_d	H'_v	0.18****	+0.62**		
	TAF	0.39**	+0.48**		
	SEL	0.12**	-0.52**		
	S_v			0.51****	+0.68**
	log N			0.18***	+0.60**
H'_d	H'_v	0.38****	+0.66**	0.40****	+0.74**
	SEL	0.12**	-0.43*	0.20***	-0.58**
J_d	H'_v	0.25**	+0.50**	0.30**	+0.54**

[a]Diet diversity indices include: species richness (S_d), species diversity (H'_d), and species evenness (J_d).

[b]Vegetation diversity indices include: species richness (S_v), species diversity (H'_v), and species evenness (J_v).

[c]Calculated as in McNaughton (1978) as $SEL = \Sigma|p_s - p_c|/2$, where p_s was proportion of the stand and p_c was proportion of the diet.

Fig. 5.6. Dietary diversity (H'_d) in relation to vegetation diversity (H'_v) at all study areas (SCNZ = Santa Cruz Nesting Zone).


● CASETA
○ CHATO
△ SCNZ
□ PINZÓN
2.6
2.2
1.8
1.4
1.0
H'd
2.0
2.2
2.4
2.6
2.8
H'v
F1,32 = 19.64
R2 = 0.38
P ≤ .0001

diversity indices, J_d was significantly higher than J_v at Caseta/Chato, with a mean increase of 0.05 ($t = 3.68$, $df = 28$, $P < .001$). There was essentially no difference at SCNZ, and a mean increase of 0.05 on Pinzón. The increase in dietary evenness over that of the available food suggests that tortoises are able to selectively consume food items in more equal proportions than are available in the environment. This ability increases with increasing vegetation diversity.

Food Preference Indices

Useful electivity indices have been developed combining an animal's diet with the availability of food items in the animal's environment to determine food selection (Ivlev 1961, Gerald 1966, Chesson 1978, Cock 1978, Strauss 1979, Vanderploeg and Scavia 1979a,b, Johnson 1980). Foods that are eaten in a higher proportion than is available are preferred, while those proportionally underrepresented in the diet are avoided. In a review of seven indices, Lechowicz (1982) found that none of them satisfied all of his criteria for a good index. Although he considered Vanderploeg and Scavia's relativized electivity index (E^*_i) (Vanderploeg and Scavia 1979b) the single most useful index, he found that the use of rank order electivities eliminated the majority of differences among six of the seven indices.

To select an electivity index for this study, three of the indices examined by Lechowicz (1982) were compared (Table 5.19). Only those food items included in the diet

Table 5.19. Three indices of feeding preference based on the proportions of food i in the diet (r_i) and in the environment (p_i)[a].

INDEX	COMMENT	REFERENCE
$E_i = (r_i - p_i)/(r_i + p_i)$	Ivlev's electivity index	Ivlev 1961
$\alpha_i = W_i = \frac{r_i/p_i}{\Sigma(r_i/p_i)}$	Chesson's alpha, Vanderploeg and Scavia's selectivity coefficient	Chesson 1978, Vanderploeg and Scavia 1979a
$E_i^* = \frac{\{W - (1/n)\}}{\{W + (1/n)\}}$	n = number of kinds of food itmes	Vanderploeg and Scavia 1979b

[a]In this study, if $p_i = 0$, but the item was eaten, p_i was set at 0.001.

were included in all preference analyses. Spearman's rank correlations among the three indices for each month at each study area was 1.0, or 100% correlation, for 40 of the 45 months, while the 5 remaining months had r_s values of 0.999. Due to the lack of difference among indices when ranked, the rank order of Ivlev's electivity index (E_i) was selected for all further analyses. To make cross-month comparisons, where each month had a different number of food items and thus rank values, rank order (lowest index value = 1) was divided by the number of food items for each month. This gave each food item a preference value between 0 and 1, with 1 the most preferred, and that closest to 0 the least preferred.

The greatest difficulty in determining food preferences is in making accurate estimates of food availability, especially in natural habitats (Johnson 1980, Crawley 1983). Whether or not a species is actually available to the animal is not always evident to the human observer. Subjectivity in naming the array of available food items was most evident on Pinzón, where the three most abundant species constituted greater than 68% of the "available" food, yet two were seldom or never eaten (Prosopis juliflora and Maytenus octogona), while the third (Alternanthera filifolia) never constituted more than 6% of the diet. Perhaps they are unavailable due to thorniness (P. juliflora), or possibly high levels of secondary compounds (A. filifolia, M. octogona). Comparing rank orders of Ivlev's electivity index

based on the available forage, including the three above-mentioned species, with that of electivity indices when the three species were eliminated from the available forage, resulted in Spearman's rank correlations of 0.83 ($P < .0001$, $df = 15$) for the hot-dry season, and 0.96 ($P < .0001$, $df = 20$) for El Niño. Therefore, use of rank order of electivity, rather than the actual index, effectively eliminated both the problem of deciding which items were available (though not which plant parts), as well as that of choosing the one best index.

Food Preferences

Food preferences at La Caseta and El Chato were similar. A paired comparison of the mean preference indices of the 56 food items common to both areas (averages include only those months a given item was in the diet), was not significant ($t = 0.30$, $df = 55$, NS), while a rank correlation of these same averages was highly significant ($r_s = 0.74$, $df = 54$, $P < .0001$).

The majority of food items in the tortoise diet had positive preference values, indicating that tortoises consume primarily what they prefer. However, there were a few dietary components that, although consumed, were avoided relative to their abundance resulting in negative preference index values. Of the 38 food items that were significant in the diet at La Caseta, on the average 36 had a positive index and only 2 were negative, while 29 of the significant food items at El Chato were positive and 2 were negative

(Tables 5.20, 5.21). However, at both areas, several species were essentially zero and could be considered taken in proportion to their availability. Desmodium canum, a staple in the tortoise diet both at La Caseta and El Chato, is a good example. However, other species with an average preference index of zero may be preferred in some seasons and avoided in others. Ageratum conyzoides, on the other hand, was avoided. In addition to the months when it occurred in the diet, there were several months when it was high in abundance in the environment but was not significant in the diet. New growth of A. conyzoides was preferred, indicating a preference change according to age of the plant. A similar selection by age was apparent for Stictocardia tiliifolia at La Caseta, where tortoises preferred the cotyledons, but otherwise avoided the species (Table 5.2). Scleria pterota, a robust, razor-edged sedge, was the only significant food item consistently avoided at both La Caseta and El Chato.

Of the 16 significant food items at SCNZ, on the average 10 had a positive preference index, while 6 were negative (Tables 5.21, 5.22). Although Bastardia viscosa had an average preference index that was negative, it could be considered a staple in the diet, similar to Desmodium canum at Caseta/Chato. Preference or avoidance of Evolvulus glaber, Sida hederifolia, and Tetramerium nervosum at SCNZ is questionable. Indices for these species vacillated between positive and negative. Only T. nervosum was significant in

Table 5.20. Food items that were significant in the diet at La Caseta and El Chato, and that had a positive average preference index (E_i, averaged over number of months significant, MO), indicating preferred tortoise foods. Those indicated equal to zero were generally eaten in proportion to their availability. Total possible number of months was 20.

	LA CASETA		EL CHATO	
FOOD ITEM	MO	$E_i \pm SD$	MO	$E_i \pm SD$
Ageratum conyzoides[a]	2	0.17 ± 1.13 = 0	3	
A. conyzoides - sprouts	2	0.74 ± 0.04	1	0.42
Alternanthera halimifolia	1	0.73		
Apium sp.	1	0.73		
Astrephia chaerophylloides	2	0.93 ± 0.02		
Azolla microphylla	4	0.96 ± 0.02	2	0.97 ± 0.02
Blechum brownei	3	0.24 ± 0.66 = 0	7	0.09 ± 0.26 = 0
Borreria laevis	1	0.90	8	0.60 ± 0.10
Cassia occidentalis	2	0.82 ± 0.07	1	0.17
Citrus spp. (lemon) - fruit	1	0.99		
Commelina diffusa	2	0.92 ± 0.01	1	0.84
Cyperus brevifolius	2	0.93 ± 0.06	2	0.89 ± 0.04
Cyperus sp.			1	0.88
Desmodium canum[b]	18		17	0.01 ± 0.25 = 0
Digitaria horizontalis	4	0.88 ± 0.03		
Dichondra repens	10	0.28 ± 0.41 = 0	13	0.60 ± 0.23
Eleocharis spp.			2	0.67 ± 0.03
Eleusine indica	1	0.93		
Enydra maritima	3	0.94 ± 0.03		
Galactia striata	4	0.76 ± 0.09		
Hippomane mancinella - fruit	8	0.56 ± 0.38	5	0.76 ± 0.28
Ichnanthus nemorosus	1	0.63		
Justicia galapagana	11	0.26 ± 0.23	6	0.54 ± 0.22
Ludwigia leptocarpa	2	0.94 ± 0.00		
Ludwigia peploides			1	0.95
Momordica charantia	6	0.57 ± 0.23	4	0.41 ± 0.22

Table 5.20 continued.

FOOD ITEM	LA CASETA MO	LA CASETA $E_i \pm SD$	EL CHATO MO	EL CHATO $E_i \pm SD$
Panicum laxum			1	0.94
Paspalum conjugatum	20	0.04 ± 0.27 = 0	20	0.22 ± 0.13
Paspalum distichum	1	0.94	2	0.95 ± 0.01
Phyla strigulosa			5	0.76 ± 0.08
Phyllanthus caroliniensis	4	0.26 ± 0.42 = 0	1	0.74
Pilea baurii	4	0.83 ± 0.09	2	0.73 ± 0.17
Psidium galapageium - fruit	6	0.60 ± 0.27	5	0.31 ± 0.46 = 0
Rhynchospora nervosa	7	0.01 ± 0.19 = 0	9	0.44 ± 0.16
Sida hederifolia	3	0.65 ± 0.10	3	0.71 ± 0.16
Sida rhombifolia	13	0.59 ± 0.29	2	0.80 ± 0.04
Sida spinosa	3	0.88 ± 0.09	5	0.88 ± 0.08
Solanum nodiflorum	2	0.77 ± 0.04	2	0.76 ± 0.06
Stenotaphrum secundatum	14	0.39 ± 0.32	13	0.50 ± 0.26
Stictocardia tiliifolia - cotyledon	1	0.04		
Thelypteris tetragona	1	0.47	1	0.43
Tillandsia insularis	3	0.94 ± 0.01		

[a]Negative preference index at El Chato, and when data from La Caseta and El Chato were combined.

[b]Negative preference index at La Caseta, and when data from La Caseta and El Chato were combined.

Table 5.21. Food items that were significant in the diet at each study area and that had a negative average preference index (E_i, averaged over number of months significant), indicating avoidance by tortoises. Those indicated equal to zero were generally eaten in proportion to their availability. Total possible number of months was 20 at La Caseta and El Chato, 3 at the Santa Cruz Nesting Zone (SCNZ), and 2 on Pinzón.

STUDY AREA	FOOD ITEM	No. MONTHS	$E_i \pm SD$
CASETA	Desmodium canum[a]	18	-0.08 ± 0.30 = 0
	Scleria pterota[a]	5	-0.29 ± 0.23
CHATO	Ageratum conyzoides[a]	3	-0.24 ± 1.02 = 0
	Scleria pterota[a]	5	-0.35 ± 0.20
SCNZ	Bastardia viscosa	3	-0.11 ± 0.17 = 0
	Blechum brownei	1	-0.42
	Commicarpus tuberosus	1	-0.26
	Evolvulus glaber	2	-0.02 ± 0.47 = 0
	Sida hederifolia	2	-0.06 ± 0.43 = 0
	Tetramerium nervosum	3	-0.25 ± 0.31 = 0
PINZÓN[b]	Alternanthera filifolia	1	-0.75
	Prosopis juliflora	1	-0.74
	Lichen	1	-0.29

[a]Also negative when data from La Caseta and El Chato were combined.

[b]When availability data exclude Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona, then Croton scouleri and Zanthoxylum fagara also have negative preference indices.

Table 5.22. Food items that were significant in the diet at the Santa Cruz Nesting Zone (SCNZ) and on Pinzón, and that had a positive average preference index (E_i, averaged over number of trips significant, TRIPS), indicating preferred tortoise foods. Those indicated equal to zero were generally eaten in proportion to their availability. Total possible number of trips was 3 at SCNZ, and 2 on Pinzón.

STUDY AREA	FOOD ITEM	TRIPS	$E_i \pm SD$
SCNZ	Alternanthera halimifolia	2	$0.04 \pm 0.17 = 0$
	Bidens riparia	1	0.69
	Blainvillea dichotroma	2	$0.06 \pm 0.34 = 0$
	Corchorus orinocensis	1	0.82
	Desmodium procumbens	1	0.72
	Ipomoea triloba	3	0.64 ± 0.11
	Opuntia echios - pads	1	0.92
	Oxalis cornellii	2	0.58 ± 0.02
	Physalis galapagensis	1	0.88
	Sida spinosa	3	$0.33 \pm 0.38 \stackrel{?}{=} 0$
PINZÓN	Commelina diffusa	2	0.73 ± 0.20
	Croton scouleri	1	0.11
	Cyperus elegans	1	0.93
	Lantana peduncularis	1	0.87
	Opuntia galapageia - fruit	1	0.94
	O. galapageia - pads	2	0.98 ± 0.02
	Panicum fasciculatum	1	0.61
	Phyla strigulosa	1	0.96
	Portulaca oleracea	2	0.73 ± 0.24
	Setaria setosa	1	0.73
	Zanthoxylum fagara	1	0.34

all three months, and it only became important in the diet in July 1983, when Ipomoea triloba, the major item in the diet during El Niño, was no longer abundant. Blechum brownei and Commicarpus tuberosus, each significant in only one month, appear to be avoided.

On Pinzón, 9 species had a positive average preference index, while 3 to 5 were negative (Tables 5.21, 5.22). Alternanthera filifolia, Prosopis juliflora (leaves), and lichen were all avoided. Only when A. filifolia, Maytenus octogona, and P. juliflora were eliminated from the available biomass did Croton scouleri and Zanthoxylum fagara have negative preference indices.

In general, most food items that were significant in the diet were preferred relative to their environmental abundance. The few that were avoided, being proportionally underrepresented in the diet, had a relatively high abundance in the available food supply. Avoidance of species by tortoises was usually close to 100%, with the result that avoided species rarely appeared as significant in the diet. Most species that consistently appeared in the available biomass, but were essentially ignored, were shrubs (Table 5.23). Occasionally tortoises were seen sampling leaves and then rejecting them. At Caseta/Chato all such rejected species were forbs, including Stictocardia tiliifolia, rejected once by each of four focal animals, and Phyla strigulosa, Teucrium vesicarium, and Passiflora foetida, each rejected once. No species was seen rejected at SCNZ. On

Table 5.23. Avoided species that were consistently available in the environment but were never significant in the diet.

FOOD TYPE	LA CASETA	EL CHATO	SANTA CRUZ NESTING ZONE	PINZÓN
SHRUB	Chiococca alba	Cassia picta	Chiococca alba	Castela galapageia
	Psychotria rufipes	Chiococca alba	Croton scouleri[a]	Maytenus octogona
	Zanthoxylum fagara[a]	Clerodendrum molle	Lantana peduncularis[b]	
		Psychotria rufipes	Tournefortia psylostachya	
		Tournefortia rufo-sericea		
		Zanthoxylum fagara[a]		
FORB	Stictocardia tiliifolia	Stictocardia tiliifolia	Galactia striata[c]	
			Heliotropium angiospermum	
			Plumbago scandens	
TREE		Psidium galapageium	Pisonia floribunda	
MOSS	Moss	Moss		

[a]Significant in the diet, but potentially avoided on Pinzón (Table 5.20).

[b]Significant and preferred on Pinzón.

[c]Significant and preferred at La Caseta.

Pinzón. Maytenus octogona was sampled but rejected by two focal animals, and Heliotropium angiospermum, an avoided species at SCNZ, was rejected by one animal. Castela galapageia, never seen eaten or even sampled by tortoises on Pinzón, was reported eaten by tortoises on Santa Cruz (Snow 1964). However, on Santa Cruz, this species is a tall, erect shrub without spines, while on Pinzón, it is extremely prostrate, with dense sharp spines along the stem.

Food Preferences in Relation to Water Content

All land tortoises may be able to exist indefinitely on a vegetation diet without free water (Cloudsley-Thompson 1971). Many authors have stressed the importance of plant water in the diet of reptiles, but have not shown whether food preferences for specific food items are dependent upon their water content. If plant water is essential, especially in dry seasons, tortoises would benefit by being able to select food higher in water content than the average water content of the available food supply.

Seasonal changes in water content of the diet of Galápagos tortoises tracked those of the available food supply, and were generally higher (Fig. 5.7, 5.8). Paired comparisons of water content of the diet versus that of the available food resulted in a mean increase of 2.4% in the diet for all study areas combined ($t = 5.16$, $df = 44$, $P < .001$), and a mean increase of 2.1% when only La Caseta and El Chato data were included ($t = 5.85$, $df = 39$, $P < .001$). The mean increase in water content of the diet ranged from only 0.3%

Fig. 5.7. Water content of the available food and of the tortoise diet at La Caseta (June 1981 to January 1983), the Santa Cruz Nesting Zone (February/March to July 1983), and Pinzón (boxes - April/May and December 1982).

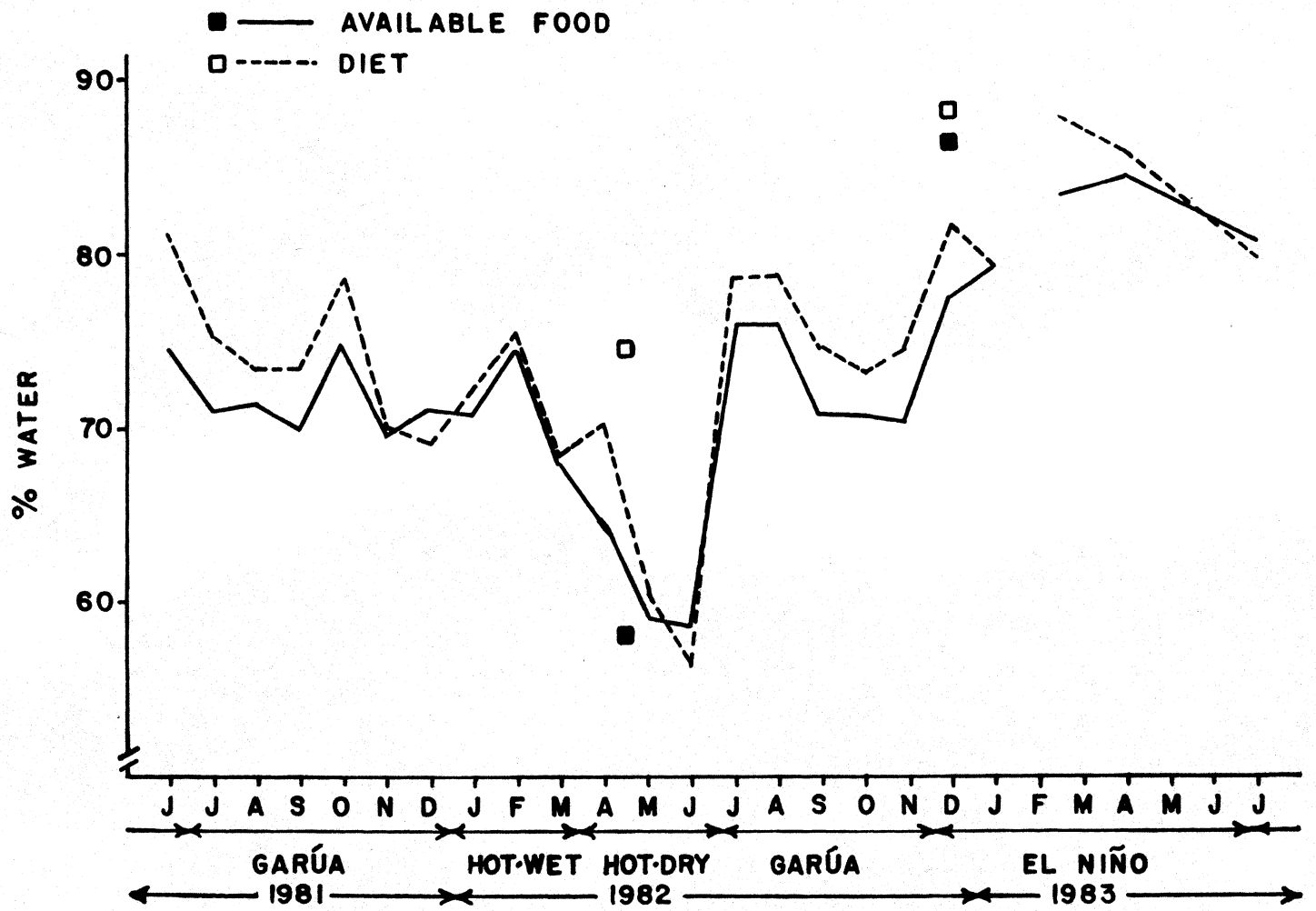
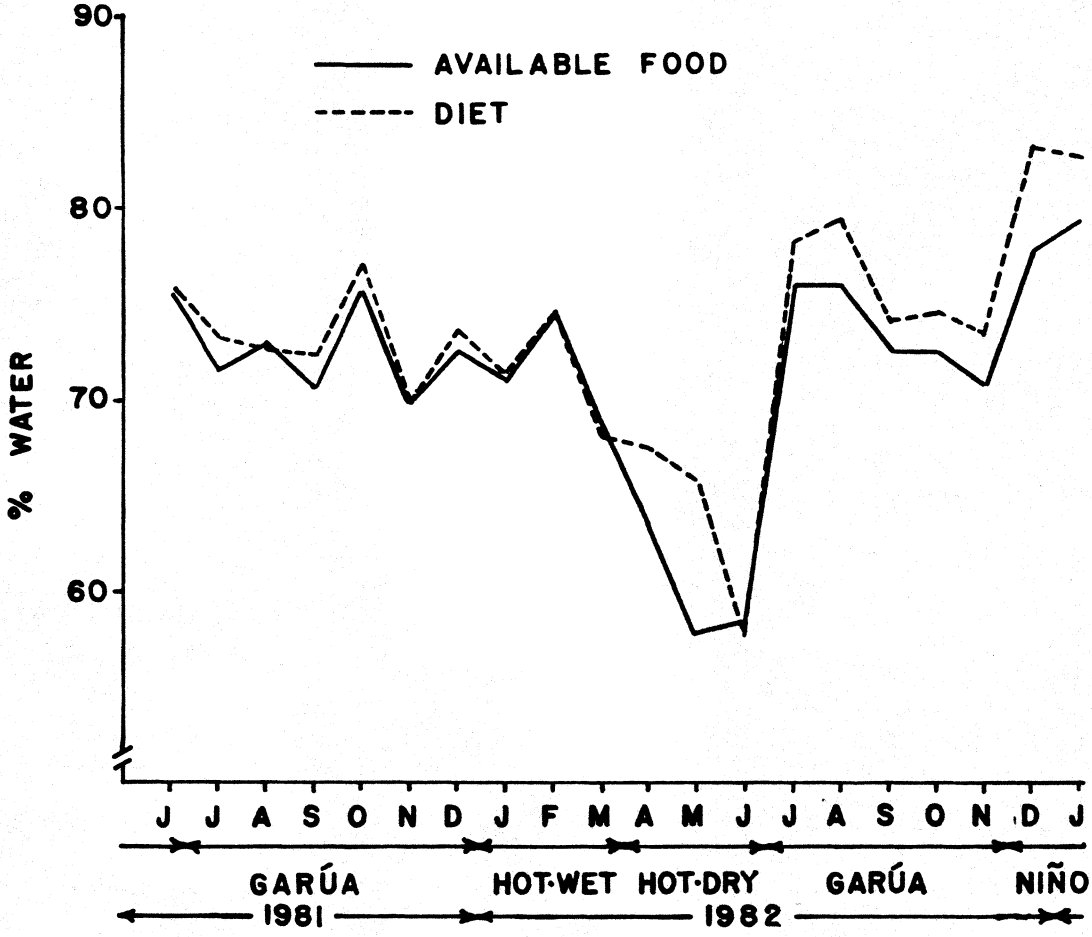

AVAILABLE FOOD
DIET
90
80
70
60
% WATER
J J A S O N D J F M A M J J A S O N D J F M A M J J
GARÚA
HOT-WET
HOT-DRY
GARÚA
EL NIÑO
1981
1982
1983

Fig. 5.8. Water content of the available food and of the tortoise diet at El Chato, June 1981 to January 1983.

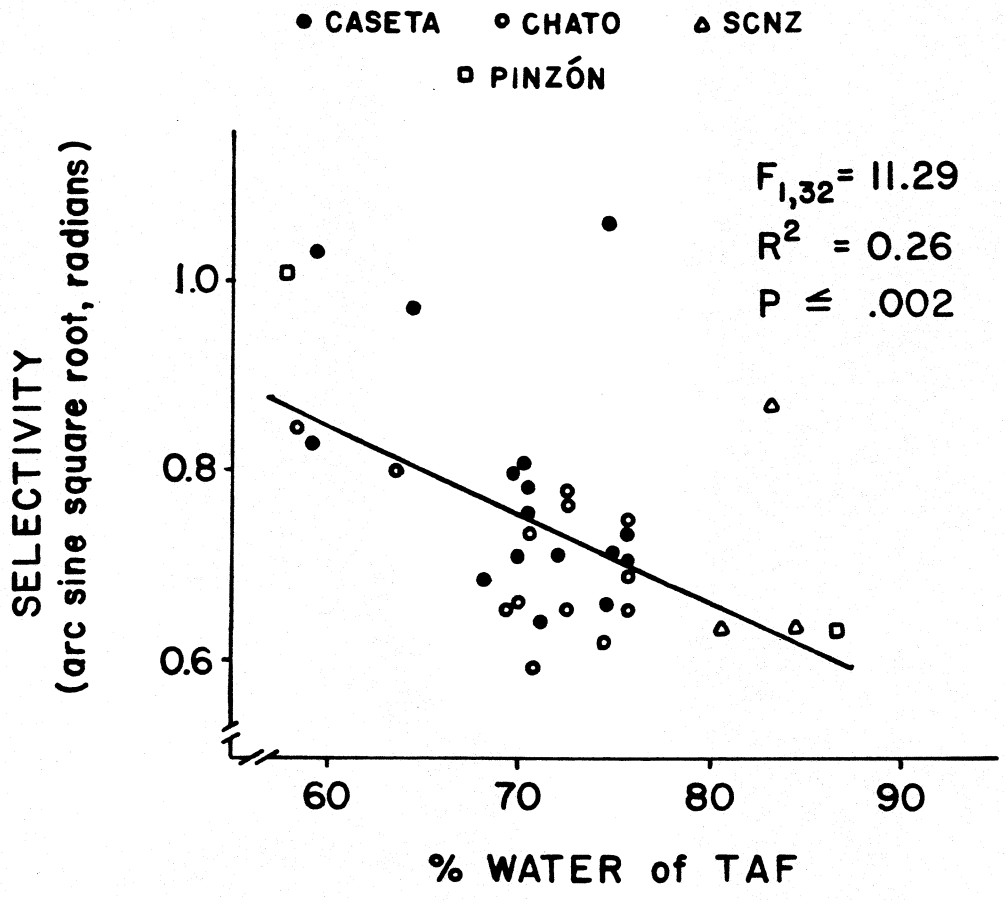
EL CHATO


90
80
70
60
% WATER
AVAILABLE FOOD
DIET
J J A S O N D J F M A M J J A S O N D J
GARÚA
HOT-WET
HOT-DRY
GARÚA
NIÑO
1981
1982

in the hot-wet season 1982, to a mean increase of 7.3% in April and May 1982, the two driest months of the study.

Water content of the diet was primarily a positive function of the water content of the available food (all study areas: $F_{1,30} = 169.38$, $P < .0001$; Caseta/Chato: $F_{1,26} = 296.73$, $P < .0001$), which explained 80% and 89% of the variance respectively, and secondarily, a positive function of selectivity (all study areas: $F_{1,30} = 13.89$, $P < .001$; Caseta/Chato: $F_{1,26} = 16.56$, $P < .0004$), which explained only 7% and 5% of the variance. Partial correlations, holding one factor constant while varying the other two, showed a positive correlation between water content of the diet and that of the available food (all study areas: $r_p = 0.93$, $P < .01$; Caseta/Chato: $r_p = 0.97$, $P < .01$), and between water content of the diet and selectivity (all study areas: $r_p = 0.59$, $P < .01$; Caseta/Chato: $r_p = 0.70$, $P < .01$). However, selectivity was negatively correlated with water content of the available food (all study areas: $r_p = -0.70$, $P < .01$; Caseta/Chato: $r_p = -0.76$, $P < .01$), and was a negative function of it (all study areas: $F_{1,32} = 11.29$, $P < .002$; Caseta/Chato: $F_{1,27} = 7.77$, $P < .01$) (Fig. 5.9). Thus, tortoises became more selective in drier periods when food and water were both scarce, with selection of food items aimed at increasing water intake per gram of forage over the average of that available, and at avoiding those species with low water content and potentially a lower level of digestability.

Fig. 5.9. Feeding selectivity of tortoises in relation to water content of the total available food (TAF) at all study areas (SCNZ = Santa Cruz Nesting Zone).


● CASETA ○ CHATO △ SCNZ
□ PINZÓN
$F_{1,32}$= 11.29
R^2 = 0.26
P ≤ .002
SELECTIVITY
(arc sine square root, radians)
1.0
0.8
0.6
60
70
80
90
% WATER of TAF

The relationship between food preferences for specific food items (E_i) and their water content (%) was examined seasonally for each study area. Rank order of E_i (lowest index value = 1) divided by the number of food items for each month was used. For each location, analyses were done for all food items and for significant food items only. Regression was used to examine potential linear relationships between preference and water content, while Spearman's rank correlation was used to determine whether tortoises simply ranked food items according to their water content.

Food preferences were positively related to water content of the food items in at least one season at each study area (Table 5.24). Water content of food items explained the most variance in preference at La Caseta in June 1981, at the end of the hot season, and on Pinzón during the hot-dry season 1982 (Fig. 5.10). In general, the strongest relationships occurred when conditions were extremely dry, continuing significant through the cool garúa seasons. Food preferences showed no relationship to water content in the hot-wet season of 1982 (see footnote, Table 5.24, for exception), or during El Niño on Pinzón. During the wet seasons the range in water content of food items was much lower than in the dry season, reducing the importance of selection for the higher water-content foods. The lack of significant relationships between preference and water content of the food at El Chato is not well understood but possibly results from the general absence of specific foods with very high

Table 5.24. Relationship between food preferences and water content of the food by season, excluding months with less than 50 feeding observations. Results from regressions and Spearman's rank correlations between the preference value[a] and % water content (arc sine square root) of food item i.

		ALL FOOD ITEMS						SIGNIFICANT FOOD ITEMS					
			REGRESSION			CORRELATION			REGRESSION			CORRELATION	
SEASON	STUDY AREA	N	$P \leq$	R^2	SLOPE	$P \leq$	r_s	N	$P \leq$	R^2	SLOPE	$P \leq$	r_s
JUNE 81	CASETA	11	.03	0.43	+	.02	+.68	6	NS			.04	+.83
GARÚA 81	CASETA	80	.001	0.14	+	.01	+.30	39	.01	0.18	+	.03	+.34
	CHATO	48	NS			NS		23	NS			NS	
HOT-WET 82	CASETA	53	NS			NS		22	NS			NS	
	CHATO	41	NS			NS		18	NS[b]			NS	
HOT-DRY 82	CASETA	23	.05	0.17	+	NS		13	NS			NS	
	CHATO	16	NS			NS		8	NS			NS	
	PINZÓN	16	.01[c]	0.36	+	.01	+.65	7	NS[d]			NS	
GARÚA 82	CASETA	143	.0001	0.11	+	.0001	+.33	63	.0001	0.23	+	.0004	+.43
	CHATO	148	.05	0.03	+	NS		62	NS			NS	
EL NIÑO	SCNZ[e]	56	.01	0.13	+	.02	+.32	30	NS			NS	
	PINZÓN	23	NS			NS		8	NS			NS	

[a] Preference value = rank of E_i/number of ranks per month.

[b] Water content is significant in regression with nitrogen content: $F_{2,2} = 3266.2$, $P \leq .0003$, $R^2 = 1.00$; water and nitrogen contents explained 13% ($P \leq .001$) and 87% ($P \leq .0002$) of the variance in feeding preference, respectively; both had significant positive partial correlations (r_p) with feeding preference.

Table 5.24 continued.

---

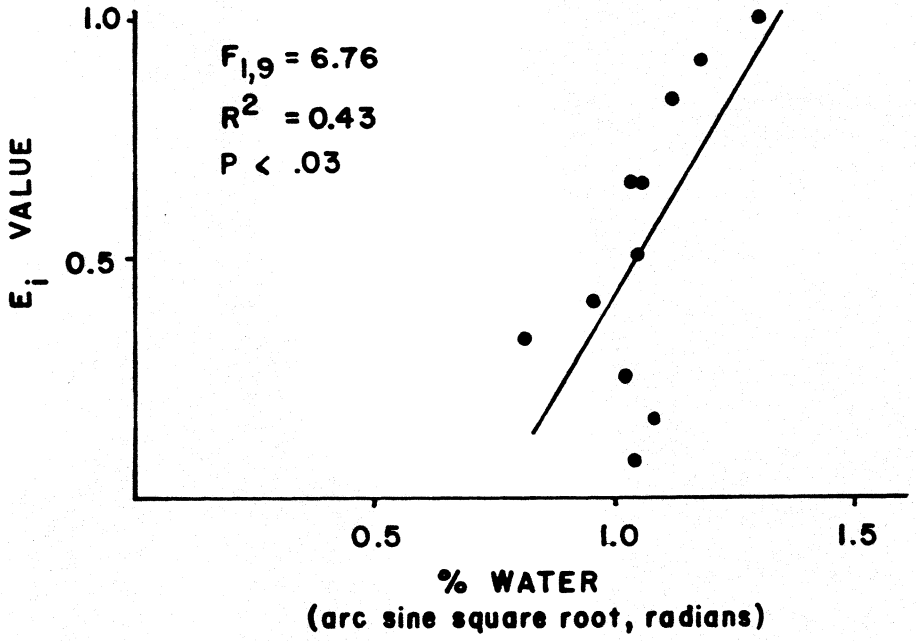
[c]Water content is significant in regression with nitrogen content: $F_{2,13} = 8.17$, $P \leq .005$, $R^2 = 0.56$; water content and nitrogen content explained 36% ($P \leq .004$) and 20% ($P \leq .03$) of the variance in feeding preference respectively; water to preference $r_p = 0.30$ ($P \leq .01$), nitrogen to preference $r_p = -0.56$ ($P \leq .05$).

[d]Water content is significant in regression with nitrogen content: $F_{2,4} = 7.86$, $P \leq .04$, $R^2 = 0.80$; water content and nitrogen content explained 35% ($P \leq .02$) and 45% ($P \leq .04$) of the variance in feeding preference, respectively; water to preference $r_p = 0.88$ ($P \leq .05$), nitrogen to preference $r_p = -0.83$ $P \leq .05$).

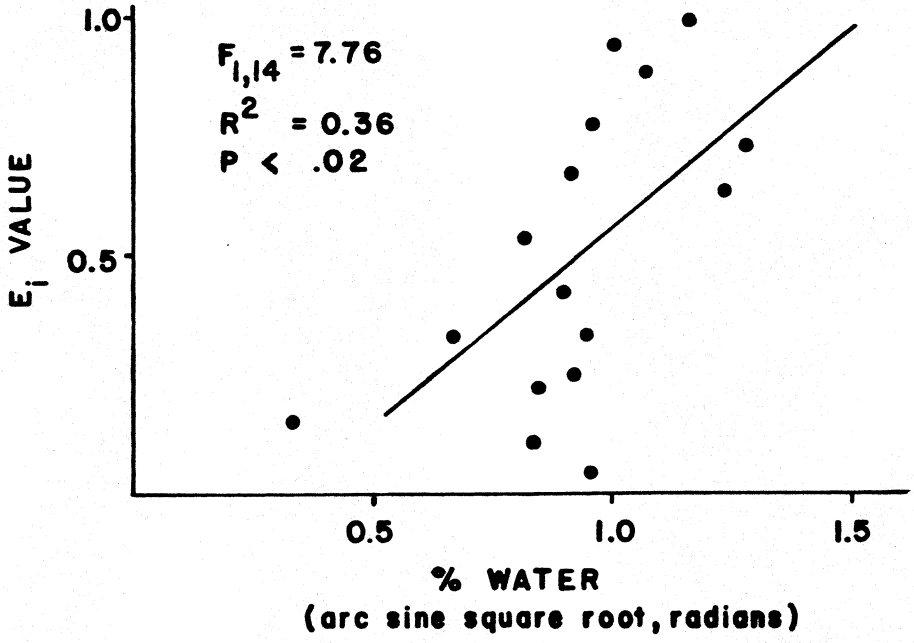
[e]Santa Cruz Nesting Zone.

Fig. 5.10. Tortoise food preferences in relation to the water content of food items at La Caseta in June 1981, and on Pinzón during the hot-dry season 1982. Preference index value (E_i value) equals the rank order of each index (lowest index value = 1) divided by the number of food items for each month. Percent water of food items ranged from 54.0 to 92.9% at La Caseta, and from 10.8 to 92.6% on Pinzón.

LA CASETA – JUNE 1981



PINZÓN – APRIL/MAY 1982



water content that are more available at La Caseta (eg., Tillandsia insularis). Overall, tortoises preferred food items with higher water content, especially in seasons when conditions were harsh, and food and water were scarce.

In general, feeding preferences of tortoises are a positive function of the water content of food items, with the strongest relationship and thus the greatest overall selectivity occurring in arid seasons when both food and water are scarce. Feeding selectivity increased with decreasing water content of the available food and decreased in periods of food abundance.

Food Preferences in Relation to Nitrogen

Nitrogen level, an important factor in determining food preferences for many vertebrates (Sinclair 1975, White 1978, Mattson 1980), is sometimes correlated with the water content of the vegetation (McNaughton 1985b). If this is true in the Galápagos Islands, preference for high-water-content foods may result from selection of foods with high nitrogen levels. Separate regression analyses of each month's nitrogen-water data set resulted in no significant relationships between the two components at El Chato (3 months), SCNZ (3 months), or on Pinzón (2 months). At La Caseta, there was a significant negative relationship in April 1982 ($F_{1,8} = 9.18$, $R^2 = 0.53$, $P < .01$), while the other three months had no significant relationship between nitrogen and water. The lack of any consistent significant relationship between nitrogen and water content of food items is most

likely due to the extremely wide variety of food types in the tortoise diet.

Regression and Spearman's rank correlation, similar to the previous analyses of preference and water content, were done to determine whether there was a significant relationship between tortoise food preferences and the nitrogen content of specific food items.

Food preference was a positive function of nitrogen content of food items only in the hot-wet season 1982, at La Caseta and El Chato when only significant food items were included (Table 5.25, Fig. 5.11). This was the only season that preferences were not significantly related to water content in at least one of the two areas (see footnote, Table 5.24, for exception).

Food preference was a negative function of nitrogen content on Pinzón in both the hot-dry season and at the onset of El Niño (Table 5.25, Fig. 5.11). In both seasons, the major reason for the negative relationship was the extremely low level of nitrogen in Opuntia galapageia pads (average nitrogen content - 0.59%), and fruits (average nitrogen content - 1.07%), both of which are highly preferred foods year-round. The negative Spearman's rank correlation at El Chato in the hot-dry season for significant food items is questionable due to the extremely low sample size.

Nitrogen content of the food is not a major factor in determining food preferences of tortoises. When conditions were favorable, as in the highlands of Santa Cruz during the

Table 5.25. Relationship between food preferences and nitrogen content of the food by season, excluding months with less than 50 feeding observations. Results from regressions and Spearman's rank correlations between the preference value[a] and % nitrogen content (arc sine square root) of food item i.

		ALL FOOD ITEMS						SIGNIFICANT FOOD ITEMS					
			REGRESSION			CORRELATION			REGRESSION			CORRELATION	
SEASON	STUDY AREA	N	P≤	R^2	SLOPE	P≤	r_s	N	P≤	R^2	SLOPE	P≤	r_s
JUNE 81	CASETA	11	NS			NS		6	NS			NS	
GARÚA 81	CASETA	21	NS			NS		10	NS			NS	
HOT-WET 82	CASETA	23	NS			NS		10	.01	0.60	+	.01	+.76
	CHATO	16	.05	0.24	+	NS		5	.04[b]	0.80	+	.04	+.90
HOT-DRY 82	CASETA	16	NS			NS		4	NS			NS	
	CHATO	10	NS			NS		3	NS			0.0	-1.0
	PINZÓN	16	NS[c]			NS		7	NS[d]			NS	
GARÚA 82	CASETA	32	NS			NS		12	NS			NS	
	CHATO	29	NS			NS		14	NS			NS	
EL NIÑO	SCNZ[e]	56	NS			NS		30	NS			NS	
	PINZÓN	23	.01	0.26	-	.05	-.41	8	NS			NS	

[a]Preference value = rank of E_i/number of ranks per month.

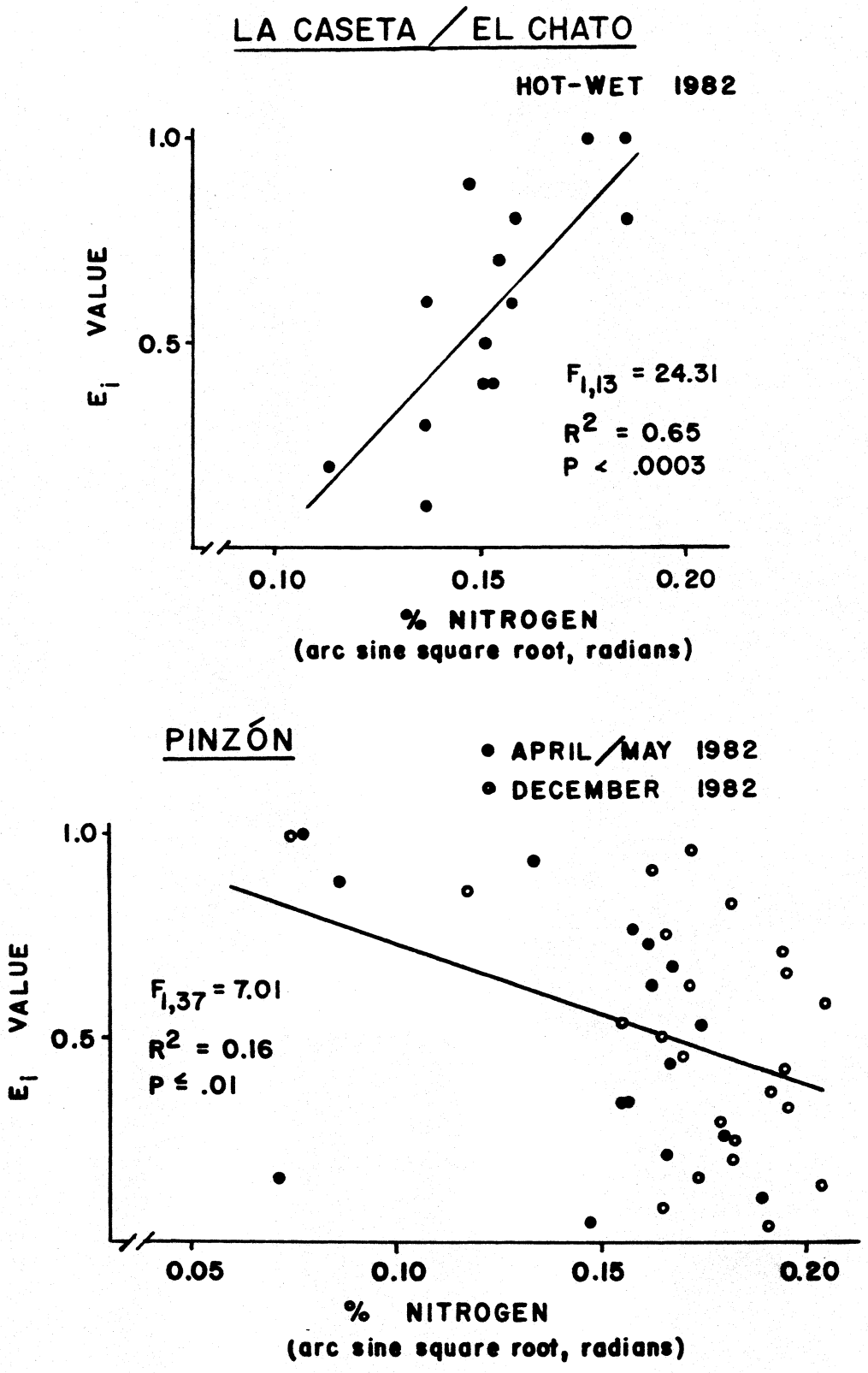
[b]Nitrogen content is significant in regression with water content (see footnote b, Table 5.22); partial correlation of nitrogen to feeding preference was 1.0 ($P \leq .01$).

[c]Nitrogen content is significant in regression with water content (see footnote c, Table 5.22); nitrogen to feeding preference $r_p = -0.56$ ($P \leq .05$).

[d]Nitrogen content is significant in regression with water content (see footnote d, Table 5.22); nitrogen to feeding preference $r_p = -0.83$ ($P \leq .05$).

[e]Santa Cruz Nesting Zone.

Fig. 5.11. Tortoise food preferences in relation to the nitrogen content of food items at La Caseta and El Chato in the hot-wet season 1982, and on Pinzón in 1982. Preference index value (E_i value) equals the rank order of each index (lowest index value = 1) divided by the number of food items for each month. Percent nitrogen of food items ranged from 1.28 to 3.43% at Caseta/Chato, and from 0.51 to 4.25% on Pinzón. All food items were included for Pinzón, while only those items significant in the diet were included for Caseta/Chato.


LA CASETA / EL CHATO
HOT-WET 1982
1.0
0.5
E_i VALUE
$F_{1,13} = 24.31$
$R^2 = 0.65$
$P < .0003$
0.10
0.15
0.20
% NITROGEN
(arc sine square root, radians)
PINZÓN
APRIL / MAY 1982
DECEMBER 1982
1.0
0.5
E_i VALUE
$F_{1,37} = 7.01$
$R^2 = 0.16$
$P \leq .01$
0.05
0.10
0.15
0.20
% NITROGEN
(arc sine square root, radians)

hot-wet season 1982, food preferences were positively related to nitrogen content of the foods. However, on Pinzón food preferences consistently showed a negative relationship to nitrogen level of food items. This may also be true in other areas of the islands, where Opuntia cactus is important in the diet.

Food Preferences in Relation to Carbohydrates

Tortoise feeding preferences had no significant relationship to the total non-structural carbohydrate (TNC) content of food items. Percent TNC was determined for food items on Pinzón for both seasons. There was no significant relationship between food preferences and %TNC of food items for either season, whether all food items or only significant food items were included. Percent TNC was negatively related to water content only in the hot-dry season when all food items were included ($F_{1,14} = 7.74$, $R^2 = 0.36$, $P < .01$). Due to the lack of importance of %TNC in the tortoise diet on Pinzón, %TNC was not analysed for plants from any other study areas.

DISCUSSION

The feeding behavior of giant tortoises, a strategy of flexible selectivity, is well suited to the aridity and unpredictability of the climate in the Galápagos Islands. Although more selective in their feeding when food is scarce, they are oppoprtunistic and remain generalists at

all times, in that they continually eat a wide variety of food types. The shift from a generalist pattern of feeding when conditions are favorable and food is abundant to a specialist or more selective feeding behavior when food is scarce is in opposition to the prediction of optimal foraging models (Ivlev 1961, MacArthur and Pianka 1966, Emlen 1966, 1968, Schoener 1971). However, it is in accordance with the majority of studies cited by Schluter (1981). This divergence from what was expected may be explained by the capability of tortoises to survive periods of 1 year or more without food or water. This capability allows them to avoid the less desirable foods when conditions are dry and food is scarce, concentrating on foods that will provide them with the most water at a time when free water is unavailable. Only when conditions were favorable and free water was plentiful did they abandon their preference for high water-content foods, and switch to a preference for high nitrogen foods.

These changes in feeding behavior over the long-term fit the type of model described by Katz (1974) for a dynamic optimization approach to foraging strategy, where there is a high dependence of present condition on past behavior. Only three types of feeding behavior are included in this strategy, maximum, nonfeeding, and minimum maintenance, with a concentration of as much feeding as possible in the lush season. A recent study of desert tortoises that fits such a long-term approach (Nagy and Medica 1986) showed that the

tortoises apparently relinquish maintenance of internal homeostasis on a daily basis, while tolerating imbalances in their water, energy, and salt budgets. This allows them to exploit periodically available resources, while balancing their salt and water budgets on an annual basis, and showing an energetic profit. Similar physiological patterns may be applicable to the long-term foraging strategies of Galápagos tortoises.

Unlike the tortoises on Aldabra, which are primarily grazers (Swingland and Lesseils 1979, Gould and Swingland 1980), major feeding behaviors of Galápagos tortoises include grazing and browsing, as well as eating fruit and cactus. It is interesting that the closest living relative of the Galápagos tortoise, Geochelone chilensis (Pritchard 1979b), which lives on the South American continent, also feeds primarily on grasses, fruit, and cactus (Pritchard 1979a).

It appears that rather than evolutionary changes in food habits, the predominant change resulting from establishment on the islands has been the change from the ancestral dome-shelled morphology to the saddle-backed morphology in tortoises on the lower arid islands. A change in feeding behavior that supports the hypothesis that the ability to reach higher for feeding was of selective advantage on the more arid islands and was a major factor in the evolution of the saddle-backed morphology (Snow 1966, Pritchard 1979a, Fritts 1983, 1984) was evident. Domed-shelled tortoises, as

those on Santa Cruz, feed close to the ground, concentrating on grasses, forbs, and fallen fruit, and seldom raise their head above their carapace; whereas the saddle-backed tortoises on Pinzón frequently stand tall, reaching for food high above them, particularly when reaching for the newest leaves of young Croton scouleri, or in attempts to knock off low-hanging cactus pads. There is a higher proportion of shrubs in the diet of tortoises on Pinzón compared to those on Santa Cruz, suggesting that the ability to reach high may be vital to their survival. Although the dome-shaped tortoises on Santa Cruz occasionally selected the top leaves of plants, the plants were rarely greater than 75 cm tall and the tortoises were not reaching to their maximum capability. On only one occasion during the 2-year study was a tortoise on Santa Cruz seen straining to reach leaves high off the ground, stepping up on a rock, and using a front foot to attempt to break the branch.

Pinzón tortoises, although not always successful, were often seen reaching up as high as possible to pull down cactus pads or to feed on the preferred shrubs Croton scouleri and Lantana peduncularis. Attempts to reach low hanging cactus pads were seen only during the hot-dry season 1982, when food was scarce, while tortoises reaching for the upper leaves of shrubs were more often seen at the onset of El Niño when food was abundant. At that time, tortoises often reached for the highest leaves although other more accessible leaves were available.

The importance of cactus in the diet of tortoises on Pinzón, and the fact that it was the primary plant for which tortoises strained to reach their maximum vertical feeding height during the dry season when food was scarce, suggest that the evolution of the saddle-backed trait may well be related to food limitations and the availability of tree-like cactus on the arid islands. The attempt to reach the highest leaves of preferred shrubs when food was relatively abundant may reflect distributional differences in nutritional quality within individual plants. If such distributional differences exist, they may have added to the forces favoring the evolution of the saddle-backed trait. It is interesting to note that the four most abundant shrubs on Pinzon, Alternanthera filifolia, Prosopis juliflora, Maytenus octogona, and Castela galapageia, all of which are avoided by tortoises, are all predominantly low-growing shrubs that do not require a feeding tortoise to extend itself vertically, while Croton scouleri and Lantana peduncularis, the more preferred shrubs, have a much taller growth form.

Although Galápagos tortoises fed on most plant species, the major portion of their diet included a narrow range of food items. This is also true of tortoises on Aldabra (Grubb 1971, Gibson and Hamilton 1983). Although there was a high preference for fruits when available, grasses (primarily Paspalum conjugatum) and forbs (primarily Desmodium canum) provided the year-round staples of the diet in the highlands of Santa Cruz. Foods that tortoises fed solely on

during long feeding bouts included fruits of Hippomane mancinella and Psidium galapageium, and the forb, Pilea baurii. Each of these items occurred seasonally. On Pinzón, Opuntia was the primary food in the dry season, while forbs, and to some extent grasses, became more important in the wet season.

Dawson (1964, 1965, 1966) following Stewart's (1911) earlier suggestion, attributed the growth patterns of Opuntia to the effect of grazing by tortoises, stating that the erect tree forms of Opuntia occurred only on islands with tortoises, while other islands had prostrate forms of Opuntia. Other authors have demonstrated that growth patterns of Opuntia in the Galápagos are dependent upon competition for light with coexisting vegetation (Arp 1973, Racine and Downhower 1974). Dawson (1966) claimed that the young Opuntia plants have extremely hard, sharp spines for defense, while the pads of the erect plants, once out of reach of tortoises, had soft hairlike spines. Although the spines may provide a certain amount of defense, tortoises were seen eating young Opuntia plants, twice at SCNZ where food was abundant, and once on Pinzón. Each tortoise had a unique method of feeding. One of the tortoises at SCNZ ate the pad, spines and all, while the second knocked off the top of the plant and managed to chew down the center. The tortoise on Pinzón ate the trunk of the small plant after discarding the spines in a pile adjacent to it. Both Heller (1903) and Slevin (quoted in Van Denburgh 1914, and Fritts and Fritts

1982) found a tortoise with its throat full of cactus spines. Heller concluded that the animal he saw was not suffering. In addition, erect Opuntia occur on Rábida, an island that never had a tortoise population according to current belief (Snow 1964). The single tortoise collected there by the California Academy of Sciences expedition in 1905, is believed to have been transported there from southern Isabela by Baur in 1892 (Van Denburgh 1914, Slevin 1931). These examples of tortoises feeding on young Opuntia plants, even in seasons of high food abundance, and the lack of tortoises historically on Rábida, an island with erect Opuntia, support the conclusion that tortoises were not the dominant factor in determining growth forms of Opuntia in the islands.

Tortoises preferred the majority of species in their diet, while avoidance of food items was usually close to 100%. Although avoided species included forbs, sedges, trees, lichen, and moss, most were shrubs. Several avoided shrub genera were also avoided by tortoises on Aldabra, including Maytenus, Psychotria, and Tournefortia (Grubb 1971). Clerodendrum, however, which was seldom eaten in Galápagos, was regularly browsed upon by tortoises on Aldabra (Grubb 1971). Aldabran tortoises are known to avoid species high in tannins (Swain 1976). This may be true for Galápagos tortoises as well. Galápagos tortoises also avoided the more thorny species, including Zanthoxylum fagara, the only abundant thorny species in the Caseta/

Chato region, and Prosopis juliflora and Castela galapageia on Pinzón. However, shrubs were important in the diet on Pinzón, where they were more abundant and where other food was less available.

Trees were seldom available to tortoises, but were generally avoided when they were. The main role of trees in the tortoise diet was in fruit production. In addition, a small portion of the diet included tree leaf litter. Although leaf litter was important in the diet of Aldabran tortoises (Gibson and Hamilton 1983), it was only occasionally eaten by Galápagos tortoises. Often, leaf litter was ingested incidentally with fruits. It was also occasionally eaten when it was wet from recent garúa or rain during periods when available free water was at a minimum.

Unlike Aldabran tortoises, whose selectivity (primarily for tortoise turf) declined as the dry season progressed (Gibson and Hamilton 1983), feeding selectivity of Galápagos tortoises was lowest when food was abundant, and increased as the dry season progressed. While portions of the Aldabran tortoise population have year-round access to free water (Gaymer 1968), tortoises in the Galápagos often go many months with no available surface water. It was at these times that selectivity was highest, and food preferences showed a positive relationship to water content of food items. Efficient use of energy resulting from poikilothermy allows tortoises to endure long periods with low food supply (Hamilton and Coe 1982). This ability allows

them to stop feeding altogether for long periods if necessary. Therefore, the food they do choose to consume when food is scarce can be those foods with the highest levels of factors that are most needed, such as water.

Nitrogen, a major factor influencing foraging of mammals (Sinclair 1975, White 1978, Mattson 1980), had little effect on food preferences of tortoises. It may be that selection pressures have not been strong enough on tortoises to produce food preferences based on nitrogen, or that other nutrients may be strongly limiting, making any preferences for food with high nitrogen of secondary importance.

Calcium has been suggested as a possible limiting factor for egg production in Galápagos tortoises (Pritchard 1979a). Female desert tortoises were observed mining exposed and subsurface mineral deposits high in calcium (Marlow and Tollestrup 1982). Sokol (1971) reported lithophagy and geophagy in tortoises, and suggested that this might be a means of obtaining supplementary calcium. Sand and gravel have been found in the feces of Galápagos tortoises (Rick and Bowman 1961). Bally (1946) reported that a tame East African leopard tortoise (Testudo pardalis) fed on small chicken bones. During this study, tortoises were seen feeding on soil, snail shells, and once, gnawing on goat horns. In addition, a few scats were found full of soil, and one was found with bones of a piglet. Few food items of tortoises in the Galápagos have been measured for calcium content, but of those that have, Opuntia has by far the highest levels (Hintz

[1972?], Sedgwick and Fowler 1972-73, Christian et al. 1984). It may be a highly preferred food both for water as well as calcium. Examination of calcium levels in other food items of tortoises may explain more of their food preferences.

Galápagos tortoises, both dome-shelled and saddle-backed, adjust their feeding behavior to current conditions. They are able to decrease the time spent feeding when food is scarce, and they selectively choose food items high in water content and perhaps other needed nutrients. Their diet consists of a wide variety of food types, with only a few items forming the majority. Few species are avoided, but avoidance of species is most often close to 100%, and may be related to thorniness and perhaps to secondary compounds. Seasonal changes in feeding behavior are highly dependent upon precipitation and the subsequent availability and water content of food items, and follow a strategy of flexible selectivity, expected in herbivores in arid and unpredictable climates.

CHAPTER SIX - HABITAT PREFERENCES

INTRODUCTION

Galápagos tortoises exhibit a hierarchy of selection, as described by Johnson (1980), beginning with selection for their physical or geographic range to selection for specific food items. Each subspecies of tortoise, limited to a single island or a single volcano on Isla Isabela, exhibits seasonal concentrations in specific regions or vegetation zones. Within each area of concentration, a higher order of selection is shown in their choice of habitat types for different activities.

The four study areas, located in regions of tortoise concentration, exhibit environmental mosaics of habitat patches, as defined by MacArthur (1971). The heterogeneity of the environment, with patches differing in "quality," should effect some degree of habitat selection (Wiens 1976), with tortoises preferring habitats of highest quality. Habitat quality may vary for different activities. For example, habitats containing highly preferred foods may be of higher quality for feeding, whereas those that have fewer preferred foods but provide shelter may be of higher quality for resting.

True selection resulting from choice is often confused with habitat correlation which results from some external agent imposing a differential distribution of individuals among patch types (Wiens 1976). Differential predation was

the main external agent in studies cited by Wiens, a factor that is non-existent for adult tortoises in the Galápagos Islands. For true habitat selection to occur, not only can there be no external agent causing differential distribution, but tortoises must also be able to move among all habitat types. With the ability to move among habitat types, substantial seasonal changes in habitat use would support a conclusion of true habitat selection. Specific habitat characteristics that are correlated with preferences may be either a cause or a result of habitat preference. Alternative interpretations will be considered.

Little information on habitat use by Galápagos tortoises is currently available. In her study of tortoises on Volcán Alcedo, Fowler (1983) noted that large-scale seasonal distributions and migrations were in response to water and possibly to food availability. However, habitat preferences within areas of seasonal concentrations have never been studied. Although some authors discussed the vegetation zones occupied by tortoises, few specific habitat types have been mentioned in the literature. Use of ponds or mud wallows by tortoises for resting and drinking have been documented by many visitors to the islands since the early 1800's (Porter 1822, Darwin 1860, Heller 1903, Van Denburgh 1914, Slevin 1935, Hendrickson 1965, Carpenter 1966, Snow 1966, Thornton 1971, MacFarland 1972, Staedeli 1972, Black 1973, Rodhouse et al. 1975, Pritchard 1979a, Fowler 1983). Hendrickson (1965) also noted that Santa Cruz tortoises con-

centrated in areas of lush pasture. Beck (1903) mentioned that tortoise trails high on Isabela often extended from one grass flat to another, and that tortoises frequented the open glades and sunny parks.

The only other landscape feature consistently mentioned was the tortoise trail, providing a corridor for movement among habitat patches, and among geographic regions (Darwin 1860, Agassiz 1892, Beck 1903, Heller 1903, Van Denburgh 1914, Slevin 1935, Carpenter 1966, Pritchard 1979a, Fritts and Fritts 1982). Descriptions by some of the earlier visitors of conditions when tortoises were more abundant show how striking these trails can be. Darwin (1860) stated, "When I landed at Chatham Island, I could not imagine what animal traveled so methodically along well-chosen tracks." Beck (1903) found that on the south side of Isabela, "the tortoise trails extend up and down the mountain side for miles...By centuries of constant use these rocks have been worn so smooth that it is almost impossible to walk over them after a rain..." At Tagus Cove on the west side of Isabela, he found "trails 2 feet deep, and just the width of a tortoise," while on Pinzón, "the trails from one cactus tree to another were as plain and as well worn as cattle trails are on a well-stocked range in California."

Habitat types in the three study areas on Santa Cruz and those in the valley of Pinzón were delineated early in the study, and tortoise use was examined in relation to habitat characteristics. If tortoises show true selection, habitat

preferences should be related to those characteristics that are most important for each activity.

RESULTS

Habitat Types - La Caseta/El Chato

Study areas at La Caseta and El Chato were situated along major drainages, indicated in the habitat type maps (Fig. 6.1, 6.2). Habitat types in these areas were defined primarily by dominant plant species and were similar for the two areas. Delineation of habitat types appeared to result from patterns of water collection and flow of flood waters during intense El Niño events (Cayot 1985). A greater mix of habitat types was found along the drainage, at the center line of each study area, than along the edges where Psidium/Zanthoxylum Woodlands were dominant (Fig. 6.1, 6.2).

Macro-habitat types included:

PZW - Psidium galapageium/Zanthoxylum fagara Woodland: relatively dense, dry woodland, predominantly on raised areas with no water collection; relatively high density of shrubs and forbs in the understory; additional tree species include Scalesia pedunculata (see micro-habitats), as well as Pisonia floribunda and Piscidia carthagenensis (rare), both of which occur where water run-off is concentrated; dominant shrubs include Psychotria rufipes, Tournefortia rufo-sericea, and Croton scouleri; the dominant forb is Desmodium canum; hanging lichens are abundant on Psidium trees.

Fig. 6.1. La Caseta. Habitat type map of the study area. Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, OF - Open Forb, GL - Grazing Lawn, SCPT - Scleria Stand, SCAL - Scalesia Stand, and DWH I/WH I - Dry Water Hole/Water Hole (type I). Habitat types were interspersed in areas where habitat patterns and/or letters are combined. Rivers and flood ponds occurred only during El Niño. Trails are indicated only where they exit the study area.

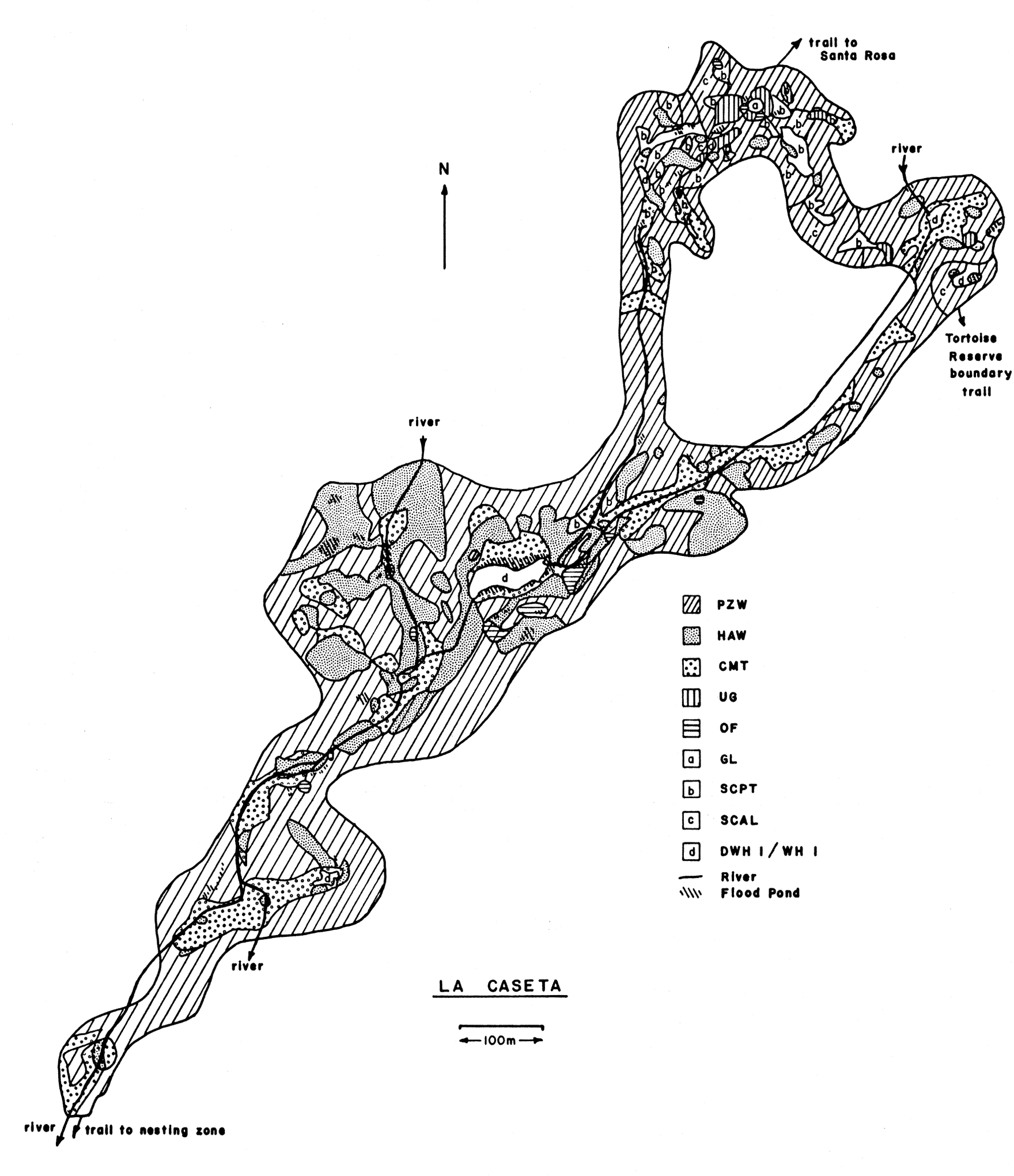
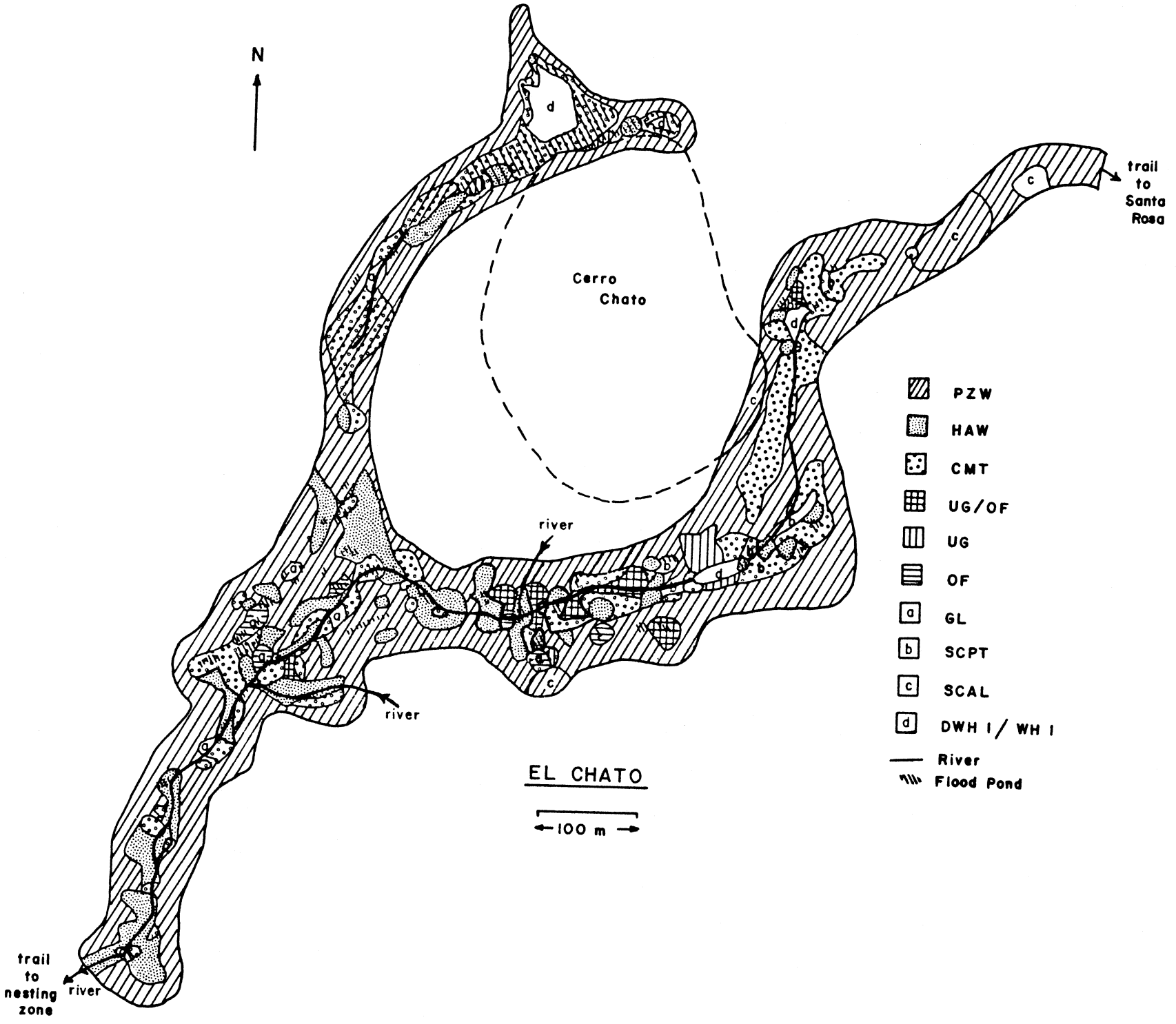

trail to
Santa Rosa
river
N
Tortoise
Reserve
boundary
trail
river
river
river
trail to nesting zone
PZW
HAW
CMT
UG
OF
GL
SCPT
SCAL
DWH I / WH I
River
Flood Pond
LA CASETA
100m

Fig. 6.2. El Chato. Habitat type map of the study area. Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, OF - Open Forb, GL - Grazing Lawn, SCPT - Scleria Stand, SCAL - Scalesia Stand, and DWH I/WH I - Dry Water Hole/Water Hole (type I). Habitat types were interspersed in areas where habitat patterns and/or letters are combined. Rivers and flood ponds occurred only during El Niño. Trails are indicated only where they exit the study area. Cerro Chato is a large hill dominating the area.


N
Cerro
Chato
trail
to
Santa
Rosa
river
river
trail
to
nesting
zone
river
PZW
HAW
CMT
UG/OF
UG
OF
GL
SCPT
SCAL
DWH I / WH I
River
Flood Pond
EL CHATO
100 m

HAW - Hippomane mancinella Woodland: open woodland associated with water collection areas and periodically flooded regions around the edges of ponds and along rivers; broad canopy with single tree species; open understory; lichens abundant on large trees; many epiphytes on larger branches and trunks.

CMT - Clerodendrum molle Thicket: dense thicket with some low herbaceous vegetation; gently sloping terrain around the outer edges of ponds and in many river bed areas.

UG - Underutilized Grassland: open areas with few to no trees, dominated by Paspalum conjugatum; grasses generally erect and not cropped to near ground level; many forb species, with Desmodium canum and Blechum brownei the most abundant.

GL - Grazing Lawn: open areas of heavy grazing by tortoises, dominated by Stenotaphrum secundatum; few to no trees; often several forb species present; heavy grazing can effect a reduction of canopy height and subsequent growth patterns of the vegetation resulting in a low-growing, dense canopy, termed a grazing lawn (McNaughton 1984); of the tortoise habitats in the Galápagos, this habitat type is the most similar to 'tortoise turf,' an extremely important habitat type for tortoises on Aldabra (Grubb 1971, Merton et al. 1976); grazing lawns disappeared when tortoise grazing was removed, either by construction of exclosures or by mass emigration of tortois-

es; S. secundatum growing in PZWs is generally much taller, less dense, and relatively ungrazed.

OF - Open Forb: open areas with few to no trees, dominated by forbs; often surrounded by PZW; important forbs include Desmodium canum and Cassia occidentalis in the drier areas, and Ageratum conyzoides in the wetter areas; Cassia picta (shrub) and Rhynchospora nervosa (sedge) often abundant in both wet and dry areas.

DWH I/WH I - Dry Water Hole I/Water Hole I: open areas ranging in size from small holes of 2 m diameter, to large areas up to 40x60 m; plant species, predominantly grasses, sedges and forbs, vary depending on locale and water conditions (Cayot 1985); ponds fill periodically with sufficient rainfall, and then the floating fern, Azolla microphylla, is often abundant.

Micro-habitats include:

SCPT - Scleria pterota Stand: dense stands of robust sedge, with few other species; usually occupies areas of 1-4 m diameter; occurs in low areas where water collects, adjacent to ponds, CMTs, or UGs, or in woodlands.

PSRU - Psychotria rufipes Thicket: areas where this shrub is extremely dense and little else is able to grow; most often associated with the two woodlands, and occasionally with UGs or CMTs.

DL - Dichondra repens Lawn: ephemeral habitat type dependent on rainfall and, possibly, tortoise grazing; absent at both low and exceptionally high levels of rain-

fall; areas of 1-3 m diameter, with low-growing, dense Dichondra repens; essentially no other species; often in openings in PZW or adjacent to UG; D. repens growing in other habitats is generally less dense, with longer, spindly stems.

SCAL - Scalesia pedunculata Stand: although this is a macro-habitat type elsewhere in the highlands of Santa Cruz, in the two study areas, Scalesia trees are less abundant and are usually found within PZWs.

DWH II/WH II - Dry Water Hole II/Water Hole II: depressions in soil beneath some Hippomane mancinella trees; often rocky with hard-packed clay soil; with almost no vegetation whether dry or wet.

RHNE - Rhynchospora nervosa Stand: a sedge, often added to HAWs or OF areas as a micro-habitat when it is a dominant part of the herbaceous layer.

RM - Rock Mound: concentration of lava boulders of 2-6 m diameter; most often covered with ferns; associated primarily with PZWs or HAWs.

LEMON or ORANGE - Lemon or Orange Tree: Citrus spp., usually a single or occasionally two trees associated with PZWs or HAWs; recorded as micro-habitats because tortoises usually located there only when foraging on citrus fruits.

WH - Water Hole: small (0.5 m diameter) to large (20 m diameter) areas that did not fit descriptions for WH I or WH II; did not appear until the onset of El Niño; usually associated with PZWs or HAWs (small WHs), or with CMTs (large WHs).

Corridor habitat types include:

Trail: a well-defined people trail or tortoise trail (often the same); generally with very little vegetation.

TS - Trailside: originally used to indicate heavily grazed areas (predominantly Paspalum conjugatum, occasionally Stenotaphrum secundatum) immediately adjacent to trails; after October 1982, trailsides included all area within 0.5 m of the trail, in association with the surrounding habitat type.

River: an El Niño phenomenon; indicates areas of flowing water, ranging from 0.5-50 m across; width changed day-to-day with flood conditions; apparently small rivers do occur in normal rainy seasons, but none was seen during this study other than during El Niño.

Percentage of area in each habitat type was estimated both from vegetation transects and habitat type maps (Table 6.1). All macro- and most micro-habitats were recorded during vegetation transects. Percentage of quadrats of each type, averaged over all sets of vegetation transects excluding those during El Niño, represents an estimate of the composition of habitat types in the regions of greatest tortoise activity or key tortoise areas. Composition of the entire study area by habitat was obtained from the habitat type maps. All macro-habitats were included, as were SCPT and DWH II/WH II. Other micro-habitats were not included. Although the trails, and the rivers during El Niño, constituted a considerable area, neither was adequately measured with the above techniques.

Table 6.1. Percent of key tortoise areas (%VT) and percent of the total study area (%SA) by habitat type[a], at La Caseta and El Chato. Habitat type SCAL was not encountered in the vegetation transects of either area, while Trail was not included at El Chato. Several micro-habitats were not mapped and therefore are not represented in %SA.

HABITAT TYPE[a]	CASETA		CHATO	
	%VT	%SA	%VT	%SA
PZW	46.79	56.78	41.80	57.92
HAW	29.91	19.12	13.98	14.23
CMT	3.99	14.34	9.35	16.84
UG	6.29	1.09	13.90	2.34
GL	0.98	0.11	1.09	1.00
OF	5.20	0.90	6.57	1.84
DWH I/WH I	1.14	1.55	5.18	2.12
SCPT	2.35	4.16	2.89	1.64
PSRU	1.60	-	2.49	-
DL	0.19	-	1.30	-
DWH II/WH II	0.56	0.12	0.70	-
SCAL	-	1.84	-	2.09
RHNE	0.21	-	0.33	-
RM	0.42	-	0.45	-
WH[b]	1.89	-	3.82	-
RIVER[c]	1.81	-	1.06	-
TRAIL	0.42	-	-	-

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerondendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, SCAL - Scalesia Stand, RHNE - Rhynchospora Stand, RM - Rock Mound, WH - Water Hole, River, and Trail.

[b]Percent values from November 1982 to January 1983 vegetation transects only; not included in the total.

[c]Percent values from December 1982 and January 1983 only; not included in the total.

Characteristics of 11 of the major habitat types were determined from the results of the vegetation transects (Table 6.2). Comparison of species richness (S_{ht}) and species diversity (H'_{ht}) among habitat types may not be reliable due to the wide range in the number of quadrats used to determine characteristics of different habitat types. However, they should be reliable within habitat types, between seasons. In addition to the dry biomass totals for available forbs, shrubs, grasses/sedges, fruit, and other food items, available biomass of significant food items, and that of preferred significant food items were summed. The majority of characteristics are potentially important in feeding by tortoises but may have little importance in habitat preferences for other activities.

Habitat Types - Santa Cruz Nesting Zone

Habitat delineation is much less distinct at the Santa Cruz Nesting Zone (SCNZ) than in the highlands of Santa Cruz, with the majority of area composed of Pisonia floribunda/Piscidia carthagenensis Woodlands (Fig. 6.3). Other tree species are relatively rare, though there are some small concentrations of Psidium galapageium. Opuntia echios, also relatively rare, were scattered throughout the study area. Shrubs, not a dominant factor in the area, were well dispersed. The primary characteristics distinguishing different habitat types were the openness of the woodland, and the amount of rock or soil surface. The rocky areas generally had greater than 50% of the ground covered by

Table 6.2. Seasonal changes in the characteristics of habitat types[a] at La Caseta/El Chato based on the results of vegetation transects. Characteristics include percent cover by rock (%ROCK), by water (%WATER), and by available food (%FOOD), species richness (S_{ht}), species diversity (H'_{ht}), available biomass (g/m^2) of all foods (FOOD), significant foods (SIGFOOD), preferred-significant foods (SIGPLUS), forbs (FORB), grasses and sedges (GRASS), shrubs (SHRUB), fruit (FRUIT), and other food items (OTHER).

HABITAT[a]	SEASON[b]	N[c]	%ROCK[d]	%WATER	%FOOD	S_{ht}	H'_{ht}	FOOD	SIG-FOOD	SIG-PLUS	FORB	GRASS	SHRUB	FRUIT	OTHER
PZW	HotWet82	284	3.10	0	24.82	42	2.74	21.40	12.49	7.70	6.48	5.76	6.10	0.04	3.02
	HotDry82	286	3.10	0	12.72	34	2.44	11.51	6.05	2.48	3.86	1.73	3.40	0.30	2.22
	Garúa82	450	3.10	0.03	48.38	55	2.67	65.59	40.33	15.21	32.84	6.57	16.17	1.63	8.38
	El Niño	130	3.10	0.12	70.27	57	2.77	76.26	52.63	27.25	40.76	12.36	12.67	1.16	9.31
HAW	HotWet82	149	3.02	0	20.20	38	2.62	19.86	12.86	10.64	4.18	4.74	4.85	3.17	2.92
	HotDry82	139	3.02	0	11.14	31	2.35	12.93	9.24	8.00	2.17	1.88	2.20	4.52	2.16
	Garúa82	183	3.02	0	36.24	48	2.81	42.02	25.42	15.45	17.02	8.84	10.36	0.49	5.31
	El Niño	67	3.02	9.41	37.61	44	2.93	39.37	27.18	19.69	12.86	11.82	5.14	1.50	8.05
CMT	HotWet82	42	2.83	0	18.40	30	2.13	20.32	15.78	9.91	6.67	8.97	2.88	0.34	1.46
	HotDry82	37	2.83	0	12.06	21	1.94	16.12	12.73	5.00	5.56	6.94	1.70	0.34	1.58
	Garúa82	62	2.83	0	43.90	35	2.19	65.10	35.78	11.58	29.71	7.63	14.54	0.11	13.11
	El Niño	12	2.83	12.08	42.42	28	2.06	62.84	41.77	10.36	12.35	28.47	12.18	0	9.84
UG	HotWet82	87	0.86	0	52.10	28	1.01	91.22	89.79	80.69	10.94	78.04	1.68	0.26	0.30
	HotDry82	86	0.86	0	18.62	24	1.56	27.70	26.86	20.79	8.17	18.28	1.08	0.13	0.04
	Garúa82	61	0.86	0	70.00	26	1.28	133.98	130.36	113.44	27.48	102.35	3.52	0.23	0.40
	El Niño	16	0.86	5.69	90.09	25	1.30	169.14	165.15	157.75	36.16	130.32	1.37	0.87	0.42
GL[e]	HotWet82	12	1.58	0	48.96	12	0.64	55.55	56.78	54.30	4.23	50.20	0.38	0.74	0
	HotDry82	13	1.58	0	16.16	8	0.69	20.28	20.23	19.70	1.06	17.16	0.28	1.78	0
	Garúa82	6	1.58	0	79.56	12	1.37	102.63	100.23	81.63	36.56	63.29	2.78	0	0

Table 6.2 continued.

HABITAT [a]	SEASON [b]	N[c]	%ROCK [d]	%WATER	%FOOD	S_{ht}	H'_{ht}	FOOD	SIG-FOOD	SIG-PLUS	FORB	GRASS	SHRUB	FRUIT	OTHER
OF	HotWet82	41	1.93	0	27.42	22	2.00	21.57	19.84	10.78	14.38	4.66	2.08	0.38	0.07
	HotDry82	31	1.93	0	8.54	17	1.78	7.04	6.38	2.67	5.46	0.43	0.75	0.38	0.02
	Garúa82	47	1.93	0.01	68.26	30	1.79	96.89	92.56	23.45	85.04	7.93	3.02	0	0.90
	El Niño	12	1.93	0	90.92	36	2.43	124.98	118.69	57.75	93.71	23.91	6.27	0	1.09
DWH I/WH I	HotWet82	205	14.40	0	47.42	24	1.62	55.63	46.52	45.35	20.49	34.78	0.32	0	0.04
	HotDry82	229	14.40	0	23.70	22	1.50	34.72	31.44	31.00	12.12	22.23	0.31	0	0.06
	Garúa82	346	14.40	18.43	75.15	33	1.85	128.58	116.90	85.53	91.34	35.79	0.92	0	0.53
	El Niño	123	14.40	95.57	58.96	14	1.33	46.24	29.95	29.95	7.38	1.59	0.86	0	36.41
SCPT	HotWet82	10	0.75	0	55.21	11	0.50	116.27	113.20	6.69	4.04	109.57	2.66	0	0
	HotDry82	7	0.75	0	24.58	7	0.35	62.48	60.97	2.98	2.25	58.71	1.52	0	0
	Garúa82	10	0.75	0	80.85	10	0.74	205.64	203.40	12.09	36.51	167.04	2.07	0	0.02
	El Niño	7	0.75	9.14	98.79	12	0.36	363.00	360.75	11.33	20.16	340.93	1.91	0	0
PSRU [f]	HotWet82	3	0.07	0	67.50	10	0.71	72.85	12.21	6.61	7.62	2.34	60.50	0	2.39
	Garúa82	3	0.07	0	79.88	10	0.93	141.19	37.14	18.58	8.40	28.12	102.72	0	1.95
	El Niño	1	0.07	85.00	92.50	2	0.24	91.00	0	0	0	0	91.00	0	0
DL [g]	HotWet82	3	1.57	0	69.17	11	1.52	25.95	25.55	23.32	19.89	5.96	0.10	0	0
	Garúa82	9	1.57	0	87.30	14	0.92	82.76	81.27	70.21	74.79	6.04	0.51	1.41	0.01
DWH II/WH II	HotWet82	6	12.33	0	21.88	14	1.38	35.77	27.68	26.92	3.39	23.18	1.22	2.15	5.83
	HotDry82	5	12.33	0	10.00	7	0.90	25.89	21.87	16.25	0.96	16.61	0.26	4.30	3.76
	Garúa82	4	12.33	85.62	20.00	13	1.67	30.55	25.40	13.55	13.51	12.15	0.17	0	4.72
	El Niño	4	12.33	94.38	34.88	12	1.37	23.06	10.75	10.75	3.04	6.86	0	0.79	12.37

Table 6.2 continued.

---

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole/Water Hole (type I), SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, and DWH II/WH II - Dry Water Hole/Water Hole (type II).

[b]Seasonal values based on averages of all quadrats of a single habitat type from both La Caseta and El Chato: HotWet82 includes January/February and March/April 1982 transects; HotDry82 includes March/April and May/June 1982 transects; Garúa82 includes July/August, September/October, and November/December 1982 transects; El Niño includes January/February 1983 transects.

[c]Total number of quadrats in each habitat type used for calculation of average values for habitat characteristics.

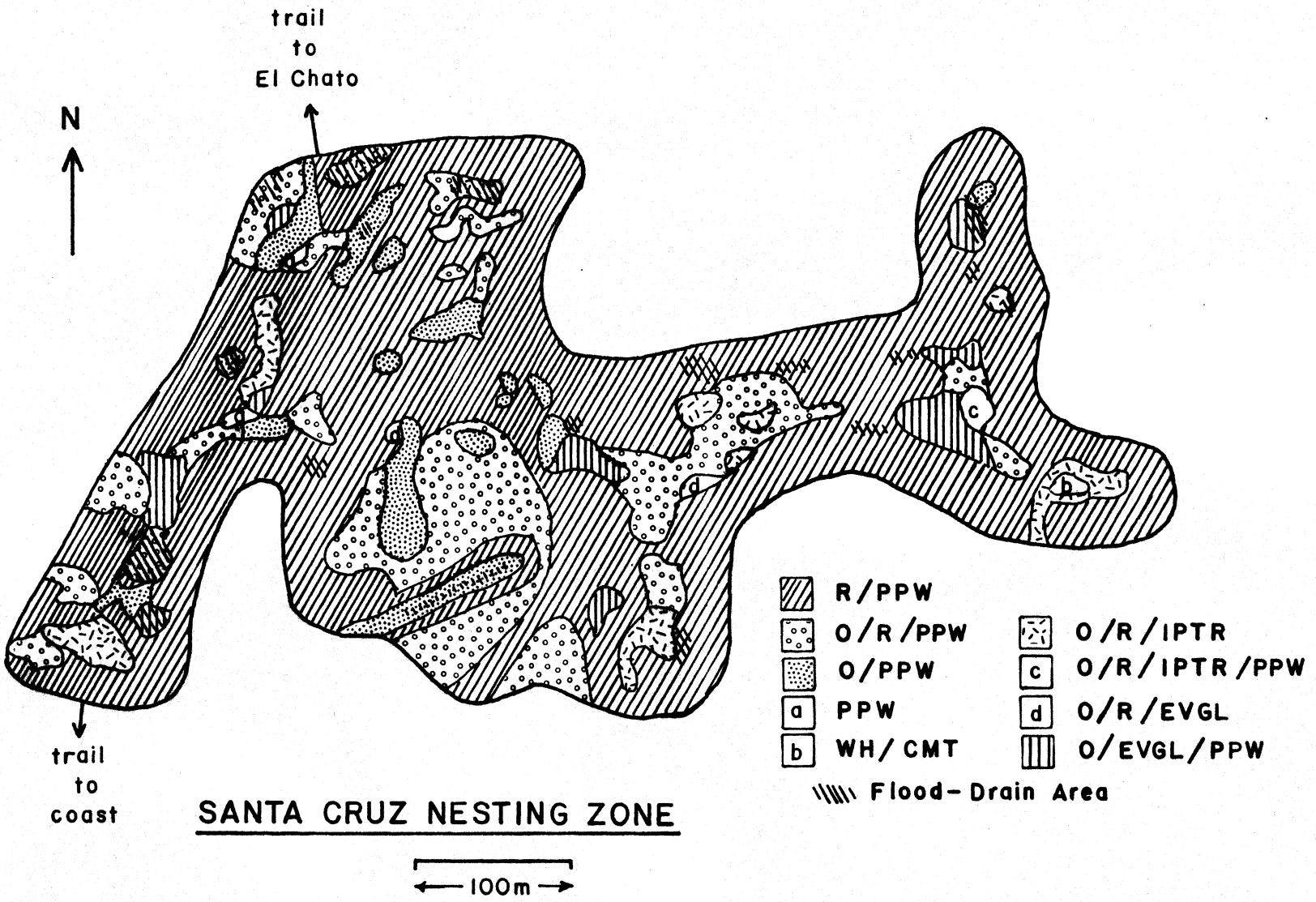
[d]Percent Rock was averaged over all quadrats for each habitat rather than by season.

[e]GL did not occur in the vegetation transects in El Niño.

[f]PSRU did not occur in the vegetation transects in the HotDry82 season.

[g]DL did not occur in the vegetation transects in the HotDry82 season, nor in El Niño.

Fig. 6.3. Santa Cruz Nesting Zone. Habitat type map of the study area during El Niño. Habitat types include various combinations of the following: R - Rock, O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea triloba, EVGL - Evolvulus glaber, WH - Water Hole, and CMT - Clerodendrum Thicket. Flood-drain areas filled with water after heavy precipitation, then drained within 2 to 3 days. Trails are indicated only where they exit the study area.



SANTA CRUZ NESTING ZONE

lava, and had very little soil. Some of the lower, relatively flat areas had much greater soil depositon. In addition, during El Niño, two forbs, the liana Ipomoea triloba, and the ground cover species Evolvulus glaber, were extremely abundant in certain areas, and were used in habitat delineation.

The habitat types used for analyses were:

R/PPW - Rock/Pisonia floribunda/Piscidia carthagenensis Woodland: fairly closed canopy with an abundance of rock; often on hilly or raised sites.

O/R/PPW - Open/Rock/Pisonia floribunda/Piscidia carthagenensis Woodland: trees generally more dispersed; more soil than in R/PPW.

O/PPW - Open/Pisonia floribunda/Piscidia carthagenensis Woodland: trees generally more dispersed; much more soil surface and less rock than in either R/PPW or O/R/PPW.

PPW - Pisonia floribunda/Piscidia carthagenensis Woodland: closed canopy woodland with less than 50% cover by rock.

O/R/IPTR - Open/Rock/Ipomoea triloba: open areas with few to no trees; lava blocks extremely abundant and covered by Ipomoea triloba; extreme flooding, in May and June 1983, caused high mortality of Ipomoea, so little was available in July 1983.

O/R/IPTR/PPW - Open/Rock/Ipomoea triloba/Pisonia floribunda/Piscidia carthagenensis Woodland: open wood-

land, with an abundance of rock covered by Ipomoea triloba; Ipomoea generally absent in July 1983.

O/R/EVGL - Open/Rock/Evolvulus glaber: open area with few to no trees; percent cover by rock and soil nearly equal; much of the ground covered by Evolvulus glaber; Evolvulus also experienced high mortality in May/June 1983, and was less abundant in July 1983.

O/R/EVGL/PPW - Open/Rock/Evolvulus glaber/Pisonia floribunda/Piscidia carthagenensis Woodland: open woodland with nearly equal cover by soil and rock; much of the ground covered by Evolvulus glaber, Evolvulus much lower in abundance in July 1983.

O/EVGL/PPW - Open/Evolvulus glaber/Pisonia floribunda/Piscidia carthagenensis Woodland: similar to O/R/EVGl/PPW, though with much less rock.

O/R - Open/Rock: extremely rocky, open areas with few to no trees; little vegetation, although sometimes covered by Plumbago scandens.

WH - Water Hole: only one major Water Hole occurred in the area, although there were other flood ponds that drained within a day or two following a heavy rain; the Water Hole was relatively open except for some large Clerodendrum molle.

CMT - Clerodendrum molle Thicket: relatively dense thicket associated with Water Holes or flood areas.

Percentage of area in each habitat type was estimated both from vegetation transects and from the habitat type

map, as described for La Caseta and El Chato (Table 6.3). All habitat types were considered macro-habitats and were noted both in vegetation transects and on the map wherever they occurred, except for WH and CMT, which did not occur in the vegetation transect areas, and O/R and O/R/EVGL/PPW, which did not have large enough patches to be mapped. Few of the "trails" in the study area were true tortoise trails, and the habitat type was not used in instantaneous tortoise observations.

Characteristics of the 10 habitat types occurring in vegetation transects were determined (Table 6.4). Measures of species richness (S_{ht}) and species diversity (H'_{ht}) are more reliable within a habitat type than among them due to the wide range in number of quadrats per habitat type. Available biomass of forbs, shrubs, grasses/sedges, and other food items, as well as significant food items and preferred significant food items were summed, as for La Caseta and El Chato.

Habitat Types - Pinzón

The Pinzón study area, situated in the southern crater of the island, consisted primarily of the crater bottom where soil deposition was substantial in some patches, and along the lower slopes of the valley, covered primarily with rock (Fig. 6.4). Habitat delineation on Pinzón was also less well defined than in the highlands of Santa Cruz. Habitat types were determined not only by the dominant plant species but by the amount of soil and rock covering the ground. Tierney (1985) described Pinzón as follows:

Table 6.3. Percent of key tortoise areas (%VT) and percent of the total study area (%SA) by habitat type[a] at the Santa Cruz Nesting Zone during El Niño 1983.

HABITAT TYPE[a]	%VT	%SA
R/PPW	38.00	66.53
O/R/PPW	29.00	17.65
O/PPW	20.00	6.78
PPW	2.00	0.21
O/R/IPTR	2.50	4.12
O/R/IPTR/PPW	3.75	0.32
O/R/EVGL	0.75	0.15
O/R/EVGL/PPW	1.75	-
O/EVGL/PPW	1.00	3.73
O/R	1.00	-
WH	-	0.21
CMT	-	0.21

[a]Habitat types include various combinations of the following: R - Rock, O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea triloba, EVGL - Evolvulus glaber, WH - Water Hole, and Clerodendrum Thicket.

Table 6.4. Characteristics of habitat types[a] at the Santa Cruz Nesting Zone during El Niño 1983, based on the results of vegetation transects. Characteristics include percent cover by rock (%ROCK) and by available food (%FOOD), species richness (S_{ht}), species diversity (H'_{ht}), available biomass (g/m^2) of all foods (FOOD), significant foods (SIGFOOD), preferred-significant foods (SIGPLUS), forbs (FORB), shrubs (SHRUB), grasses and sedges (GRASS), and other food items (OTHER).

HABITAT[a]	MONTH	N[b]	%ROCK[c]	%FOOD	S_{ht}	H'_{ht}	FOOD	SIG-FOOD	SIG-PLUS	FORB	SHRUB	GRASS	OTHER
R/PPW	April	89	80.20	47.80	32	2.47	26.64	21.10	6.21	15.60	9.75	0.05	1.24
	July	63	80.20	39.46	24	2.28	24.88	17.02	3.37	19.66	4.35	0	0.87
O/R/PPW	April	52	72.80	58.03	33	2.78	31.78	23.58	9.77	21.13	8.58	0.18	1.89
	July	64	72.80	51.26	29	2.45	37.05	25.60	5.02	26.07	9.28	0.06	1.64
O/PPW	April	33	30.72	55.21	26	2.50	31.82	26.81	11.95	25.94	3.56	0.03	2.29
	July	47	30.72	49.51	29	2.28	38.15	27.32	6.39	29.50	3.19	0.30	5.16
PPW[d]	July	8	34.69	24.69	14	2.03	16.69	14.46	3.09	15.19	0.13	0	1.37
O/R/IPTR	April	6	87.75	60.83	13	1.74	28.38	18.84	14.92	22.76	1.72	3.90	0
	July	4	87.75	17.50	6	1.18	12.42	12.42	1.95	8.04	4.38	0	0
O/R/IPTR/PPW	April	9	87.83	66.94	15	1.66	28.39	26.91	17.32	20.85	6.37	0	1.17
	July	6	87.83	12.50	11	1.85	12.18	8.86	3.85	7.28	4.70	0	0.20
O/R/EVGL	April	2	62.50	72.50	8	0.89	43.70	42.80	12.08	43.52	0	0	0.18
	July	1	62.50	37.50	4	1.07	15.34	15.25	3.00	10.09	5.25	0	0
O/R/EVGL/PPW	April	5	48.21	86.50	16	1.16	53.91	51.02	7.61	49.30	2.22	1.95	0.44
	July	2	48.21	38.75	7	0.87	43.35	39.45	0.15	39.42	0.18	0	3.75
O/EVGL/PPW[e]	July	4	27.50	61.25	10	1.36	25.73	21.61	3.37	24.67	0.08	0.98	0
O/R	April	3	88.12	38.50	8	1.31	35.93	13.06	2.40	19.52	10.58	0	5.83
	July	1	88.12	100.00	1	0	68.25	0	0	68.25	0	0	0

Table 6.4 continued.

---

[a]Habitat types include various combinations of the following: R - Rock, O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea triloba, and EVGL - Evolvulus glaber.

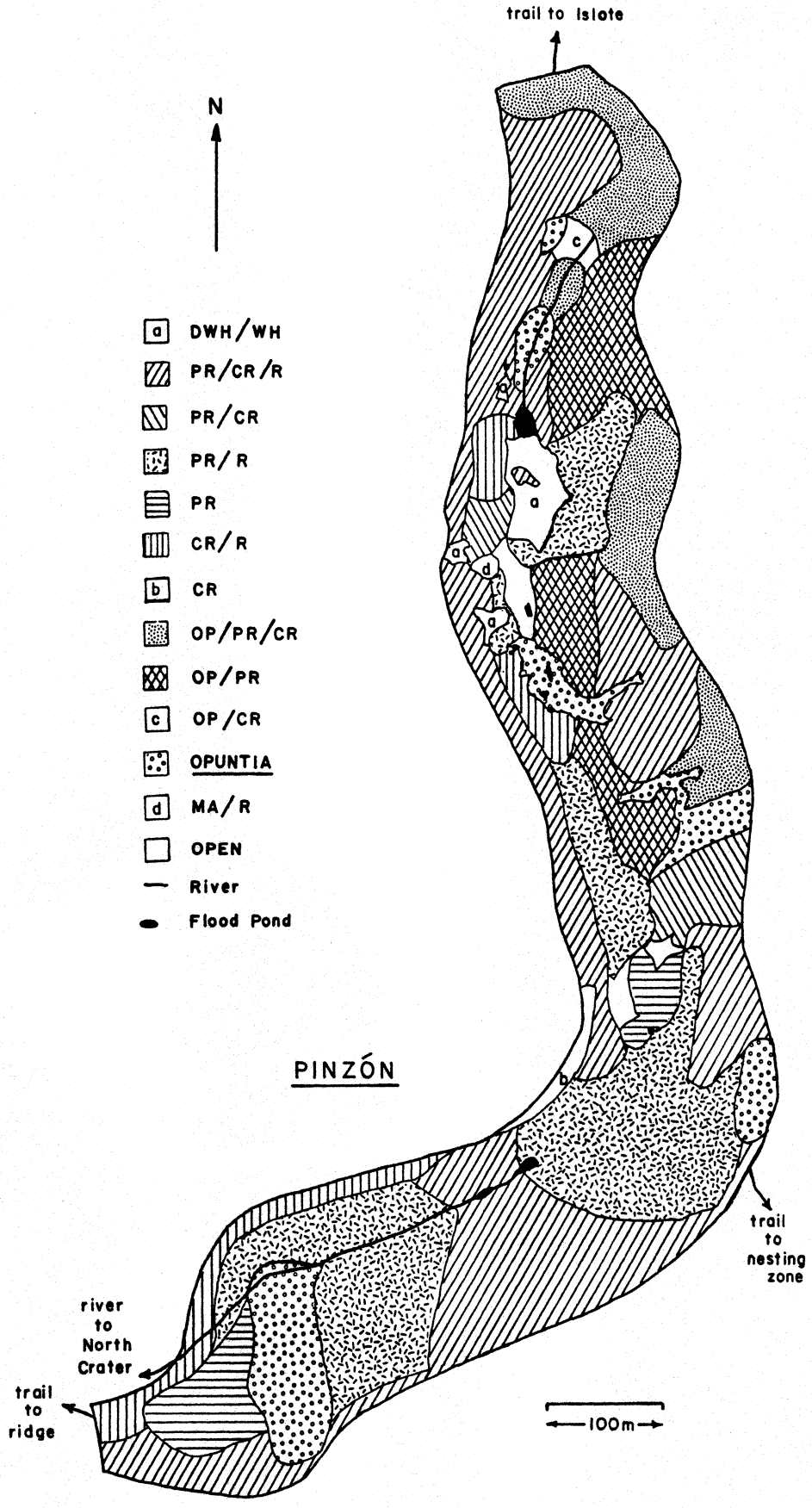
[b]Total number of quadrats in each habitat type used for calculation of average values for habitat characteristics.

[c]Percent Rock was averaged over all quadrats for each habitat type from the two months of transects.

[d]PPW was not recorded during vegetation transects in April.

[e]O/EVGL/PPW was not recorded during vegetation transects in April.

Fig. 6.4. South Crater, Pinzón. Habitat type map of the study area. Habitat types include various combinations of the following: DWH/WH - Dry Water Hole/Water Hole, R - Rock, PR - Prosopis, CR - Croton, OP - Opuntia, MA - Maytenus, and Open. Rivers and flood ponds first appeared in December 1982, at the onset of El Niño. By June 1983, ponds covered much more of the valley floor than is indicated. Trails are indicated only where they exit the study area.


trail to Islote
N
a DWH/WH
PR/CR/R
PR/CR
PR/R
PR
CR/R
b CR
OP/PR/CR
OP/PR
c OP/CR
OPUNTIA
d MA/R
OPEN
River
Flood Pond
PINZÓN
trail to nesting zone
river to North Crater
trail to ridge
100m

> "Pinzón Island is basically one large thornbush, and the bush covers a 1300-foot-high volcano ---- nine square miles of lava rocks and parched thickets."

Although this describes the island as a whole, in the bottom of the two craters soil deposition has been substantial and some areas are relatively free of lava at the surface. The majority of habitat types were based on the occurrence or absence of two shrub species, Prosopis juliflora and Croton scouleri. The most abundant shrub, Alternanthera filifolia, was well represented in nearly all habitat types, and thus was not included in habitat type names. Two additional fairly abundant shrubs that were not represented in habitat type names were Zanthoxylum fagara and Lantana peduncularis. Both were more closely associated with Croton than with Prosopis.

Habitat types used in analyses included:

DWH/WH - Dry Water Hole/Water Hole: open areas ranging in size from small holes of 2 m diameter to the large central Water Hole, approximately 50x90 m; ground cover by rock and soil about equal; generally low-growth plants consisting of forbs, grasses, and sedges; these depressions fill only when there is substantial precipitation, due to drainage of initial rainfall into an underground river system (Cayot 1985).

PR/CR/R - Prosopis juliflora/Croton scouleri/Rock: extremely rocky areas with shrubs generally between 50-150 cm tall; few areas with shrubs taller than 150 cm; Alternanthera filifolia, Maytenus octogona, and Zanthoxylum fagara also fairly common.

PR/CR - Prosopis juliflora/Croton scouleri: similar to PR/CR/R, but with much less cover by lava and more by soil; Prosopis generally 50-150 cm tall, while Croton was often taller than 150 cm.

PR/R - Prosopis juliflora/Rock: lava extremely abundant; Alternanthera filifolia and Maytenus octogona common; Prosopis from 50-150 cm tall.

PR - Prosopis juliflora: similar to PR/R but with less lava and more soil; Alternanthera filifolia and Maytenus octogona common; Prosopis from 50-150 cm tall.

CR/R - Croton scouleri/Rock: moderate amount of cover by lava; Alternanthera filifolia, Lantana peduncularis, Maytenus octogona, and Zanthoxylum fagara relatively common; Croton usually taller than 150 cm.

CR - Croton scouleri: similar to CR/R but with less lava; Alternanthera filifolia, Lantana peduncularis, Maytenus octogona, and Zanthoxylum fagara relatively common; Croton usually taller than 150 cm.

OP/PR/CR - Opuntia galapageia/Prosopis juliflora/Croton scouleri: rock abundant in about 50% of the habitat type; Opuntia trees relatively dense with open soil areas between; Croton and Prosopis ranging from 50 cm to greater than 150 cm tall; Alternanthera filifolia, Maytenus octogona, and Zanthoxylum fagara relatively common.

OP/PR - Opuntia galapageia/Prosopis juliflora: moderately rocky areas with scattered Opuntia; Prosopis generally between 50-150 cm tall; Alternanthera filifolia common.

OP/CR - Opuntia galapageia/Croton scouleri: high amount of soil deposition; Opuntia relatively dense; Alternanthera filifolia and Zanthoxylum fagara common; Croton usually taller than 150 cm.

OPUNTIA - Opuntia galapageia: open area with scattered Opuntia and a high level of soil deposition; little understory vegetation; low-growth Alternanthera filifolia, Castela galapagana, and Maytenus octogona most common.

MA/R - Maytenus octogona/Rock: very rocky area covered with low-growth Maytenus octogona and Alternanthera filifolia, both less than 50 cm tall; little other vegetation except for Commelina diffusa which became abundant at the onset of El Niño.

OPEN: open areas of soil with little rock and very little vegetation; herbaceous vegetation was abundant during El Niño.

O/R - Open/Rock: open areas covered by lava with very little soil or vegetation.

Percentage of area in each habitat type was estimated both from vegetation transects and from the habitat type map, as described for La Caseta and El Chato (Table 6.5). All habitat types were considered macro-habitats and were noted both in the vegetation transects and on the map, except for O/R which constituted a relatively small amount of the study area. Few of the "trails" in the study area were true tortoise trails and the habitat type was not used in instantaneous tortoise observations.

Table 6.5. Percent of key tortoise areas (%VT) and percent of the total study area (%SA) by habitat type[a] on Pinzón.

HABITAT TYPE[a]	%VT	%SA
DWH	18.54	1.76
PR/CR/R	15.03	32.43
PR/CR	11.79	2.97
PR/R	4.64	25.05
PR	11.16	3.99
CR/R	4.00	4.69
CR	4.76	0.52
OP/PR/CR	9.27	9.53
OP/PR	4.12	8.57
OP/CR	7.52	0.52
OPUNTIA	3.38	8.50
MA/R	4.26	0.18
OPEN	1.50	1.23

[a]Habitat types include various combinations of the following: DWH - Dry Water Hole, R - Rock, PR - Prosopis, CR - Croton, OP - Opuntia, MA - Maytenus, and Open.

Characteristics of the 13 habitat types occurring in vegetation transects were determined (Table 6.6). Measures of species richness (S_{ht}) and species diversity (H'_{ht}) are more reliable within a habitat type than among them due to the wide range in the number of quadrats per habitat type. Available biomass of forbs, shrubs, grasses/sedges, cactus, and other food items, as well as significant food items and preferred significant food items, were summed, as for La Caseta and El Chato.

Movement Among Habitat Types

Both the number of different habitat types visited and the number of times a tortoise is able to change habitat types each day are important measures of the ability of tortoises to select specific habitat types for specific activities. Potential movement among habitat types per day by an individual tortoise was determined by examining movement of focal animals. A total of 22 animals, or 44 days, was monitored at Caseta/Chato. However, because substitute observers without adequate knowledge of the habitat types worked during a portion of 9 days, those days were eliminated from the analysis. At the Santa Cruz Nesting Zone, 8 focal animals, or 16 days of observation, were used. To examine movement among habitat types on Pinzón, only the 9 focal animals, or 18 days, from December 1982, were used. Constant monitoring of focal animals was initiated on the first trip to Pinzón, and habitat types were not yet well-defined nor always recorded.

Table 6.6. Characteristics of habitat types[a] on Pinzón, based on results of vegetation transects. Characteristics include percent cover by rock (%ROCK) and by available food (%FOOD), species richness (s_{ht}), species diversity (H'_{ht}), available biomass (g/m^2) of all foods (FOOD), of significant foods (SIGFOOD), of preferred-significant foods (SIGPLUS), of forbs (FORB), shrubs (SHRUB), grasses and sedges (GRASS), Opuntia (CACTUS), and other food items (OTHER).

HABITAT[a]	SEASON	N[b]	%ROCK[c]	%FOOD	S_{ht}	H'_{ht}	FOOD	SIG-FOOD	SIG-PLUS	FORB	SHRUB	GRASS	CACTUS	OTHER
DWH	HotDry82	27	53.29	4.72	11	1.05	10.77	10.23	1.22	1.28	8.50	0.01	0.39	0.59
	El Niño	32	53.29	30.39	22	1.19	38.93	36.77	20.58	19.52	16.22	1.90	0.88	0.41
PR/CR/R	HotDry82	22	79.92	37.16	18	1.67	96.13	72.27	12.89	0.96	89.05	0.20	0	5.92
	El Niño	38	79.92	65.07	33	1.74	131.92	109.72	20.57	10.61	116.19	1.12	0	3.99
PR/CR	HotDry82	29	31.80	28.97	19	1.65	71.58	56.18	3.88	0.37	64.36	0.19	0	6.66
	El Niño	15	31.80	35.83	25	1.71	47.42	38.98	7.43	5.63	39.52	1.20	0	1.07
PR/R	HotDry82	6	77.36	45.83	11	1.20	128.96	98.24	1.52	1.52	127.00	0.08	0	0.36
	El Niño	12	77.36	74.58	21	1.39	149.69	134.04	18.79	19.13	127.17	2.91	0	0.48
PR	HotDry82	14	29.15	36.43	15	1.24	104.15	75.81	1.48	0.99	102.56	0.04	0	0.56
	El Niño	17	29.15	56.62	21	1.67	60.16	50.98	10.16	10.33	46.43	0.98	1.76	0.66
CR/R	HotDry82	5	66.83	24.00	13	1.47	69.80	56.52	5.85	1.51	54.24	0.10	0	13.95
	El Niño	10	66.83	40.50	28	1.62	80.84	65.93	10.11	5.40	68.84	1.15	0	5.45
CR	HotDry82	10	28.74	25.25	17	1.87	60.84	33.83	10.10	1.35	45.19	0.35	0	13.95
	El Niño	7	28.74	29.29	24	2.16	34.32	25.05	10.61	6.83	22.80	0.19	0	4.50
OP/PR/CR	HotDry82	18	47.33	26.94	21	1.78	67.32	52.46	6.89	0.85	60.75	0.92	2.41	2.39
	El Niño	19	47.33	48.03	32	1.42	92.40	78.46	9.90	5.34	85.05	1.56	0.26	0.19

Table 6.6 continued.

HABITAT[a]	SEASON	N[b]	%ROCK[c]	%FOOD	S_{ht}	H'_{ht}	FOOD	SIG-FOOD	SIG-PLUS	FORB	SHRUB	GRASS	CACTUS	OTHER
OP/PR	HotDry82	12	50.69	25.21	14	1.22	64.74	61.21	2.18	1.23	59.82	0.04	0.39	3.26
	El Niño	4	50.69	54.38	15	1.65	92.22	74.97	8.20	11.43	75.40	1.96	0	3.43
OP/CR	HotDry82	14	33.90	11.25	14	1.65	30.67	27.01	4.50	1.29	18.33	0	4.12	6.93
	El Niño	16	33.90	37.47	29	1.44	70.27	48.82	7.39	6.05	61.34	1.48	0.26	1.14
OPUNTIA	HotDry82	8	31.58	14.38	11	1.49	36.21	21.71	1.46	0.58	29.25	0	0	6.38
	El Niño	5	31.58	38.50	20	1.54	62.45	44.39	8.95	3.61	56.55	2.27	0	0.02
MA/R	HotDry82	6	75.68	53.33	12	0.87	117.65	43.41	3.26	2.42	113.98	1.25	0	0
	El Niño	5	75.68	82.50	10	1.13	241.27	127.91	24.27	16.78	222.95	1.54	0	0
OPEN	HotDry82	2	25.08	2.50	0	0	0	0	0	0	0	0	0	0
	El Niño	4	25.08	8.75	11	1.75	4.84	4.48	3.81	1.26	0.67	2.91	0	0

[a]Habitat types include various combinations of the following: DWH - Dry Water Hole, R - Rock, PR - Prosopis, CR - Croton, OP - Opuntia, MA - Maytenus, and Open.

[b]Total number of quadrats in each habitat type used for calculation of average values for habitat characteristics.

[c]Percent rock was averaged over all quadrats for each habitat rather than by season.

Tortoises were recorded using nearly all of the available habitat types in each study area. Of the 22 possible habitat types at Caseta/Chato (Dry Water Holes I and II separate from Water Holes I and II), focal animals were recorded in all except LEMON. A range from 2 to 11 habitat types was visited per day, with 2 to 39 changes among habitat types (Table 6.7). Of the 12 possible habitat types at SCNZ, focal animals were seen in all except O/R/EVGL, O/EVGL/PPW, and CMT. In addition, tortoises were noted using trails, and one tortoise was found in a Rock/Psidium galapageium Woodland. A range of 1 to 5 habitat types was visited per day, with tortoises moving among habitat types 0 to 14 times (Table 6.7). Focal animals were recorded in all 15 of the defined habitats on Pinzón, and were also seen using trails. They visited between 2 to 12 habitat types per day, moving among them 2 to 40 times (Table 6.7).

The reasons for the wide range in the number of habitat types visited and in the number of changes among habitat types per day may be important in determining the ability of tortoises to select high quality habitats in different seasons. Although the original position of each focal animal in the study area may affect the ease with which it can move among habitats due to the uneven distribution of habitat types, movement among habitats is primarily dependent on the amount of activity per day. For each study area, stepwise regressions were run between the number of habitat types visited or the number of changes in habitat type and the

Table 6.7. The number of different habitat types used per day (HT/DAY) by focal animals, and the number of times they moved from one habitat type to another (ΔHT/DAY). N = the total number of focal-animal days.

STUDY AREA	VARIABLE	N	$\bar{X}$	SD	RANGE
CASETA/CHATO	HT/DAY	35	6.29	2.50	2 - 11
	ΔHT/DAY	35	16.26	9.79	2 - 39
SCNZ[a]	HT/DAY	16	3.62	1.26	1 - 5
	ΔHT/DAY	16	5.06	3.32	0 - 14
PINZÓN	HT/DAY	18	6.28	2.93	2 - 12
	ΔHT/DAY	18	13.72	9.72	2 - 40

[a]Santa Cruz Nesting Zone.

number of minutes per day spent feeding, traveling, and the sum of the two. Number of minutes feeding was included because tortoises often moved substantial distances while steadily feeding.

The number of habitats visited by a tortoise in a day at Caseta/Chato was most significantly related to the sum of the number of minutes spent traveling and feeding (Fig. 6.5). Although no significant results were found for tortoises at SCNZ or Pinzón, tortoises on Pinzón exhibited a trend of an increasing number of habitat types visited with increasing time spent traveling ($F_{1,16} = 3.33$, $R^2 = 0.17$, $P < .09$).

The number of times a tortoise moved from one habitat to another per day at Caseta/Chato was most significantly related to the time spent traveling (Fig. 6.6). No significant results were found for tortoises at SCNZ or Pinzón, although those at SCNZ showed a trend of increasing movement among habitats with increases in the total time spent feeding and traveling ($F_{1,14} = 3.91$, $R^2 = 0.22$, $P < .07$).

As the amount of time spent feeding and traveling increases, a tortoise is able to increase its movement among habitat types, visiting more different habitat types each day, enabling it to better select specific habitat types. This suggests that selection of habitat types may be stronger when tortoises are more active, ie., when conditions are favorable. With less activity during stressful times, it is possible that tortoises select the highest quality habitat

Fig. 6.5. The number of different habitat types visited/day in relation to the total number of minutes feeding and traveling/day, for focal animals at La Caseta and El Chato.

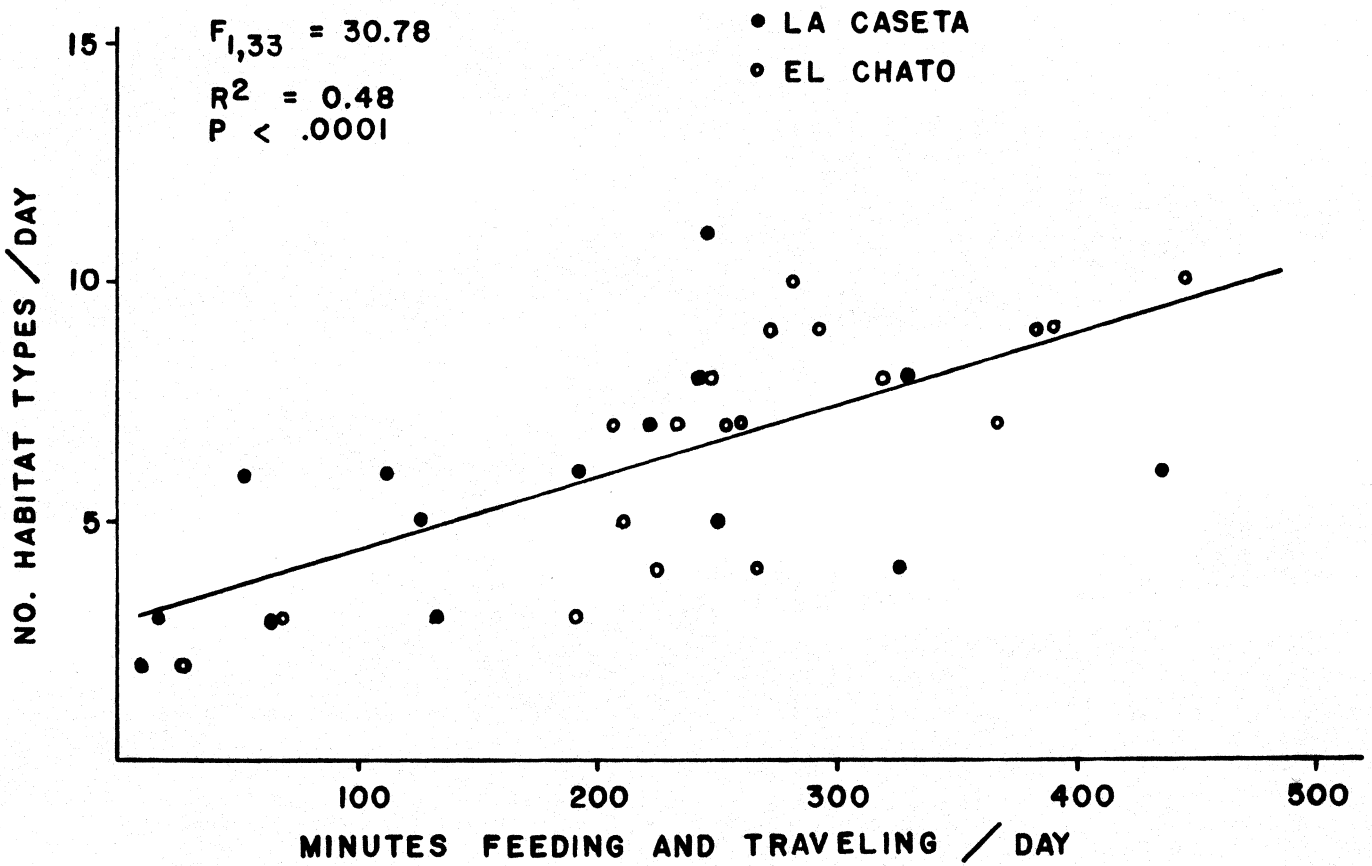
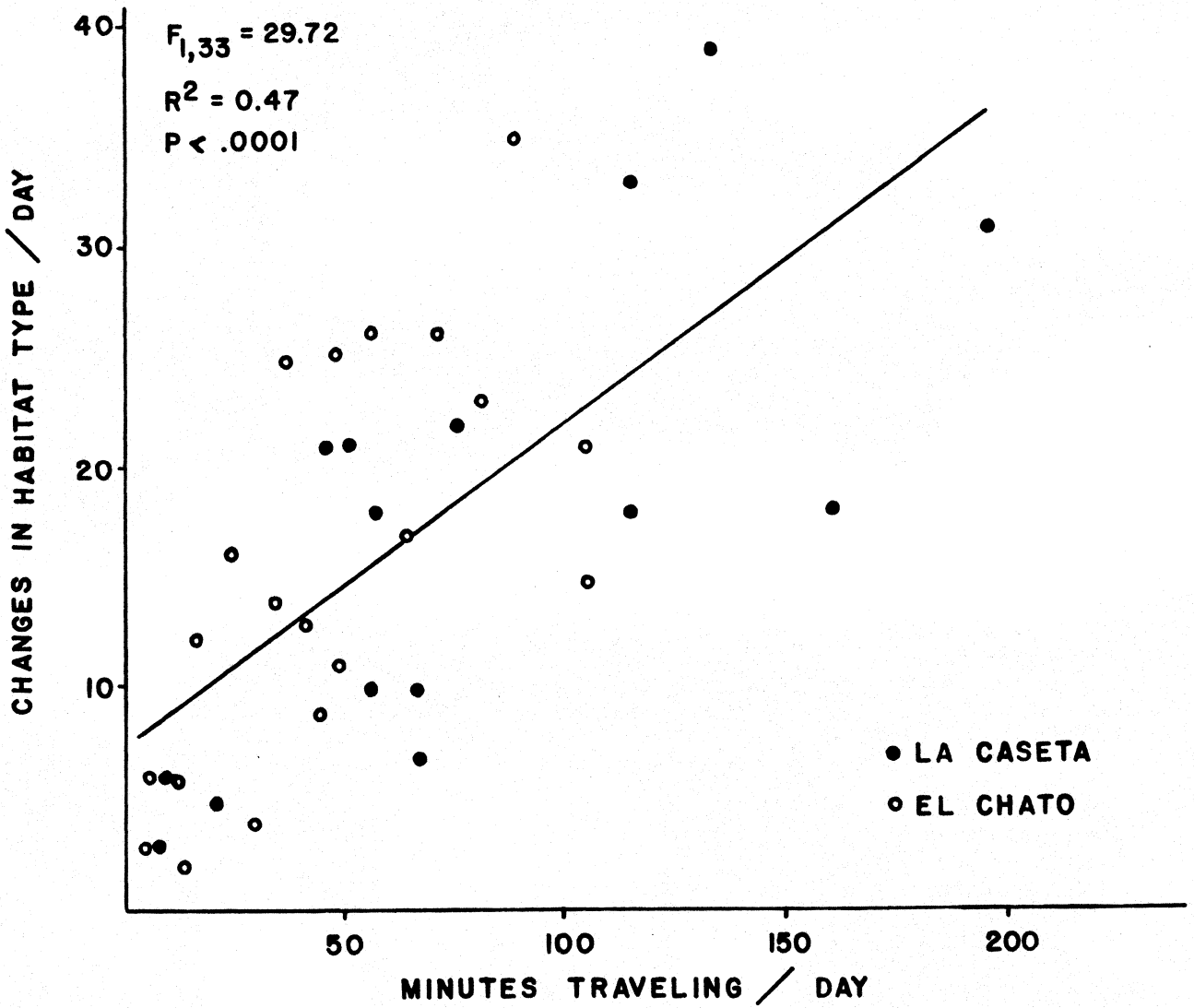

$F_{1,33}$ = 30.78
R^2 = 0.48
P < .0001
● LA CASETA
○ EL CHATO
NO. HABITAT TYPES / DAY
15
10
5
100
200
300
400
500
MINUTES FEEDING AND TRAVELING / DAY

Fig. 6.6. The number of times a tortoise moved from one habitat type to another/day in relation to the total number of minutes traveling/day, for focal animals at La Caseta and El Chato.


$F_{1,33} = 29.72$
$R^2 = 0.47$
$P < .0001$
CHANGES IN HABITAT TYPE / DAY
40
30
20
10
50
100
150
200
MINUTES TRAVELING / DAY
LA CASETA
EL CHATO

types for the single most important activity and remain in them, forfeiting habitat selection for other activities. In general, tortoises are able to move freely among habitat types, allowing them to select specific habitat types for their various activities except when conditions are poor and some compromise in habitat choice is necessary.

Habitat Selectivity

Seasonal changes in selectivity of habitats for different activities were examined to determine the effect of environmental conditions on the intensity of habitat choice by tortoises. Indices of habitat selectivity (SEL), where $SEL = \Sigma|p_s - p_c|/2$, and p_s is the proportion of the total area in each habitat type, and p_c is the proportion of tortoise activity occurring in each habitat type (after McNaughton 1978), were calculated by month for the three major activities of tortoises, resting, feeding, and traveling. Two selectivity indices were possible for each month, the first based on percent area from vegetation transects (SELVT), and the second on percent of the total study area from habitat type maps (SELMAP).

Habitat selectivity may differ by activity, by location, or by season. To determine to what extent these factors effect habitat selectivity, general linear models were run for all study areas and all activities combined, with location, and activity as discrete variables. Similar analyses were done for La Caseta and El Chato only, with activity as the only discrete variable. To determine the significance

of season on habitat selectivity, selectivity for each activity was run separately against season. Tukey's Studentized Range Tests were then run for those ANOVAs with significant discrete variables.

With all study areas included, habitat selectivity was significantly related to location for both SELVT ($F_{3,95}$ = 10.84, R^2 = 0.25, P < .0001) and SELMAP ($F_{3,93}$ = 8.26, P < .0001). Using either measure, SCNZ had the lowest level of selectivity (Table 6.8). Low levels of habitat selectivity at SCNZ correspond to the lack of distinct habitat delineation in that study area. SELMAP was also related to activity ($F_{2,93}$= 6.56, P < .002), with habitat selectivity highest for feeding, while there were no significant differences between resting and traveling (Table 6.8). SELMAP was also correlated with activity at La Caseta and El Chato ($F_{2,81}$ = 6.56, R^2 = 0.14, P < .002), but SELVT was not. Again, habitat selectivity was highest for feeding, with no significant differences between resting and traveling (Table 6.8).

When habitat selectivity for feeding was considered alone, location was again significant (SELVT: $F_{3,29}$= 9.66, R^2 = 0.50, P < .0001; SELMAP: $F_{3,29}$= 11.65, R^2 = 0.55, P < .0001), with selectivity lowest at SCNZ (Table 6.8). There were no significant seasonal effects on habitat selectivity for feeding.

When all study areas were considered together, location was significant for SELVT for resting ($F_{3,29}$ = 3.25, R^2 = 0.25, P < .04), but Tukey's Range Test showed no significant

Table 6.8. Results of Tukey's Studentized Range Tests based on significant results of ANOVAs analysing the effect of study area (LOC) and activity (ACT) on habitat selectivity (SELVT, SELMAP)[a] for feeding, resting, and traveling at all study areas, and the effect of season and study area on habitat selectivity for each activity separately. All differences significant at $P < .05$.

ALL ACTIVITIES

ALL STUDY AREAS

SELVT = LOC, df = 95

LOC	Caseta	Chato	Pinzón	SCNZ[b]
N	42	42	6	9
MEAN	0.68	0.67	0.57	0.47

SELMAP = LOC + ACT, df = 93

LOC	Pinzón	Chato	Caseta	SCNZ[b]
N	6	42	42	9
MEAN	0.87	0.77	0.70	0.57

ACT	Feeding	Traveling	Resting
N	33	33	33
MEAN	0.80	0.70	0.69

CASETA/CHATO

SELMAP = ACT, df = 81

ACT	Feeding	Traveling	Resting
N	28	28	28
MEAN	0.82	0.72	0.69

FEEDING - ALL STUDY AREAS

SELVT = LOC, df = 29

LOC	Chato	Caseta	Pinzón	SCNZ[b]
N	14	14	2	3
MEAN	0.70	0.64	0.58	0.40

Table 6.8 continued.

FEEDING - ALL STUDY AREAS

SELMAP = LOC, df = 29

LOC	Chato	Pinzón	Caseta	SCNZ[b]
N	14	2	14	3
MEAN	0.90	0.84	0.73	0.63

RESTING - CASETA/CHATO

SELMAP = SEASON, df = 23

SEASON	Garúa81	Garúa82	Niño	HotWet82	HotDry82
N	2	10	4	6	6
MEAN	0.94	0.73	0.71	0.66	0.54

TRAVELING

ALL STUDY AREAS

SELVT = LOC + SEASON, df = 25

LOC	Caseta	Chato	Pinzón	SCNZ[b]
N	14	14	2	3
MEAN	0.71	0.68	0.56	0.56

SEASON	Garúa81	HotWet82	HotDry82	Garúa82	Niño
N	2	6	7	10	8
MEAN	0.84	0.77	0.71	0.64	0.58

SELMAP = LOC + SEASON, df = 25

LOC	Pinzón	Chato	Caseta	SCNZ[b]
N	2	14	14	3
MEAN	0.87	0.73	0.70	0.46

SEASON	Garúa81	HotWet82	HotDry82	Garúa82	Niño
N	2	6	7	10	8
MEAN	0.87	0.81	0.71	0.67	0.60

Table 6.8 continued.

TRAVELING

CASETA/CHATO

SELVT = SEASON, df = 23

SEASON	Garúa81	HotWet82	HotDry82	Garúa82	Niño
N	2	6	6	10	4
MEAN	0.84	0.77	0.72	0.64	0.62

[a]SELVT = habitat selectivity based on habitat availability in the key tortoise areas; SELMAP = habitat selectivity based on habitat availability in the total study area. Both values transformed to arc sine square root, in radians.

[b]Santa Cruz Nesting Zone.

differences between study areas. Season was significant for SELMAP for resting when only La Caseta and El Chato were included ($F_{4,23}$= 3.45, R^2 = 0.37, P < .02), but not when all study areas were included. The seasonal trend in habitat selectivity for resting at La Caseta and El Chato was from highest selectivity in the garúa seasons, mid-levels in the hot-wet seasons, to lowest levels of selectivity in the hot-dry season (Table 6.8).

Habitat selectivity for traveling was significantly related to both study area (SELVT: $F_{3,25}$= 5.09, P < .007; SELMAP: $F_{3,25}$= 6.07, P < .003) and season (SELVT: $F_{4,25}$= 6.12, P < .001; SELMAP: $F_{4,25}$ = 2.69, P < .05) when all study areas were included, and season (SELVT: $F_{4,23}$ = 6.44, R^2 = 0.53, P < .001) when only La Caseta and El Chato were included. Differences among study areas were dependent upon selectivity measure (Table 6.8). The seasonal trend ran from the highest selectivity at the beginning of the study to the lowest at the end (Table 6.8). This may be complicated by changes in recording trail and trailside habitats at La Caseta and El Chato during the course of the study. Also, results for habitat selectivity for traveling were based on many fewer observations than either feeding or resting and may be less reliable.

Habitat selectivity is significantly higher for feeding than for resting and traveling. There are no seasonal effects on habitat selectivity for feeding, suggesting that tortoises maintain high levels of habitat selectivity for

feeding regardless of environmental conditions. The lowest levels of habitat selectivity for resting were in the hot-dry season when conditions were least favorable. This corresponds to the period when tortoises are least active, and when they have the highest selectivity for food items. These two factors may require them to remain in high quality habitat types for feeding, forcing them to compromise in terms of habitat selectivity for resting.

Habitat Preference Indices

Due to the lack of difference among the three preference indices tested for feeding when ranked (see Feeding Behavior chapter), the rank order of Ivlev's electivity index (E_i) (Ivlev 1961) was selected for use in all analyses. For habitat preferences, $E_i = (r_i - p_i)/(r_i + p_i)$, where r_i is the proportion of total activity of tortoises in habitat i, and p_i is the proportion of the total area encompassing habitat i.

Percent use by tortoises was determined separately for each activity from the instantaneous observations. Number of observations per month varied for all activities (Table 6.9). Due to the low number of observations for mating, agonistic interactions, and drinking, these activities were eliminated from the analyses of habitat preferences.

Proportion of the environment in habitat i had two separate estimates, resulting in two sets of preference indices. The first estimate (E_iVT) is based on vegetation transects which represent the composition of habitats in the key tor-

Table 6.9. Monthly totals of instantaneous tortoise observations for each activity with habitat type recorded.

STUDY AREA	MONTH	REST	FEED	TRAVEL	DRINK	MATING	AGONISTIC INTERACTION
CASETA	DEC81	125	104	38	2	6	0
	JAN82	58	97	42	2	14	8
	FEB82	51	75	39	5	4	0
	MAR82	124	120	61	1	12	14
	APR82	127	68	28	0	6	2
	MAY82	355	27	34	0	14	10
	JUN82	426	56	68	0	13	10
	JUL82	116	97	16	18	2	0
	AUG82	194	111	39	23	6	2
	SEP82	116	104	30	4	0	0
	OCT82	122	90	16	6	0	2
	NOV82	133	124	16	10	0	2
	DEC82	102	22	31	1	0	0
	JAN83	118	8	23	1	0	0
CHATO	DEC81	114	121	18	24	6	0
	JAN82	126	98	39	26	22	3
	FEB82	10	55	9	3	12	0
	MAR82	72	79	41	5	26	2
	APR82	38	63	14	0	14	0
	MAY82	56	12	16	0	8	8
	JUN82	83	49	17	0	8	0
	JUL82	225	142	29	7	8	2
	AUG82	45	167	25	21	2	0
	SEP82	161	221	27	5	0	0
	OCT82	152	210	39	11	2	4
	NOV82	205	141	10	8	4	0
	DEC82	33	27	21	0	2	0
	JAN83	62	34	22	0	4	0

Table 6.9 continued.

STUDY AREA	MONTH	REST	FEED	TRAVEL	DRINK	MATING	AGONISTIC INTERACTION
SCNZ[a]	FEB/MAR83	207	123	26	2	16	2
	APR83	273	169	16	3	18	2
	JUL83	290	147	25	7	8	0
PINZÓN	APR/MAY82	545	132	120	19	6	15
	DEC82	546	257	83	8	4	2

[a]Santa Cruz Nesting Zone.

toise areas, while the second estimate ($E_i SA$) is based on habitat type maps which represent the proportion of the entire study area in habitat i. If a habitat type used by tortoises was not included in either of these methods, its percent availability was set at 0.1%. All of the habitat types that constituted a portion of the vegetation transects were included in all of the analyses whether or not they were used by tortoises in a given month.

To determine whether the rank of the two habitat preference indices differed significantly, Spearman's rank correlations (r_s) were run by activity and month for each study area (Table 6.10). The two preference indices were significantly correlated for resting, feeding, and traveling at La Caseta and El Chato in all months, except for tortoises feeding at El Chato in July 1982. However, r_s for resting ranged from 0.60 to 0.99, for feeding from 0.49 (NS) to 0.99, and for traveling from 0.66 to 1.00. Correlations at SCNZ were not always significant for resting and feeding, and on Pinzón, the only significant correlation was for traveling, in December 1982.

Lack of significance and the occasional low levels in rank correlations are due primarily to tortoise use of those habitat types whose estimated abundances differed most between the key tortoise areas and the surrounding study area. Two examples of this in the macro-habitats were Underutilized Grasslands and Clerodendrum Thickets at La Caseta and El Chato (Table 6.1). Underutilized Grasslands were

Table 6.10. Comparison of habitat preference indices for resting, feeding, and traveling based on percent of key tortoise areas (E_iVT) with those based on percent of the total study area (E_iSA). Results list Spearman's rank correlation coefficients (r_s) at P < .05*, .01**, .001***, .0001****.

STUDY		RESTING		FEEDING		TRAVELING	
AREA	MONTH	N	r_s	N	r_s	N	r_s
CASETA	Dec81	15	.83****	14	.92****	12	.96****
	Jan82	13	.88****	13	.63*	13	.94****
	Feb82	14	.94****	14	.71**	12	.91****
	Mar82	12	.86***	14	.81***	12	.70**
	Apr82	12	.85***	11	.91****	11	.99****
	May82	14	.85****	12	.99****	12	.92****
	Jun82	14	.70**	13	.73**	12	.82***
	Jul82	13	.90****	12	.81**	12	.89****
	Aug82	15	.75***	14	.83***	11	.92****
	Sep82	12	.75**	12	.86***	11	.85***
	Oct82	13	.86***	17	.81****	12	.98****
	Nov82	17	.83****	16	.74***	12	.93****
	Dec82	13	.91****	15	.90****	14	.93****
	Jan83	12	.87***	12	.98****	13	.86***
CHATO	Dec81	14	.87****	14	.82***	12	.96****
	Jan82	13	.60*	14	.75**	12	.91****
	Feb82	12	.99****	13	.92****	12	.97****
	Mar82	11	.95****	13	.77**	13	.66**
	Apr82	11	.92****	11	.83**	10	1.00****
	May82	11	.66*	10	.90***	11	.94****
	Jun82	12	.74**	12	.79**	12	.95****
	Jul82	15	.76***	14	.49	10	.67*
	Aug82	13	.81***	14	.71**	12	.96****
	Sep82	13	.86****	16	.79***	12	.98****
	Oct82	14	.80***	15	.62**	13	.79***
	Nov82	15	.75***	14	.68**	12	.97****
	Dec82	13	.89****	14	.86****	12	.81***
	Jan83	13	.84***	15	.74**	12	.85***

Table 6.10 continued.

STUDY AREA	MONTH	RESTING N	RESTING r_s	FEEDING N	FEEDING r_s	TRAVELING N	TRAVELING r_s
SCNZ[a]	Feb/Mar83	10	.87***	9	.83**	9	.96****
	Apr83	10	.80**	10	.47	9	.93***
	Jul83	11	.58	10	.68*	10	.95****
PINZÓN	Apr/May82	14	.48	13	.54	14	.35
	Dec82	13	.33	14	.18	14	.53*

[a]Santa Cruz Nesting Zone.

well represented in the vegetation transects but only constituted between 1-3% of the total study area. Clerodendrum Thickets, a habitat not usually frequented by tortoises, were much less abundant in the vegetation transects than in the study area as a whole. Because of these discrepancies, both of these habitat types were better measured in the mapping procedure, which suggests that the preference index E_iSA would be more appropriate. On the other hand, abundance of micro-habitats was better measured in the vegetation transects, or key tortoise areas. Many of the micro-habitats were too small to map, resulting in their E_iSA values being unrealistically high whenever tortoises used them, even if percent use was insignificant.

In addition, although ranks may be similar, the actual preference index values, positive indicating preference and negative indicating avoidance, may differ greatly between the two calculations of preference. Preference indices based on the entire study area may be positive for all of the micro-habitats which are represented primarily in the key tortoise areas, while the same habitats may appear avoided when using the index based on vegetation transects. Therefore both calculations of E_i were used in all further analyses, and differences between the two discussed when necessary.

To make cross-month comparisons of habitat preference, where each month had a different total number of habitat types and thus rank values, rank order (lowest index value = 1) was divided by the number of habitat types for each

month. This gives each habitat a preference value between 0 and 1, with 1 the most preferred, and that closest to 0 the least preferred.

Habitat Preferences - Feeding

Percent use of habitat types and the corresponding habitat preferences of tortoises feeding at La Caseta and El Chato changed seasonally for many habitats (Tables 6.11, 6.12). Directional changes were similar in both study areas. Feeding in Hippomane Woodlands increased dramatically during the hot season 1982, when tortoises were dependent upon the fruit of Hippomane trees. Otherwise, the habitat type was little used. Underutilized Grasslands, generally preferred, were of greater importance to tortoises feeding at El Chato where UGs are more abundant, but were used least in both study areas during the hot-dry season 1982, when much of the herbaceous vegetation was dry. Open Forb areas and Dry Water Holes (type 1) showed the same drop in use during the hot-dry season when herbaceous vegetation was dry. The ephemeral lawns of Dichondra repens were non-existent in this period, but were highly preferred when available.

Significant seasonal correlations between the average indices of habitat preference for the 13 major habitat types at La Caseta with those at El Chato validate the habitat preference:avoidance patterns of tortoises when feeding (Table 6.13). Tortoises never used Psidium/Zanthoxylum Woodlands to the extent of their availability, resulting in

Table 6.11. Seasonal averages of the percent of observations of feeding tortoises at La Caseta in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
PZW	%USE	43.1	31.3	32.9	38.4	33.5
	E_iVT	-.04	-.20	-.19	-.10	-.17
	E_iSA	-.14	-.29	-.28	-.19	-.26
HAW	%USE	4.8	27.4	36.9	6.6	9.9
	E_iVT	-.72	-.10	+.02	-.65	-.51
	E_iSA	-.60	+.11	+.22	-.51	-.33
CMT	%USE	6.7	4.8	2.1	1.3	0
	E_iVT	+.26	+.05	-.44	-.55	-1.0
	E_iSA	-.36	-.51	-.77	-.84	-1.0
UG	%USE	4.8	7.8	3.3	22.0	21.6
	E_iVT	-.13	+.04	-.41	+.54	+.54
	E_iSA	+.63	+.69	+.09	+.90	+.90
GL	%USE	5.8	3.3	8.0	5.8	13.1
	E_iVT	+.71	+.49	+.20	+.69	+.86
	E_iSA	+.96	+.92	+.32	+.96	+.98
OF	%USE	6.6	2.5	0.3	3.0	4.3
	E_iVT	+.12	-.47	-.90	-.28	-.15
	E_iSA	+.76	+.18	-.67	+.51	+.59
DWH I/WH I	%USE	14.4	9.3	4.3	12.8	0
	E_iVT	+.85	+.77	+.13	+.70	-1.0
	E_iSA	+.81	+.70	+.08	+.63	-1.0
SCPT	%USE	0	0.2	1.2	2.0	2.3
	E_iVT	-1.0	-.88	-.42	-.22	-.43
	E_iSA	-1.0	-.93	-.59	-.43	-.48
PSRU	%USE	0	0.5	0.3	0.5	0
	E_iVT	-1.0	-.50	-.76	-.58	-1.0
	E_iSA	-1.0	+.68	-.40	+.06	-1.0
DL[b]	%USE	5.6	3.8	0	1.1	3.4
	E_iVT	+.93	+.68		+.40	-.03
	E_iSA	+.96	+.81		+.49	-.01

Table 6.11 continued.

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
DWH II/WH II	%USE	1.0	2.3	0.5	0.1	0
	E_iVT	+.26	+.04	-.52	-.80	-1.0
	E_iSA	+.78	+.25	-.38	-.67	-1.0
TRAIL	%USE	1.9	4.0	2.4	2.4	2.2
	E_iVT	+.64	+.81	+.60	+.60	-.08
	E_iSA	+.90	+.95	+.88	+.87	-.02
OTHER[c]	%USE	5.3	2.8	7.8	4.0	9.7

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, and Trail.

[b]DL non-existent in HotDry82.

[c]Includes Scalesia Stand, Rhynchospora Stand, Rock Mound, Lemon, Orange, Trailside, River, and Water Hole.

Table 6.12. Seasonal averages of the percent of observations of feeding tortoises at El Chato in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
PZW	%USE	19.0	19.8	16.2	19.8	31.3
	E_iVT	-.37	-.36	-.50	-.36	-.14
	E_iSA	-.51	-.49	-.60	-.49	-.30
HAW	%USE	1.6	13.0	45.4	4.1	2.0
	E_iVT	-.79	-.18	+.45	-.57	-.78
	E_iSA	-.79	-.19	+.44	-.58	-.78
CMT	%USE	3.7	5.3	1.9	3.1	0
	E_iVT	-.43	-.31	-.70	-.51	-1.0
	E_iSA	-.64	-.54	-.81	-.70	-1.0
UG	%USE	33.1	23.4	18.9	25.5	34.6
	E_iVT	+.41	+.24	+.06	+.29	+.42
	E_iSA	+.87	+.81	+.72	+.83	+.87
GL	%USE	3.3	4.7	1.6	2.0	0
	E_iVT	+.50	+.40	-.19	+.24	-1.0
	E_iSA	+.54	+.43	-.17	+.27	-1.0
OF	%USE	2.9	6.0	0.8	10.0	5.1
	E_iVT	-.39	-.05	-.83	+.16	-.15
	E_iSA	+.22	+.53	-.62	+.65	+.44
DWH I/WH I	%USE	18.2	9.3	9.0	17.2	13.1
	E_iVT	+.56	+.21	+.17	+.50	+.43
	E_iSA	+.79	+.56	+.53	+.75	+.72
SCPT	%USE	1.6	0	0.3	1.4	0.6
	E_iVT	-.27	-1.0	-.86	-.41	-.70
	E_iSA	0	-1.0	-.78	-.18	-.57
PSRU	%USE	0	1.2	2.5	0.7	0.6
	E_iVT	-1.0	-.43	-.06	-.57	-.67
	E_iSA	-1.0	+.26	+.90	+.71	-.08
DL[b]	%USE	5.8	3.1	0	12.1	2.1
	E_iVT	+.63	+.34		+.79	+.18
	E_iSA	+.97	+.92		+.98	+.89

Table 6.12 continued.

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
DWH II/WH II	%USE	0.8	0.6	2.1	0.1	0
	E_iVT	+.08	-.29	-.40	-.84	-1.0
	E_iSA	+.78	+.18	-.34	-.67	-1.0
TRAIL	%USE	1.6	6.0	0.9	1.4	5.0
	E_iVT	+.89	+.96	+.23	+.80	+.92
	E_iSA	+.89	+.96	+.23	+.80	+.92
OTHER[c]	%USE	8.4	7.6	0.4	2.6	5.6

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, and Trail.

[b]DL non-existent in HotDry82.

[c]Includes Scalesia Stand, Rhynchospora Stand, Rock Mound, Lemon, Trailside, River, and Water Hole.

Table 6.13. Seasonal comparisons of habitat preference indices for feeding (E_iVT , based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area) at La Caseta, with those at El Chato. Results list Spearman's rank correlation coefficients (r_s) at P < .01*, .001**, .0001***.

SEASON	N	r_s (E_iVT)	r_s (E_iSA)
All	13	0.90***	0.88***
Dec81	13	0.81**	0.83**
HotWet82	13	0.83**	0.88***
HotDry82	12	0.79*	0.90***
Garúa82	13	0.84**	0.73*
El Niño	13	0.45	0.44

negative preference indices for all seasons. However, the woodlands were used extensively, most likely due to their high occurrence in the study areas, especially at La Caseta. Hippomane Woodlands had an average preference index that was negative, although they did become important and preferred when fruit was available, expecially if other foods were not.

Underutilized Grasslands, Grazing Lawns, Dichondra Lawns, and Dry Water Holes (type I) were preferred habitats for feeding throughout the study, with few exceptions. Underutilized Grasslands, always preferred at El Chato, had a negative preference index (based on vegetation transects) at La Caseta during December 1981, and in the hot-dry season 1982. These grasslands were concentrated in the area of vegetation transects which caused an over-estimate of their availability, and thus the negative indices. Grazing Lawns, always positive at La Caseta, had a negative preference index at El Chato in the hot-dry season 1982, and during El Niño. There was little forage available in these areas during the hot-dry season. The reason for the negative preference during El Niño is probably due to the low number of feeding observations in December 1982, and January 1983, and to the gradual disappearance of the habitat type at that time. Dichondra Lawns were preferred at all seasons except the hot-dry season 1982, when they were non-existent, and at the start of El Niño, when the habitat type was disappearing once again. Dry Water Holes (type I) were always preferred.

However, tortoises avoided ponds filled with water at the onset of El Niño at La Caseta, presumably because they were too deep, and preferred foods were covered and subsequently killed.

Preference indices for Open Forb areas alternated more than for other habitats between positive and negative values. The areas were preferred in most seasons. Most of the negative index values resulted from availability calculations based on vegetation transects, which included a majority of the Open Forb areas, and thus over-estimated their abundance in the study area. However, the areas were avoided by tortoises during the hot-dry season 1982, when little forage was available.

Areas that were consistently avoided by feeding tortoises included dense stands of Scleria pterota, Clerodendrum and Psychotria Thickets, and Dry Water Holes (type II). The only positive values for CMTs occurred in December 1981, and early 1982, at La Caseta. Both were based on availability figures from the vegetation transects in which CMTs were under-represented. Positive values for PSRU, a microhabitat, occurred only in indices based on habitat maps. The PSRU habitat type was never recorded on the maps, so any use of them by tortoises, no matter how insiginificant, would result in a positive value. Dry Water Holes (type II) were avoided by tortoises except during some of the periods when Hippomane fruits were available.

Of the three dominant habitat types at the Santa Cruz Nesting Zone (no other habitat types constituted greater than 5% of the total area based on either vegetation transects or the habitat type map), tortoises preferred the more open, less rocky woodlands (Table 6.14). R/PPW, although used more than any other area, was never preferred. Both O/R/PPW and O/PPW were preferred habitats for feeding, with O/PPW the most preferred. The negative indices for these two habitat types, both barely less than zero, occurred only when based on vegetation transects that were concentrated in the more open areas. The O/R/IPTR habitat was the only type that was always preferred regardless of which index value was used. This correlated well with the importance of Ipomoea in the diet during El Niño.

The other habitat types at SCNZ, constituting a small portion of the study area, were seldom used (Table 6.14). Their index values were all negative when availability was based on vegetation transects because these habitats were more concentrated in the transect regions. The positive value for some, corresponding to indices where availability was based on the habitat type map, suggest that these areas may be slightly preferred. However, they are probably relatively unimportant to tortoises.

Tortoises on Pinzón also tended to avoid the more rocky habitats (Table 6.15). Prosopis/Croton/Rock, the most abundant habitat type in the study area, was always avoided, as was Croton/Rock. Prosopis/Rock had a positive index, indi-

Table 6.14. Average percent of observations of feeding tortoises at the Santa Cruz Nesting Zone during El Niño 1983, in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas and E_iSA, based on habitat availability in the total study area). N = 3.

HABITAT TYPE[a]	%USE	E_iVT	E_iSA
R/PPW	34.9	-.05	-.32
O/R/PPW	26.3	-.07	+.18
O/PPW	20.3	-.01	+.48
PPW	1.7	-.25	+.23
O/R/IPTR	6.6	+.38	+.17
O/R/IPTR/PPW	4.3	-.18	+.26
O/R/EVGL	1.4	-.04	+.23
O/R/EVGL/PPW	3.0	-.06	+.30
O/EVGL/PPW	0.6	-.37	-.73
O/R	0.4	-.48	+.15
WH	0.2	-.47	-.51

[a]Habitat types include various combinations of the following: R - Rock. O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea triloba, EVGL - Evolvulus glaber, and WH - Water Hole.

Table 6.15. Percent of observations of feeding tortoises on Pinzón in 1982, in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	APRIL/MAY			DECEMBER		
	%USE	E_iVT	E_iSA	%USE	E_iVT	E_iSA
DWH/WH	9.8	-.31	+.70	17.9	-.02	+.82
PR/CR/R	0.8	-.90	-.95	3.5	-.62	-.80
PR/CR	8.0	-.19	+.46	11.9	0	+.60
PR/R	0.8	-.71	-.94	8.9	+.31	-.48
PR	5.3	-.36	+.14	10.9	-.01	+.46
CR/R	0	-1.0	-1.0	2.3	-.27	-.34
CR	4.5	-.03	+.79	4.9	+.01	+.81
OP/PR/CR	26.5	+.48	+.47	8.2	-.06	-.08
OP/PR	11.4	+.47	+.14	7.8	+.31	-.05
OP/CR	15.9	+.36	+.94	5.6	-.15	+.83
OPUNTIA	8.3	+.42	-.01	6.4	+.31	-.14
MA/R	7.2	+.26	+.95	3.1	-.16	+.89
OPEN	1.5	0	+.10	5.1	+.55	+.61
O/R	0	-1.0	-1.0	3.5	+.94	+.94

[a]Habitat types include various combinations of the following: DWH/WH - Dry Water Hole/Water Hole, PR - Prosopis, CR - Croton, OP - Opuntia, MA - Maytenus, R - Rock, and O - Open.

cating preference, only in December 1982, when availability was based on vegetation transects in which that habitat type was under-represented. Open/Rock areas were only used in December 1982. However, because the habitat type was never recorded for either vegetation transects or on the habitat type map, any activity in that habitat would result in a high index value. Open/Rock areas did support an increase in herbaceous vegetation in December 1982, which could explain the minimal use. Maytenus/Rock areas had positive preference indices in both seasons. However, in April and May, only 4 observations, or 3% of the total, were completely in Maytenus/Rock, while the remaining 4.2% recorded for Maytenus/Rock resulted from 11 observations of tortoises feeding on the edge between Maytenus/Rock and other more preferred habitats. In December, 5 observations, or 2% of the total, were completely in Maytenus/Rock, while the remaining 1.1% recorded for Maytenus/Rock resulted from 4 observations of tortoises feeding on the edge between Maytenus/Rock and other more preferred habitats. Also in December, available biomass of Maytenus had decreased, and many of the plants were covered by Commelina diffusa, a highly preferred food species.

Tortoises on Pinzón preferred the less rocky areas for feeding, concentrating in habitats containing Opuntia cactus during the hot-dry period of 1982, when little other forage was available. These areas were also used in December, but less often, resulting in slightly negative preference indi-

ces in some cases. Dry Water Holes were another important habitat type for feeding. The negative preference indices, based on availability measurements from vegetation transects, are due to the extreme over-representation of Water Holes in the transect area. Vegetation transects ran straight through the central large Water Hole. On the whole, Dry Water Holes were highly preferred. Open areas, and less rocky areas dominated by Prosopis and/or Croton, were also generally preferred. Negative index values for these habitat types were either very close to zero, or resulted from higher concentrations of these habitat types in the region of vegetation transects.

Habitat Preferences for Feeding in Relation to Habitat Characteristics

Habitat preferences for feeding at La Caseta and El Chato were most closely correlated with the occurrence of preferred-significant food items. Habitat preference indices for feeding were tested relative to habitat characteristics by stepwise regression. Characteristics of habitats were determined from the results of vegetation transects and included species richness (S_{ht}), species diversity (H'_{ht}), available biomass (dry weight) of all food items, of significant food items, of preferred-significant food items, and of forbs, grasses and sedges, shrubs, and fruit, the percent of ground covered by available food, by water, and by rock, and lastly, the percent of the total available food that included significant food items only, and that including

preferred-significant food items only. The 11 major habitat types that were consistently in the vegetation transects were included in the analyses.

Percent of the total available food that was preferred-significant (%SIGPLUS) was directly related to habitat preferences for feeding at La Caseta and El Chato, and was the primary significant variable in most seasons (Table 6.16, Figs. 6.7, 6.8). This factor alone explained between 15 to 71% of the variance in preference indices, depending on season and study area. Only when food became extremely abundant at the end of the garúa season 1982, at La Caseta, and continuing on into El Niño at both study areas, did the total abundance of preferred-significant foods (SIGPLUS) become more significant than %SIGPLUS in relation to habitat preferences (Table 6.16, Figs. 6.9, 6.10). Due to the cluster of habitats with low levels of SIGPLUS (Fig. 6.9, 6.10), Spearman's rank correlations (r_s) were also run for these data. In all cases there was a significant positive rank correlation between habitat preference and SIGPLUS (La Caseta: E_iVT, garúa 1982 - $r_s = 0.73$, df = 47, $P < .0001$; E_iSA, garúa 1982 - $r_s = 0.74$, df = 47, $P < .0001$; E_iVT, El Niño - $r_s = 0.56$, df = 18, $P < .01$; E_iSA, El Niño - $r_s = 0.62$, df = 18, $P < .004$; El Chato: E_iVT, El Niño - $r_s = 0.80$, df = 18, $P < .0001$; E_iSA, El Niño - $r_s = 0.76$, df = 18, $P < .0001$). At La Caseta in garúa 1982, %SIGPLUS was the second most significant variable, and in the case of E_iVT, %SIGPLUS became the dominant variable when SIGPLUS was later removed.

Table 6.16. Primary variables explaining habitat preferences for feeding at La Caseta and El Chato, based on stepwise regressions with preference index values $(E_i)^a$ versus the following habitat characteristics: percent cover (arc sine square root) by rock, by water, and by available food, species richness, species diversity, total available biomass (g/m^2) of all foods, of significant foods, of preferred-significant foods (SIGPLUS), of forbs, grasses and sedges, shrubs, and fruit, and the percent of total available food (arc sine square root) including significant foods, and that including only preferred-significant foods (%SIGPLUS). Results list statistics for models with the single most significant variable only, at $P < .05$*, .01**, .001***, .0001****. All relationships shown are positive.

STUDY AREA	SEASON	E_i [a]	VARIABLE	F	df	R^2	%OMIT[b]
CASETA	All	VT	%SIGPLUS	79.13	1,136	0.37****	
		SA	%SIGPLUS	98.40	1,136	0.42****	
	Dec81	VT	%SIGPLUS	12.88	1,9	0.59**	7.21
		SA	%SIGPLUS	22.47	1,9	0.71***	7.21
	HotWet82	VT	%SIGPLUS	31.86	1,29	0.52****	7.12
		SA	%SIGPLUS	30.69	1,29	0.51****	7.12
	HotDry82	VT	%SIGPLUS	4.38	1,25	0.15*	10.44
		SA	%SIGPLUS	9.16	1,25	0.27**	10.44
	Garúa82	VT	SIGPLUS	44.96	1,47	0.49****	6.75
		SA	SIGPLUS	47.09	1,47	0.50****	6.75
	El Niño	VT	SIGPLUS	9.47	1,18	0.34**	18.18
		SA	SIGPLUS	9.94	1,18	0.36**	18.18
CHATO	All	VT	%SIGPLUS	99.64	1,136	0.42****	
		SA	%SIGPLUS	66.95	1,136	0.33****	
	Dec81	VT	%SIGPLUS	9.36	1,9	0.51**	9.91
		SA	%SIGPLUS	11.71	1,9	0.56**	9.91
	HotWet82	VT	%SIGPLUS	31.34	1,29	0.52****	14.75
		SA	%SIGPLUS	15.89	1,29	0.35***	14.75
	HotDry82	VT	%SIGPLUS	12.85	1,25	0.34***	3.73
		SA	%SIGPLUS	8.79	1,25	0.26**	3.73

Table 6.16 continued.

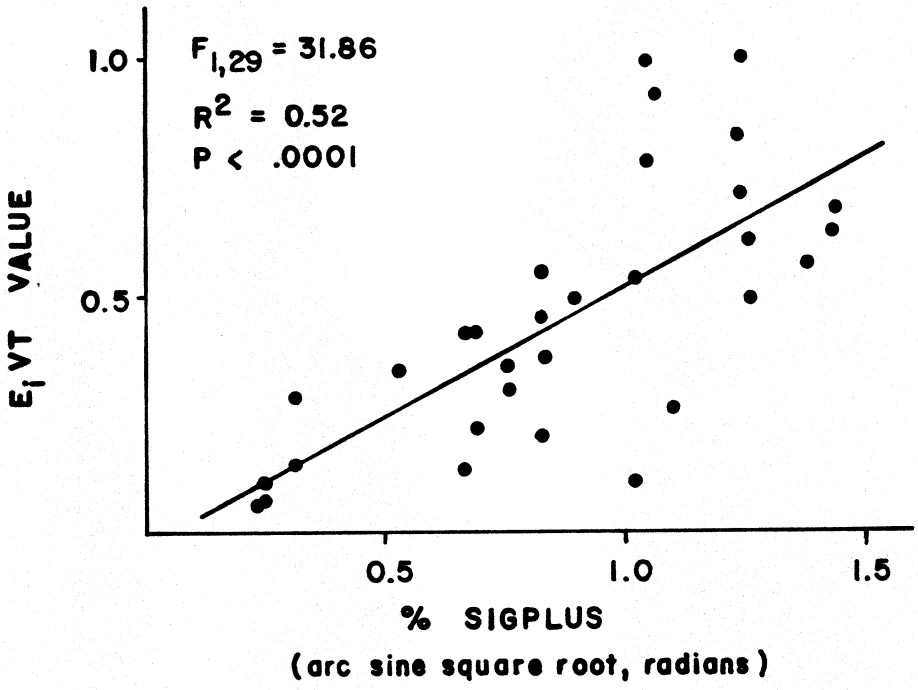
STUDY AREA	SEASON	E_i[a]	VARIABLE	F	df	R^2	%OMIT[b]
CHATO	Garúa82	VT	%SIGPLUS	45.79	1,47	0.49****	4.31
		SA	%SIGPLUS	26.63	1,47	0.36****	4.31
	El Niño	VT	SIGPLUS	12.17	1,18	0.40**	11.98
		SA	SIGPLUS	14.45	1,18	0.44***	11.98

[a]Index of habitat preference based on habitat availability in key tortoise areas (VT) or on habitat availability in the total study area (SA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]Percent of tortoise observations omitted from the analysis because the observations occurred in habitats for which there were no measurements of environmental characteristics.

Fig. 6.7. Habitat preferences of tortoises for feeding at La Caseta in the hot-wet season 1982, in relation to the percent of the total available food including preferred-significant food items only (%SIGPLUS). Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month. Percent SIGPLUS ranged from 5.3 to 98.1%.

LA CASETA — HOT-WET 1982



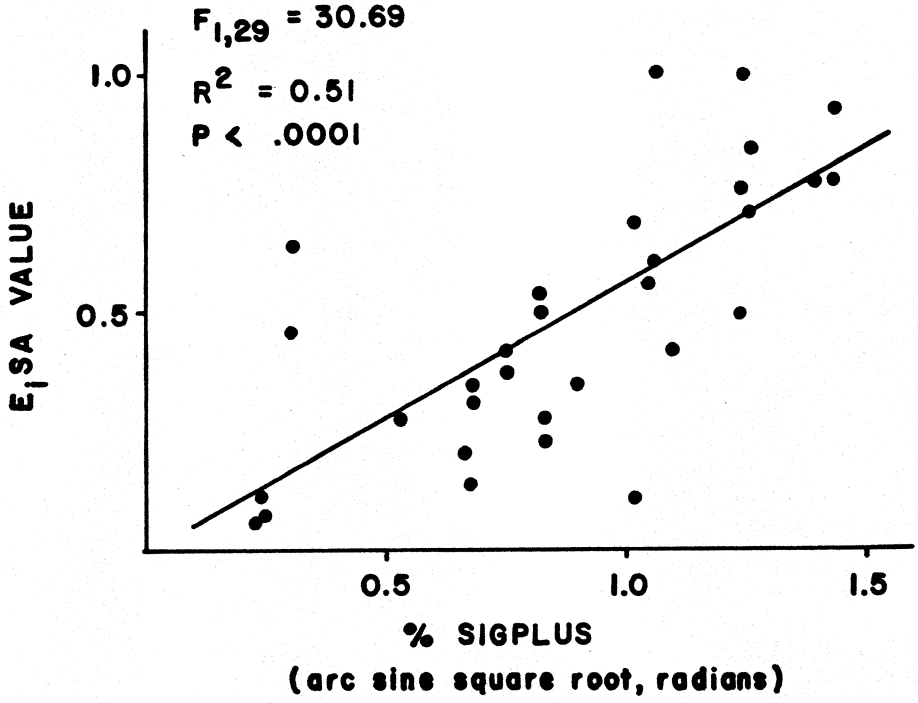
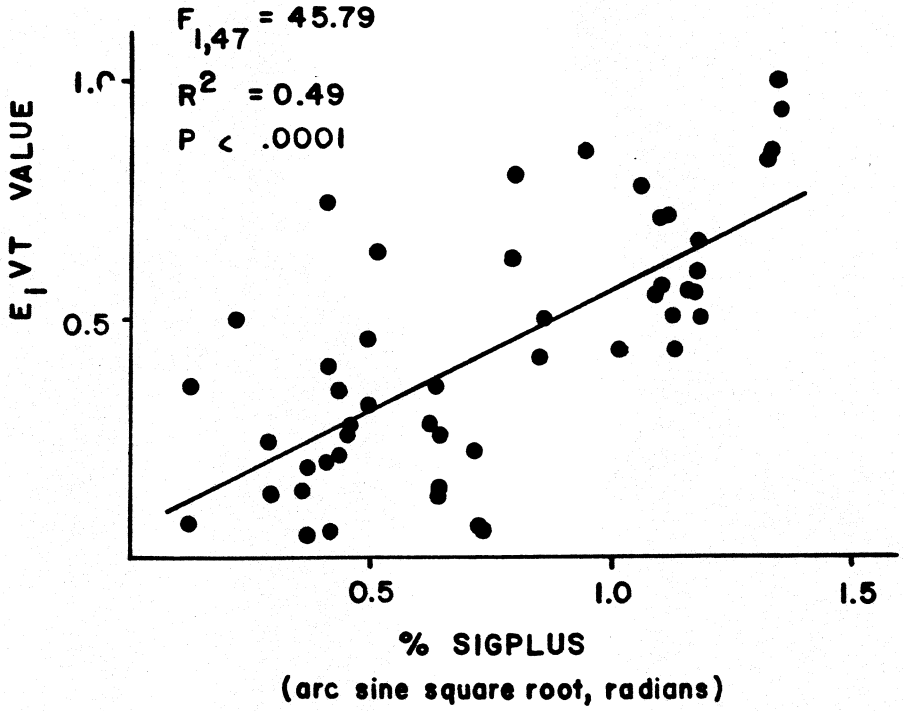


Fig. 6.8. Habitat preferences of tortoises for feeding at El Chato in garúa season 1982, in relation to the percent of the total available food including preferred-significant food items only (%SIGPLUS). Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month. Percent SIGPLUS ranged from 1.5 to 95.7%.

EL CHATO - GARÚA 1982



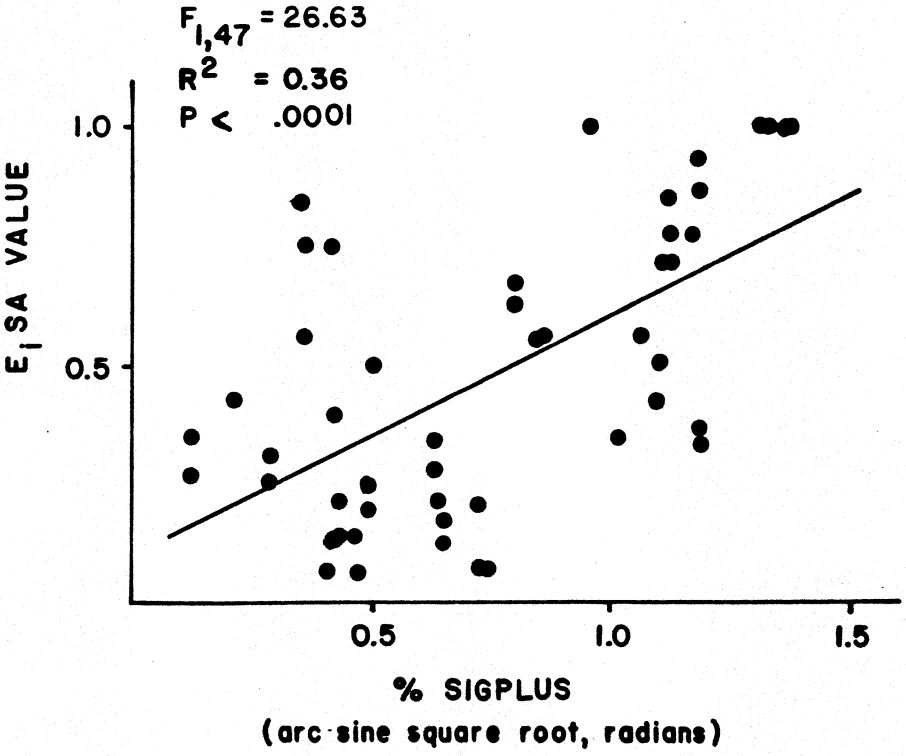
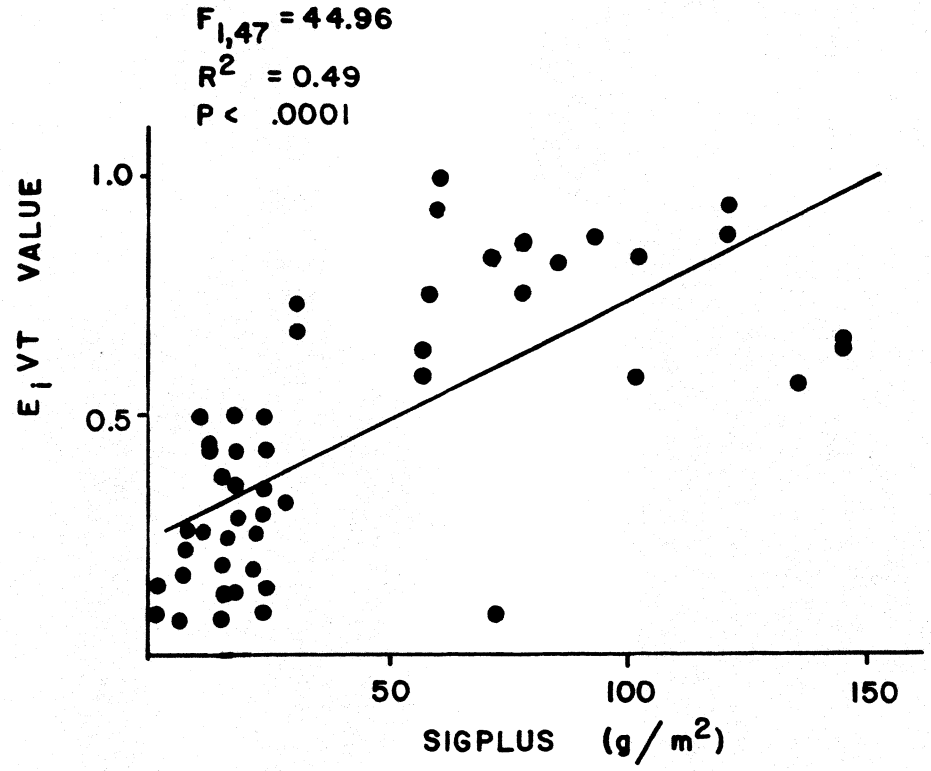


Fig. 6.9. Habitat preferences of tortoises for feeding at La Caseta in garúa season 1982, in relation to the total available biomass of preferred-significant foods (SIGPLUS). Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month.

LA CASETA - GARÚA 1982



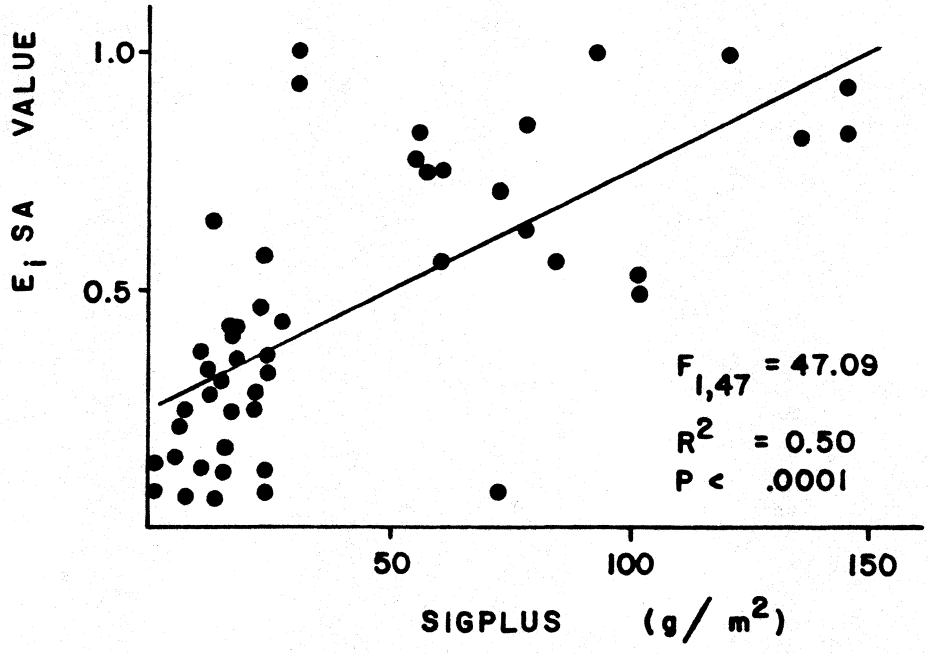
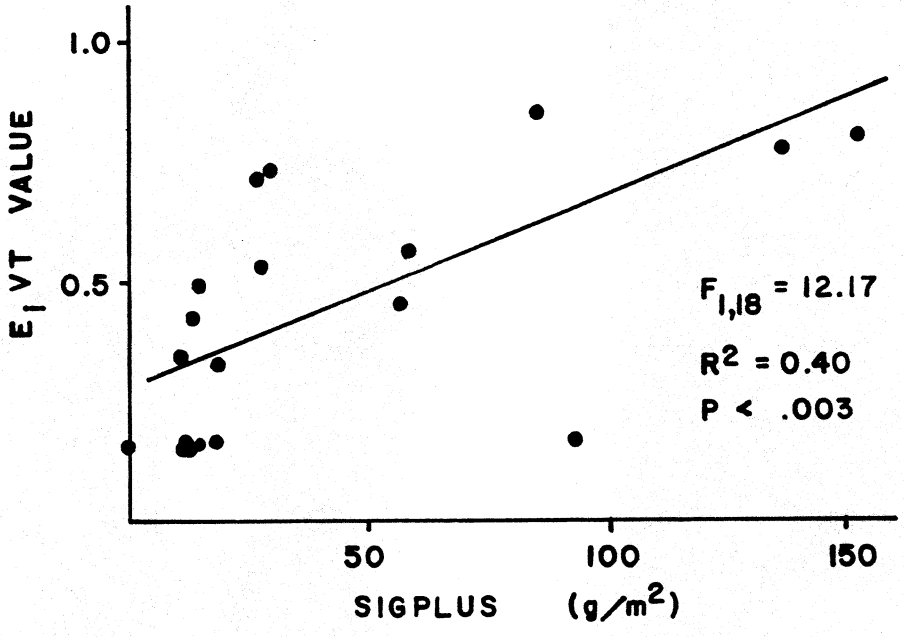
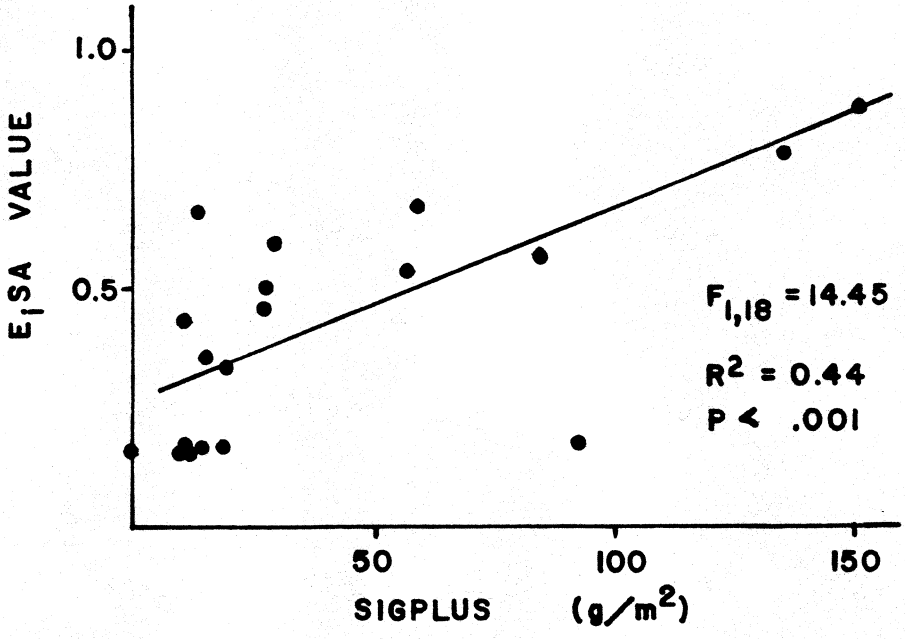


Fig. 6.10. Habitat preferences of tortoises for feeding at El Chato at the onset of El Niño, in relation to the total available biomass of preferred-significant foods (SIGPLUS). Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month.

EL CHATO — EL NIÑO





These results suggest that under conditions of low to moderate levels of food availability, tortoises prefer habitats where the search for preferred species among all available species will be relatively easy; whereas, when there is an overabundance of food, time spent searching within a habitat becomes less important. Search time could either actually decrease due to the large size and apparency of all species, or it may simply become less important because tortoises have much more food than they can eat.

Additional characteristics of habitats related to habitat preferences for feeding were not consistently significant (Table 6.17, 6.18). However, results were similar for the two study areas. In addition to %SIGPLUS, only total forbs, the total available food, and the percent of ground covered by available food were always positively related to habitat preferences when significant. Of these, only %SIGPLUS and total available forbs were important in several seasons. The only season in which available forbs explained greater than 10% of the variance in habitat preference indices was garûa 1982, when consumption of forbs was highest. When included in the final model, SIGPLUS was positively related to habitat preference except at La Caseta in December 1981, and at El Chato during garûa 1982. Reasons for the negative relationships are unknown.

Percent cover by rock, relatively high only in Dry Water Holes/Water Holes, was positively related to habitat preferences during both garûa seasons at La Caseta when tortoises

Table 6.17. Significant variables explaining habitat preferences for feeding at La Caseta, based on stepwise regressions with preference index values (E_i)[a] versus the following habitat characteristics: percent cover[b] by rock (%ROCK), by water (%WATER), and by available food (%COVER-FOOD), species richness, species diversity, total available biomass (g/m^2) of all foods, of significant foods (SIGFOOD), of preferred-significant foods (SIGPLUS), of forbs (FORB), grasses and sedges, shrubs (SHRUB), and fruit (FRUIT), and the percent of the total available food[b] including significant foods only, and that including only preferred-significant foods (%SIGPLUS). Results list statistics for the model with the most variables that were significant. Percent variance explained is indicated beneath each variable, along with its correlation coefficient with the preference index value in parentheses. Partial correlations are used when more than one variable was significant. Significance levels at P < .05*, .01**, .001***, .0001****. Significance of correlations are not noted beyond .01**.

	MODEL				HABITAT CHARACTERISTICS								
SEASON	E_i[a]	F	df	R^2	%SIG-PLUS[b]	%COVER-FOOD[b]	%WATER[b]	%ROCK[b]	SIG-FOOD	SIG-PLUS	FORB	SHRUB	FRUIT
Dec81	E_iVT	26.10	4,6	0.95***	58.86*** (+.95**)	8.31** (+.85*)		8.74* (+.78*)		18.65** (-.91**)			
	E_iSA	33.26	3,7	0.93***	71.40**** (+.96**)	12.29** (+.81**)				9.75** (-.87**)			
HotWet82	E_iVT	16.94	3,27	0.65****	52.35**** (+.66**)						7.46** (+.50**)		5.50* (+.37*)
	E_iSA	21.99	3,27	0.71****	51.41**** (+.80**)	4.43* NS						15.12** (+.48**)	
HotDry82	E_iVT	4.38	1,25	0.15*	14.91* (+.39*)								
	E_iSA	9.16	1,25	0.27**	26.82** (+.52**)								
Garúa82	E_iVT	24.82	4,44	0.69****	48.33**** (+.76**)		3.69* (-.33*)	3.15** (+.42**)	14.13**** (+.57**)				
	E_iSA	30.06	2,46	0.57****	6.60** (+.36*)					50.04** (+.40**)			

Table 6.17 continued.

	MODEL				HABITAT CHARACTERISTICS								
SEASON	E_i[a]	F	df	R^2	%SIG-PLUS[b]	%COVER-FOOD[b]	%WATER[b]	%ROCK[b]	SIG-FOOD	SIG-PLUS	FORB	SHRUB	FRUIT
El Niño	E_iVT	8.92	2,17	0.51**			16.73* (-.50*)			34.46** (+.57*)			
	E_iSA	8.67	2,17	0.50**			14.94* (-.48*)			35.57** (+.57*)			

[a]Index of habitat preference based on habitat availability in key tortoise areas (E_iVT) or on habitat availability in the total study area (E_iSA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]Percent data transformed to its arc sine square root, in radians.

Table 6.18. Significant variables explaining habitat preferences for feeding at El Chato, based on stepwise regressions with preference index values (E_i)[a] versus the following habitat characteristics: percent cover[b] by rock (%ROCK), by water, and by available food (%COVER-FOOD), species richness (S_{ht}), species diversity (H'_{ht}), total available biomass (g/m^2) of all foods, of significant foods (SIGFOOD), of preferred-significant foods (SIGPLUS), of forbs (FORB), grasses and sedges, shrubs (SHRUB), and fruit (FRUIT), and the percent of the total available food[b] including significant foods only (%SIGFOOD), and that including only preferred-significant foods (%SIGPLUS). Results list statistics for the model with the most variables that were significant. Percent variance explained is indicated beneath each variable, along with its correlation coefficient with the preference index value in parentheses. Partial correlations are used when more than one variable was significant. Significance levels at P < .05*, .01**, .001***, .0001****. Significance of correlations are not noted beyond .01**.

	MODEL				HABITAT CHARACTERISTICS										
SEASON	E_i[a]	F	df	R^2	%SIG-FOOD[b]	%SIG-PLUS[b]	%COVER-FOOD[b]	%ROCK[b]	SIG-FOOD	SIG-PLUS	FORB	SHRUB	FRUIT	S_{ht}	H'_{ht}
Dec81	E_iVT	15.60	3,7	0.87**			27.30*** (+.89**)	13.19* (+.71*)				46.51** (-.79*)			
	E_iSA	18.44	4,6	0.92**		56.54*** (+.95**)			8.50* (+.73**)				14.09** (-.86**)	13.34* (-.79**)	
HotWet82	E_iVT	17.89	4,26	0.73****		51.94**** (+.73**)		6.35* (-.44*)			9.50** (+.57**)		5.57*** (+.58**)		
	E_iSA	11.54	2,28	0.45***		35.35*** (+.54**)					9.84* (+.39*)				
HotDry82	E_iVT	9.97	2,24	0.45***	11.43* (-.42*)	33.94*** (+.64**)									
	E_iSA	8.80	1,25	0.26**		26.02** (+.51**)									
Garúa82	E_iVT	38.30	5,43	0.82****		49.35**** (+.76**)				2.01* (-.31*)	26.25**** (+.72**)			1.48* (+.32*)	2.57** (-.43**)
	E_iSA	30.42	5,43	0.78****		36.16**** (+.77**)					3.82** (+.38*)	6.66*** (+.53**)		7.70** (+.46**)	23.62**** (-.63**)

Table 6.18 continued.

	MODEL				HABITAT CHARACTERISTICS										
SEASON	E_i[a]	F	df	R^2	%SIG-FOOD[b]	%SIG-PLUS[b]	%COVER-FOOD[b]	%ROCK[b]	SIG-FOOD	SIG-PLUS	FORB	SHRUB	FRUIT	S_{ht}	H'_{ht}
El Niño	E_iVT	12.17	1,18	0.40**						40.34** (+.64**)					
	E_iSA	14.44	1,18	0.44***						44.52*** (+.68**)					

[a]Index of habitat preference based on habitat availability in key tortoise areas (E_iVT) or on habitat availability in the total study area (E_iSA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]Percent data transformed to its arc sine square root, in radians.

were often concentrated in those habitats. The reason for the negative relationship in the hot-wet season at El Chato is unknown. Percent cover by water, occurring to any great extent only at the end of 1982, and during El Niño, was negatively related to habitat preferences for feeding, presumably because it covered and eventually killed much of the preferred food previously available.

The relationship between habitat preferences for feeding and diversity indices at El Chato is not understood. Whichever index entered the equation first was negatively related to habitat preferences. If the remaining index entered later, it was positively related to habitat preferences.

Overall, individual habitat characteristics other than preferred-significant foods (% or total dry weight) were not of major importance in relation to habitat preferences of tortoises at La Caseta and El Chato when feeding.

Habitat preferences for feeding at the Santa Cruz Nesting Zone were mainly correlated with food availability (Table 6.19). For analysis of habitat preferences at SCNZ, habitat characteristics included in the stepwise regressions were available biomass (dry weight) of all food items, of significant food items, of preferred-significant food items, of forbs, and of shrubs, percent of ground covered by food items and by rock, and the percent of the total available food that included significant food items only, and that including preferred-significant food items only. Percent

Table 6.19. Significant variables explaining habitat preferences for feeding at the Santa Cruz Nesting Zone during El Niño 1983. Results are based on stepwise regressions with preference index value (E_i)[a] versus the following habitat characteristics: percent cover[b] by rock (%ROCK), and by available food (%COVER-FOOD), total available biomass (g/m^2) of all foods, of significant foods (SIGFOOD), of preferred-significant foods, of forbs (FORB), and of shrubs (SHRUB), and the percent of the total available food[b] including significant foods only (%SIGFOOD), and that including only preferred-significant foods (%SIGPLUS). Results list statistics for the model with the most variables that were significant. Percent variance explained (%VE) and the corresponding correlation coefficient (r) with the preference index value are indicated. Partial correlations are used when more than one variable was significant. Significance levels at P < .05*, .01**, .001***, .0001****. Significance of correlations are not noted beyond .01**.

	MODEL				HABITAT CHARACTERISTICS					
MONTH	E_i[a]	F	df	R^2	1st VARIABLE	%VE	r	2nd VARIABLE	%VE	r
All	E_iVT			NS						
	E_iSA	3.84	1,16	0.19[c]	SIGFOOD	19.35[c]	+ .44			
Feb/Mar	E_iVT	6.04	1,4	0.60[c]	%SIGPLUS[b]	60.14[c]	+ .78			
	E_iSA	22.76	1,4	0.85**	%SIGPLUS[b]	85.05	+ .92**			
April	E_iVT	15.72	2,3	0.91*	%ROCK[b]	49.43**	+ .95*	SHRUB	41.86*	-.91*
	E_iSA	16.15	1,4	0.80*	%COVER-FOOD[b]	80.15	+ .90*			
July	E_iVT	167.58	2,3	0.99***	SIGFOOD	86.10**	+ .98**	FORB	13.02**	-.97**
	E_iSA	691.07	2,3	1.00****	SIGFOOD	90.98****	+1.00**	%SIGFOOD[b]	8.81**	+.99**

[a]Index of habitat preference based on habitat availability in key tortoise areas (E_iVT) or on habitat availability in the total study area (E_iSA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]Percent data transformed to its arc sine square root, in radians.

[c]P < .07.

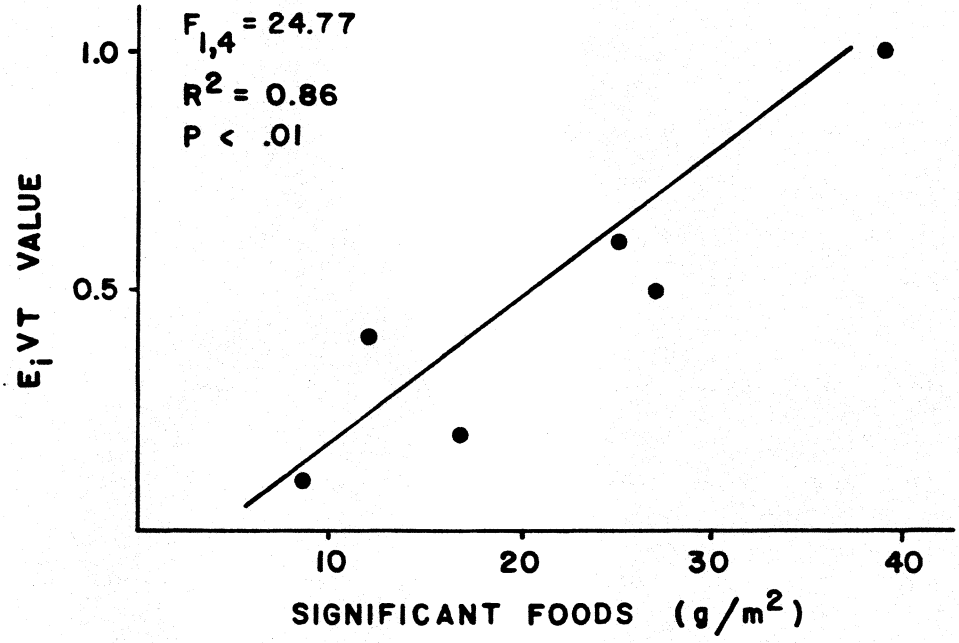
cover by water was omitted because it was always less than 1%. Food type totals, other than forbs and shrubs, were insignificant and were omitted. Diversity indices, which were too dependent on the number of quadrats per habitat type, were also omitted. Only the six major habitat types, R/PPW, O/R/PPW, O/PPW, O/R/IPTR, O/R/IPTR/PPW, and O/R/EVGL/PPW, were included in the analyses.

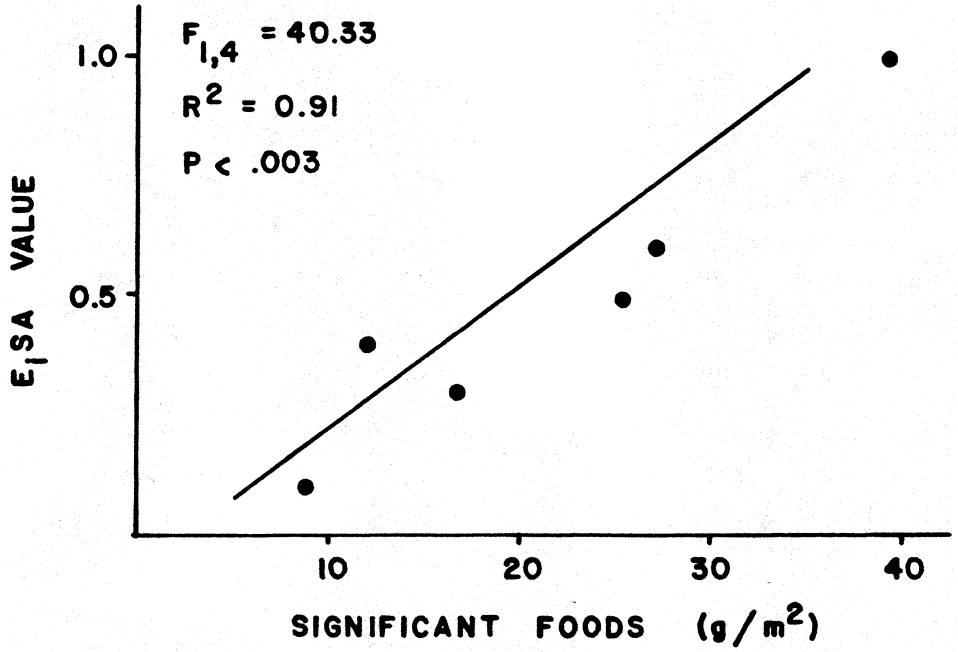
Total biomass of available significant food items was the most significant ($P < .07$) habitat characteristic correlated to habitat preferences for feeding for the season, and it was the primary variable significant in July (Table 6.19, Fig. 6.11). El Niño was a time of food abundance in all regions of the tortoise range, and the importance of total abundance of significant foods at SCNZ corresponds to that of the abundance of preferred-significant foods in the highlands of Santa Cruz. Significant foods at SCNZ included 16 species, 6 of which had average negative preference indices that eliminated them from the total of preferred-significant foods. However, preference indices for at least 3 of the eliminated species vacillated between positive and negative values and the same species were all preferred in other study areas. If they were also actually preferred at SCNZ, the total biomass of significant food items may more closely represent the preferred forage of tortoises than does the total biomass of preferred-significant foods from which the 3 species were eliminated.

Fig. 6.11. Habitat preferences of tortoises for feeding at the Santa Cruz Nesting Zone in July 1983, in relation to the total available biomass of significant foods. Preference index values, where $E_i VT$ was based on habitat availability in the key tortoise areas and $E_i SA$ was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month.

SANTA CRUZ NESTING ZONE

JULY 1983





Percent of the total available food that was preferred-significant was the only habitat factor correlated with habitat preferences for feeding in February and March (Fig. 6.12). It was positively related to habitat preference, as were percent cover by rock and by available food in April. The positive relationship between rock and habitat preference was driven primarily by tortoise use of O/R/IPTR and O/R/IPTR/PPW in April, when Ipomoea triloba constituted 29.4% of the diet. Tortoises avoided habitats with an abundance of shrubs in April (Table 6.19). A similar relationship between habitat preference and abundance of forbs is not understood.

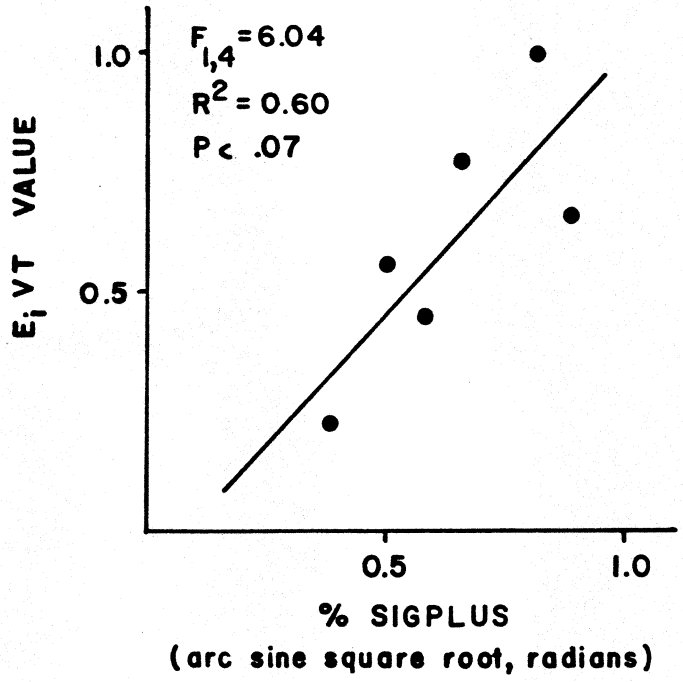
Tortoises feeding at SCNZ during El Niño, when food was over-abundant, preferentially used those habitats that had more available biomass of food items that were significant in their diet and potentially preferred. This pattern of preference was similar to that exhibited by tortoises at La Caseta and El Chato at the onset of El Niño.

Habitat preferences of tortoises feeding on Pinzón appear to be closely correlated with avoidance of certain factors as well as with attraction to preferred characteristics in the habitats (Table 6.20). Stepwise regression analyses of habitat preferences on Pinzón included the following habitat characteristics: total biomass of all available food items (TAF1), of significant food items, of preferred-significant food items, of shrubs, of cactus, and of forbs, grasses, and sedges combined; percent cover by

Fig. 6.12. Habitat preferences of tortoises for feeding at the Santa Cruz Nesting Zone in February/March 1983, in relation to the percent of the total available food including preferred-significant food items only (%SIGPLUS). Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month. Percent SIGPLUS ranged from 6.7 to 52.6%.

SANTA CRUZ NESTING ZONE

FEBRUARY - MARCH 1983



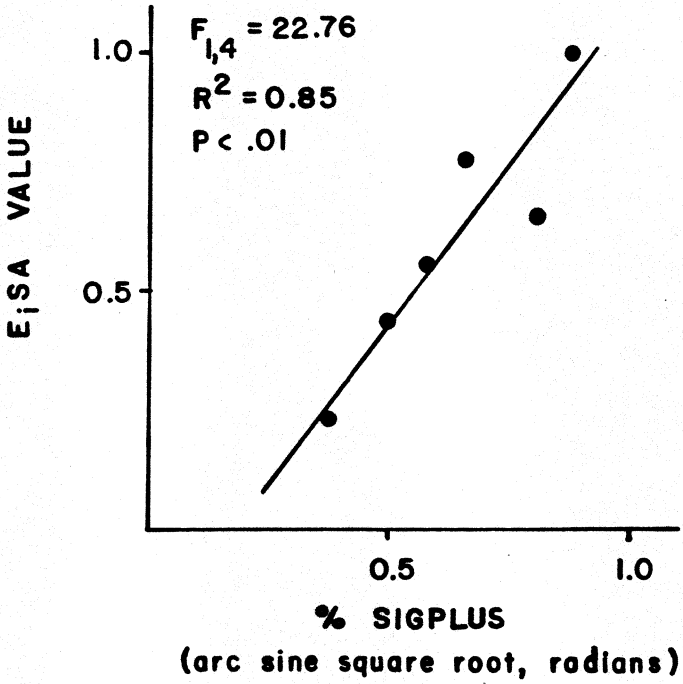


Table 6.20. Significant variables explaining habitat preferences for feeding on Pinzón in 1982. Results are based on stepwise regressions with preference index values (E_i)[a] versus the following habitat characteristics: percent cover[b] by rock (%ROCK), and by available food, total available biomass (g/m^2) of all foods (FOOD), of significant foods (SIGFOOD), of preferred-significant foods (SIGPLUS), of shrubs, forbs, grasses and sedges combined (FORBGRASS), and of Opuntia (CACTUS), and the percent of the total available food[b] including significant foods only, and that including preferred-significant foods only. The total available food (g/m^2) when the three most abundant, but avoided species, were eliminated, and the percent of that total[b] that included preferred-significant foods only (%SIGPLUS-II) were also included. Results list statistics for the model with the most variables that were significant. Percent variance explained (%VE) and the corresponding correlation coefficient (r) with the preference index value, in parentheses, are indicated. Partial correlations are used when more than one variable was significant. Significance levels at P < .05*, .01**, .001***, .0001****. Significance of correlations are not noted beyond .01**.

	MODEL				HABITAT CHARACTERISTICS					
MONTH	E_i[a]	F	df	R^2	1st VARIABLE	%VE (r)	2nd VARIABLE	%VE (r)	3rd VARIABLE	%VE (r)
All	E_iVT	5.93	1,24	0.20*	%ROCK[b]	19.81* (-.44*)				
	E_iSA	10.90	3,22	0.60****	SIGFOOD	14.04**** (-.73**)	FOOD	31.65*** (+.69**)	CACTUS	14.10** (+.51*)
Apr/May	E_iVT	3.23	1,11	0.23[c]	CACTUS	22.68[c] (+.48)				
	E_iSA	11.13	3,8	0.81**	SIGFOOD	30.63* (-.69*)	%SIGPLUS-II[b]	21.30** (+.85**)	%ROCK[b]	28.75** (-.77**)
Dec	E_iVT	4.07	2,10	0.45*	FORBGRASS	0.26* (NS)	SIGPLUS	44.64* (-.67*)		
	E_iSA			NS						

[a]Index of habitat preference based on habitat availability in key tortoise areas (E_iVT) or on habitat availability in the total study area (E_iSA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]Percent data transformed to its arc sine square root, in radians.

[c]P < .10.

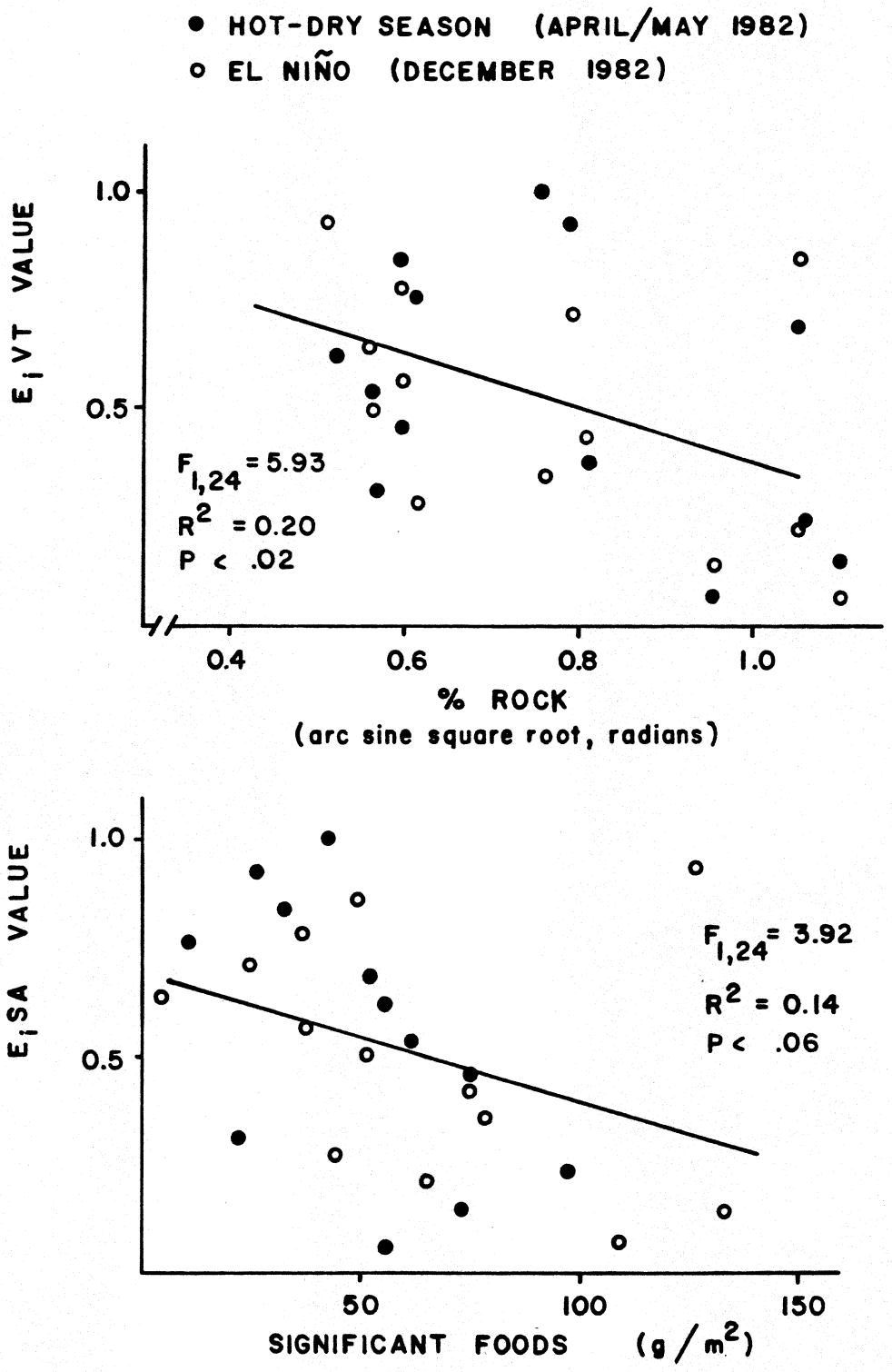
rock, and by available food; and the percent of TAF1 that included significant food items only, and that including preferred-significant food items only. Also included were the total biomass of available food items when the three most abundant but avoided species, Alternanthera filifolia, Prosopis juliflora, and Maytenus octogona, were omitted (TAF2), and the percent of TAF2 that was preferred-significant.

Tortoises avoided the more rocky habitats, and those with a high biomass of significant food items (Table 6.20, Fig. 6.13). Alternanthera filifolia and Prosopis juliflora, both avoided species, constituted the largest proportion of significant food items in nearly all habitat types. It is likely that tortoises avoided habitats in which these species were exceptionally abundant.

Tortoises concentrated in areas with preferred foods, as did the tortoises on Santa Cruz. They fed in Opuntia areas 62.1% of the time during the hot-dry season when Opuntia constituted the majority of the diet and little other food was available. Total available biomass of Opuntia was positively related to habitat preference. Tortoises also preferred habitats in which %TAF2 that was preferred-significant was higher, and those with greater amounts of forbs and grasses. The positive partial correlation between total available food and habitat preference when both seasons are combined, and the negative partial correlation between SIGPLUS and habitat preference are not understood. Neither of these variables was significant when alone.

Fig. 6.13. Habitat preferences of tortoises for feeding on Pinzón in 1982, in relation to the percent cover by rock (%ROCK), and to the total available biomass of significant foods. Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month. Percent rock ranged from 25.1 to 79.9%.

PINZÓN


● HOT-DRY SEASON (APRIL/MAY 1982)
○ EL NIÑO (DECEMBER 1982)
E_iVT VALUE
1.0
0.5
F_1,24 = 5.93
R^2 = 0.20
P < .02
0.4
0.6
0.8
1.0
% ROCK
(arc sine square root, radians)
E_iSA VALUE
1.0
0.5
F_1,24 = 3.92
R^2 = 0.14
P < .06
50
100
150
SIGNIFICANT FOODS (g / m^2)

Overall, tortoises on Pinzón preferred to feed in habitats where there was more soil and less rock. They also fed preferentially in areas with more preferred-significant foods, as did the tortoises on Santa Cruz.

Habitat Preferences - Resting

Percent use of habitat types and the corresponding habitat preferences of tortoises for resting at La Caseta and El Chato changed seasonally (Tables 6.21, 6.22). In both study areas, major changes in habitat use were primarily due to seasonal changes in ambient temperature. During the cool garúa seasons, tortoises increased their use of open areas where they could receive direct sunlight, while during both the hot-wet and the hot-dry periods of 1982, tortoises greatly increased their use of the habitat types that provided shade where they could escape direct sunlight (Table 6.23). During El Niño, a hot season with an unusually high level of precipitation, tortoises again increased their use of the more shaded habitat types, often resting in small water holes within the woodlands and thickets (see footnote, Table 6.23).

Significant seasonal correlations between the average indices of habitat preference for the 13 major habitat types at La Caseta with those at El Chato validate the habitat preference:avoidance patterns of tortoises when resting (Table 6.24). Lower levels of correlation for resting in relation to feeding may result from the unimportance, and therefore more random use, of micro-habitats for resting.

Table 6.21. Seasonal averages of the percent of observations of resting tortoises at La Caseta in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
PZW	%USE	28.4	38.1	66.8	36.6	31.8
	E_iVT	-.24	-.12	+.18	-.13	-.19
	E_iSA	-.33	-.21	+.08	-.23	-.28
HAW	%USE	1.2	23.6	9.1	2.2	6.2
	E_iVT	-.92	-.14	-.57	-.87	-.66
	E_iSA	-.88	+.07	-.42	-.81	-.51
CMT	%USE	0.8	11.5	9.8	4.3	2.2
	E_iVT	-.67	+.44	+.42	-.10	-.30
	E_iSA	-.89	-.14	-.19	-.57	-.74
UG	%USE	4.0	0	1.3	21.5	1.0
	E_iVT	-.22	-1.0	-.68	+.45	-.76
	E_iSA	+.57	-1.0	0	+.86	-.36
GL	%USE	3.5	0	0	0.6	0
	E_iVT	+.56	-1.0	-1.0	-.40	-1.0
	E_iSA	+.94	-1.0	-1.0	+.07	-1.0
OF	%USE	4.7	0.3	0.6	2.5	0
	E_iVT	-.05	-.90	-.81	-.42	-1.0
	E_iSA	+.68	-.67	-.47	+.20	-1.0
DWH I/WH I	%USE	43.6	16.4	2.6	8.6	6.9
	E_iVT	+.95	+.81	+.16	+.46	+.70
	E_iSA	+.93	+.75	+.04	+.38	+.61
SCPT	%USE	3.2	0.4	1.4	13.3	11.5
	E_iVT	+.15	-.77	-.36	+.44	+.61
	E_iSA	-.13	-.85	-.54	+.26	+.40
PSRU	%USE	0	1.8	5.2	6.1	1.6
	E_iVT	-1.0	-.26	+.52	+.40	-.05
	E_iSA	-1.0	+.26	+.96	+.90	+.86
DL[b]	%USE	2.4	0	0	0	0
	E_iVT	+.85	-1.0		-1.0	-1.0
	E_iSA	+.92	-1.0		-1.0	-1.0

Table 6.21 continued.

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
DWH II/WH II	%USE	0	3.1	0.1	0.4	0.2
	E_iVT	-1.0	-.37	-.81	-.51	-.57
	E_iSA	-1.0	-.34	-.56	-.30	-.22
TRAIL	%USE	4.0	3.4	1.0	1.3	3.4
	E_iVT	+.81	+.67	+.22	+.43	+.76
	E_iSA	+.95	+.91	+.69	+.82	+.94
OTHER[c]	%USE	4.2	1.4	2.1	2.6	35.2[d]

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, and Trail.

[b]DL non-existent in HotDry82.

[c]Includes Scalesia Stand, Rhynchospora Stand, Rock Mound, Lemon, Trailside, Mora, and Water Hole.

[d]Water Hole = 34.5%.

Table 6.22. Seasonal averages of the percent of observations of resting tortoises at El Chato in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
PZW	%USE	16.7	20.3	27.0	39.6	50.4
	E_iVT	-.43	-.44	-.24	-.04	+.09
	E_iSA	-.55	-.54	-.38	-.20	-.07
HAW	%USE	0.9	23.6	21.1	1.8	6.5
	E_iVT	-.88	+.22	+.16	-.79	-.42
	E_iSA	-.88	+.21	+.15	-.80	-.43
CMT	%USE	3.5	25.7	20.8	9.1	3.5
	E_iVT	-.45	+.40	+.36	-.03	-.47
	E_iSA	-.66	+.15	+.09	-.32	-.66
UG	%USE	29.4	8.9	5.8	9.8	2.0
	E_iVT	+.36	-.39	-.50	-.21	-.75
	E_iSA	+.85	+.09	+.03	+.56	-.10
GL	%USE	9.6	0.5	0.8	0	0.8
	E_iVT	+.80	-.60	-.35	-1.0	-.42
	E_iSA	+.81	-.59	-.32	-1.0	-.26
OF	%USE	5.3	0.3	1.8	6.3	1.5
	E_iVT	-.11	-.93	-.70	-.09	-.68
	E_iSA	+.48	-.80	-.50	+.47	-.38
DWH I/WH I	%USE	18.4	3.1	7.7	14.3	5.4
	E_iVT	+.56	-.41	+.14	+.40	+.02
	E_iSA	+.79	-.14	+.51	+.70	+.44
SCPT	%USE	2.2	0.1	2.0	2.8	0
	E_iVT	-.14	-.92	-.35	-.18	-1.0
	E_iSA	+.14	-.87	-.17	+.02	-1.0
PSRU	%USE	0	2.3	7.7	7.7	0.8
	E_iVT	-1.0	-.36	+.51	+.24	-.61
	E_iSA	-1.0	+.25	+.97	+.58	-.06
DL[b]	%USE	5.3	0	0	1.8	0
	E_iVT	+.60	-1.0		-.04	-1.0
	E_iSA	+.96	-1.0		+.51	-1.0

Table 6.22 continued.

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
DWH II/WH II	%USE	0	4.4	3.1	1.0	3.9
	E_iVT	-1.0	-.02	+.54	-.23	+.69
	E_iSA	-1.0	+.25	+.91	+.09	+.95
TRAIL	%USE	4.4	9.9	1.0	1.2	6.3
	E_iVT	+.96	+.93	+.31	+.47	+.97
	E_iSA	+.96	+.93	+.31	+.47	+.97
OTHER[c]	%USE	4.3	0.9	1.2	4.6	18.9[d]

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, and Trail.

[b]DL non-existent in HotDry82.

[c]Includes Scalesia Stand, Rhynchospora Stand, Rock Mound, Lemon, Trailside, and Water Hole.

[d]Water Hole = 18.3%.

Table 6.23. Seasonal averages of the percent of observations of resting tortoises at La Caseta and El Chato in open habitats and in shaded habitats. Open, treeless habitat types include Underutilized Grasslands, Grazing Lawns, Open Forb, Dichondra Lawns, and Dry Water Holes/Water Holes (type I). Shaded habitat types include Psidium/Zanthoxylum and Hippomane Woodlands, Clerodendrum and Psychotria Thickets, and Dry Water Holes/Water Holes (type II).

	LA CASETA		EL CHATO	
SEASON	OPEN	SHADED	OPEN	SHADED
Dec81	58.2	30.4	68.0	21.1
HotWet82	16.7	78.1	12.8	76.3
HotDry82	4.5	91.0	16.1	79.7
Garúa82	33.2	49.6	32.2	59.2
El Niño	7.9	42.0[a]	10.4	65.1[a]

[a]An additional 34.5% (Caseta) and 18.3% (Chato) of observations were of tortoises in Water Holes, a habitat type that was most often associated with woodlands and thickets.

Table 6.24. Seasonal comparisons of habitat preference indices for resting (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area) at La Caseta, with those at El Chato. Results list Spearman's rank correlation coefficients (r_s) at P <.05*, .01**, .0001****.

SEASON	N	r_s (E_iVT)	r_s (E_iSA)
All	13	0.67**	0.66**
Dec81	13	0.90****	0.87****
HotWet82	12	0.63*	0.68*
HotDry82	11	0.55	0.45
Garúa82	13	0.48	0.76**
El Niño	13	0.41	0.59*

In addition, habitat selectivity for resting was significantly lower than for feeding, resulting in a relaxation of preference:avoidance patterns for resting relative to those for feeding.

Habitat characteristics measured in the vegetation transects were at times significantly correlated with habitat preferences for resting. However, the significant characteristics appeared unrelated to habitat quality for resting. This suggests that these correlations resulted from habitat choice based on other factors, and that the significant characteristics were not the cause of habitat choice. The characteristics measured had to do primarily with food availability, while resting behavior appeared to result primarily from sun:shade patterns, dominated by the presence or absence of overstory. Therefore, results of stepwise regressions were uninteresting and will not be reported.

In the Santa Cruz Nesting Zone, tortoises concentrated their resting in the three major woodland habitats, preferring areas with less rock (Table 6.25). Although more tortoises rested in R/PPW, the more open, less rocky woodlands, especially O/PPW and PPW, were preferred. The three major woodlands constituted between 87-91% of the study area, and were used for resting 90.1% of the time. This suggests that tortoises do not seek out the other less abundant habitat types for resting. The Water Hole was the only other habitat that was preferred for resting.

Table 6.25. Average percent of observations of resting tortoises at the Santa Cruz Nesting Zone during El Niño 1983, in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_i SA, based on habitat availability in the total study area). N = 3.

HABITAT TYPE[a]	%USE	E_iVT	E_iSA
R/PPW	39.7	-.01	-.27
O/R/PPW	22.4	-.17	+.06
O/PPW	28.0	+.14	+.58
PPW	2.4	+.04	+.81
O/R/IPTR	1.1	-.49	-.63
O/R/IPTR/PPW	2.8	-.19	+.74
O/R/EVGL	1.3	-.44	-.36
O/R/EVGL/PPW	0.3	-.75	-.39
O/EVGL/PPW	0.1	-.83	-.94
O/R	0.3	-.66	-.39
WH	1.5	+.85	+.71

[a]Habitat types include various combinations of the following: R - Rock, O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea triloba, EVGL - Evolvulus glaber, and WH - Water Hole.

Stepwise regressions of preference indices versus habitat characteristics revealed few significant correlations. As at La Caseta and El Chato, measurement of habitat characteristics was aimed primarily at feeding behavior and did not measure available shade. Tortoises did avoid the open areas with no trees when resting, preferring wooded areas where shade was available.

Tortoises on Pinzón rested most often in habitats with less rock (Table 6.26). In the hot-dry season when shade was at a premium, tortoises concentrated in Opuntia areas, where they spent 52.5% of their total time resting. They often rested at the base of an Opuntia tree, shifting around the trunk as the one line of shade moved around it during the day. Other areas that were preferred included Prosopis/Croton and Croton areas, both of which were habitats where Croton often grew taller than 150 cm, providing more shade than was available in most other habitats.

The Dry Water Hole was also a preferred habitat for resting. The negative value for E_iVT was due to the placement of the vegetation transects across the largest Dry Water Hole, resulting in an over-estimate of its availability. Although not offering much shade, Dry Water Holes were preferred feeding areas and tortoises may have rested there, under whatever shade was available, in connection with feeding bouts, rather than expend more energy traveling elsewhere when under the stressful conditions of the hot-dry season.

Table 6.26. Percent of observations of resting tortoises on Pinzón in 1982, in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	APRIL/MAY			DECEMBER		
	%USE	E_iVT	E_iSA	%USE	E_iVT	E_iSA
DWH/WH	10.6	-.27	+.72	12.1	-.21	+.75
PR/CR/R	2.4	-.72	-.86	1.3	-.84	-.92
PR/CR	14.3	+.10	+.66	13.2	+.06	+.63
PR/R	1.6	-.49	-.88	3.8	-.10	-.74
PR	6.9	-.24	+.27	26.8	+.41	+.74
CR/R	1.1	-.57	-.62	1.3	-.51	-.57
CR	5.3	+.05	+.82	8.6	+.29	+.89
OP/PR/CR	25.0	+.46	+.45	9.2	0	-.02
OP/PR	8.7	+.36	+.01	6.3	+.21	-.15
OP/CR	12.7	+.26	+.92	6.6	-.06	+.85
OPUNTIA	6.1	+.29	-.16	5.5	+.24	-.21
MA/R	3.1	-.16	+.89	1.8	-.41	+.82
OPEN	1.1	-.15	-.06	3.5	+.40	+.48
O/R	1.1	+.83	+.83	0	-1.0	-1.0

[a]Habitat types include various combinations of the following: DWH/WH - Dry Water Hole/Water Hole, R - Rock, O - Open, PR - Prosopis, CR - Croton, OP - Opuntia, and MA - Maytenus.

In December, tortoises preferred areas with less rock for resting (Table 6.26). Shade and the necessity of remaining in higher quality habitats for feeding were less important in December than in the hot-dry season, and resting activity was spread out among all of the preferred habitats. Overall height of the vegetation was probably less important, allowing tortoises to spend more time in Prosopis areas. All of the Opuntia areas alternated between being preferred and avoided, suggesting that use of Opuntia areas for resting was consistent with their availability during this season.

Seven of the measured habitat characteristics were thought to be of potential importance to resting behavior of tortoises on Pinzón, and only they were included in stepwise regression analyses. Abundance of rock was the only significant variable correlated with use of habitats for resting, and the two were inversely related (Table 6.27, Fig. 6.14). The stronger negative relationship between rock abundance and habitat preference at the onset of El Niño in comparison to the hot-dry season may be related to the increase in activity in December allowing more movement among habitat types and to the change in the absolute need for shade. Increased activity, cooler temperatures, and greater availability of shade in all habitats, due to the general increase in leaf production, allowed tortoises to be more selective in terms of rock:soil surfaces. Availability of shade, particularly in the hot-dry season, and lower levels

Table 6.27. Significant seasonal relationships between percent cover by rock (arc sine square root, in radians) and habitat preference indices[a] for resting on Pinzón in 1982. B value equals the slope of the regression. Results of regression models significant at P < .05*, .001***, .0001****.

SEASON	E_i[a]	F	df	R^2	B VALUE
Both	VT	26.62	1,24	0.53****	-0.98
	SA	5.26	1,24	0.18*	-0.59
HotDry	VT	5.72	1,11	0.34*	-0.76
	SA			NS	
El Niño	VT	31.15	1,11	0.74***	-1.20
	SA	3.79	1,11	0.26[b]	-0.71

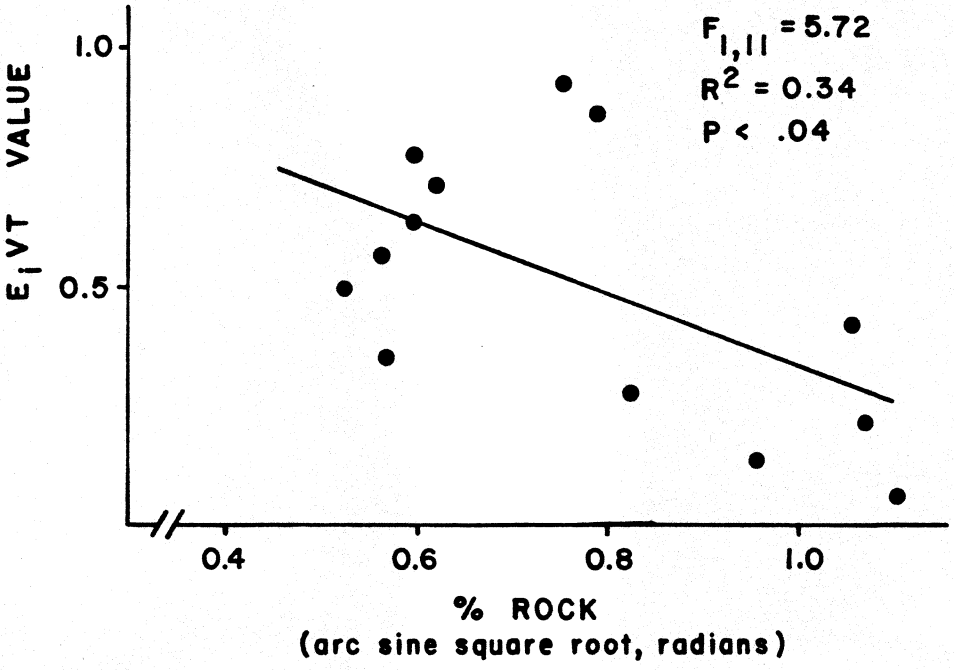
[a]Index of habitat preference based on habitat avilability in key tortoise areas (VT) or on habitat availability in the total study area (SA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]P < .08.

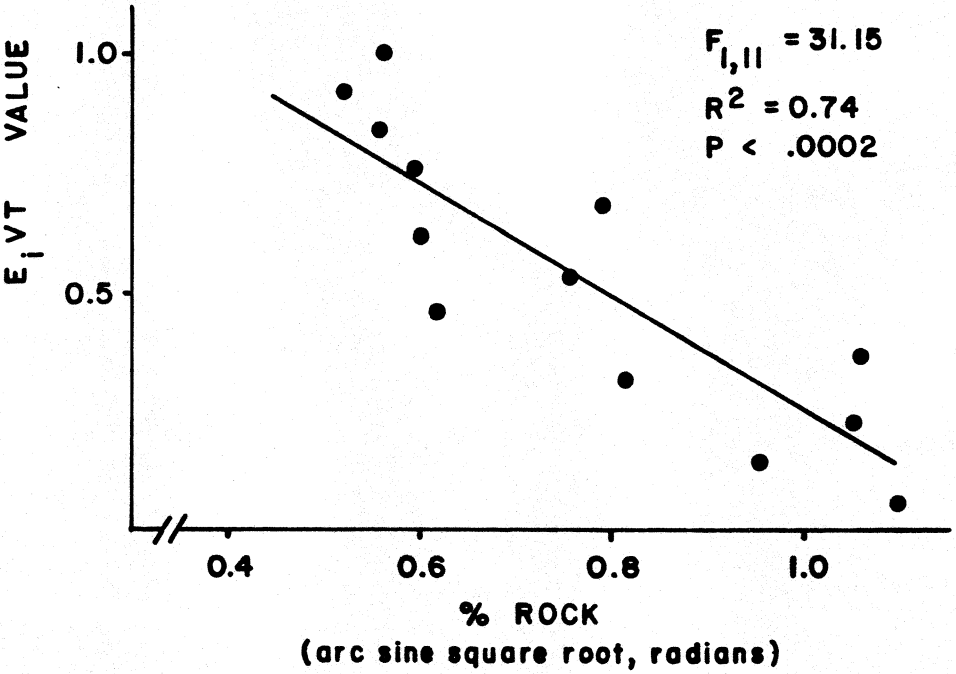
Fig. 6.14. Habitat preferences of tortoises for resting on Pinzón in 1982, in relation to the percent cover by rock (%ROCK). Preference index value, where E_iVT was based on habitat availability in the key tortoise areas, equals the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month. Percent rock ranged from 25.1 to 79.9%.

PINZÓN

HOT-DRY SEASON (APRIL/MAY 1982)



EL NIÑO (DECEMBER 1982)



of rock cover were the major factors in determining habitat preferences for resting on Pinzón.

Habitat Preferences - Traveling

Percent use of habitat types and the corresponding habitat preferences of tortoises traveling at La Caseta and El Chato changed seasonally (Tables 6.28, 6.29). The tortoise trail, little used for either feeding or resting, was the most important habitat type for traveling. Trails represented from 25-33% of the observations of traveling tortoises at La Caseta, and between 19-31% at El Chato. Although Psidium/Zanthoxylum Woodlands were also often used, they were never used at a level greater than their availability.

As with resting, changes in habitat use for traveling were due in part to seasonal changes in ambient temperatures. There was a major reduction in the use of open habitats that received direct sunlight, during the hot-dry season 1982, when conditions were most stressful for the tortoises (Table 6.30). The apparent increase in use of shaded areas (primarily Psidium/Zanthoxylum and Hippomane Woodlands) in garúa 1982, and at the onset of El Niño, reflects a change in method of recording habitat types relative to trails (see footnote c, Tables 6.28, 6.29). In October 1982, the habitat surrounding the trail was included in all trail notations to improve habitat use data for feeding. Prior to that time, surrounding habitats had been included in few of the observations. The majority of observations of trail coupled with a surrounding habitat was

Table 6.28. Seasonal averages of the percent of observations of traveling tortoises at La Caseta in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
PZW	%USE	28.9	25.3	42.8	38.3	36.2
	E_iVT	-.24	-.31	-.06	-.11	-.13
	E_iSA	-.32	-.39	-.15	-.20	-.22
HAW	%USE	10.5	14.6	6.3	11.0	11.3
	E_iVT	-.48	-.35	-.66	-.48	-.47
	E_iSA	-.29	-.15	-.52	-.30	-.29
CMT	%USE	5.3	11.2	8.9	8.5	6.5
	E_iVT	+.14	+.44	+.24	-.16	+.20
	E_iSA	-.46	-.15	-.32	-.47	-.39
UG	%USE	0	4.5	0.7	8.1	7.9
	E_iVT	-1.0	-.34	-.83	-.06	+.07
	E_iSA	-1.0	+.11	-.55	+.41	+.72
GL	%USE	0	1.3	0	1.6	1.9
	E_iVT	-1.0	-.11	-1.0	-.40	+.31
	E_iSA	-1.0	+.26	-1.0	-.23	+.89
OF	%USE	0	0.5	0.2	1.6	0
	E_iVT	-1.0	-.84	-.92	-.65	-1.0
	E_iSA	-1.0	-.57	-.70	-.35	-1.0
DWH I/WH I	%USE	23.7	10.8	6.8	7.0	4.4
	E_iVT	+.91	+.70	+.67	+.68	-.11
	E_iSA	+.88	+.62	+.58	+.59	-.15
SCPT	%USE	0	0.4	0.3	2.0	1.9
	E_iVT	-1.0	-.76	-.80	-.52	-.11
	E_iSA	-1.0	-.84	-.87	-.62	-.38
PSRU	%USE	0	1.0	1.1	2.5	1.1
	E_iVT	-1.0	-.37	-.39	+.01	-.42
	E_iSA	-1.0	+.25	+.23	+.54	-.04
DL[b]	%USE	0	0	0	0	0
	E_iVT	-1.0	-1.0		-1.0	-1.0
	E_iSA	-1.0	-1.0		-1.0	-1.0

Table 6.28 continued.

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
DWH II/WH II	%USE	0	1.3	0	1.2	0
	E_iVT	-1.0	+.04	-1.0	-.63	-1.0
	E_iSA	-1.0	+.26	-1.0	-.61	-1.0
TRAIL	%USE	31.6	28.0	30.8	17.5	16.5
	%USE[c]	31.6	28.7	31.9	25.3	32.9
	E_iVT	+.96	+.97	+.97	+.92	+.95
	E_iSA	+.99	+.99	+.99	+.98	+.99
OTHER[d]	%USE	0	1.1	2.1	0.7	12.3[e]

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, and Trail.

[b]DL non-existent in HotDry82.

[c]Real %USE of trails. Observations of tortoises on trails were sometimes recorded with the surrounding habitat type, so that %USE was divided between them. These values eliminate the surrounding habitat type from any trail observations, resulting in the true percent of observations of tortoises traveling that were on the trails.

[d]Includes Trailside, Rock Mound, River, and Water Hole.

[e]River recorded only in January, equaling 9.7% for that month.

Table 6.29. Seasonal averages of the percent of observations of traveling tortoises at El Chato in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
PZW	%USE	0	16.6	33.7	39.5	47.2
	E_iVT	-1.0	-.44	-.17	-.04	+.04
	E_iSA	-1.0	-.56	-.31	-.20	-.12
HAW	%USE	16.7	13.4	11.2	4.9	11.3
	E_iVT	+.09	-.12	-.19	-.54	-.12
	E_iSA	+.08	-.13	-.20	-.55	-.12
CMT	%USE	22.2	6.8	16.8	10.1	4.5
	E_iVT	+.41	-.23	+.15	-.13	-.51
	E_iSA	+.14	-.47	-.11	-.35	-.65
UG	%USE	27.8	6.9	4.1	3.5	1.2
	E_iVT	+.33	-.39	-.61	-.65	-.85
	E_iSA	+.84	+.37	-.10	-.07	-.50
GL	%USE	0	0.8	0	0	0
	E_iVT	-1.0	-.53	-1.0	-1.0	-1.0
	E_iSA	-1.0	-.52	-1.0	-1.0	-1.0
OF	%USE	0	2.9	1.0	6.6	2.4
	E_iVT	-1.0	-.47	-.78	-.03	-.58
	E_iSA	-1.0	-.07	-.58	+.53	-.28
DWH I/WH I	%USE	5.6	14.5	2.9	14.0	8.1
	E_iVT	+.04	+.44	-.58	+.38	+.17
	E_iSA	+.45	+.72	-.46	+.68	+.53
SCPT	%USE	0	0.4	0	1.3	0.8
	E_iVT	-1.0	-.80	-1.0	-.60	-.66
	E_iSA	-1.0	-.72	-1.0	-.49	-.52
PSRU	%USE	0	3.9	6.6	2.2	4.6
	E_iVT	-1.0	-.07	+.38	-.34	+.22
	E_iSA	-1.0	+.31	+.96	+.15	+.94
DL[b]	%USE	0	1.3	0	1.3	0
	E_iVT	-1.0	-.56		-.48	-1.0
	E_iSA	-1.0	-.36		-.24	-1.0

Table 6.29 continued.

HABITAT TYPE[a]	VAR	Dec81 (N = 1)	HotWet82 (N = 3)	HotDry82 (N = 3)	Garúa82 (N = 5)	El Niño (N = 2)
DWH II/WH II	%USE	0	1.2	0	1.0	2.3
	E_iVT	-1.0	-.44	-1.0	-.65	+.54
	E_iSA	-1.0	-.35	-1.0	-.61	+.92
TRAIL	%USE	27.8	30.8	21.6	14.6	14.6
	%USE[c]	27.8	30.8	22.7	19.7	27.7
	E_iVT	+.99	+.99	+.33	+.98	+.99
	E_iSA	+.99	+.99	+.33	+.98	+.99
OTHER[d]	%USE	0	0.5	2.1	1.0	3.0

[a]Habitat types include: PZW - Psidium/Zanthoxylum Woodland, HAW - Hippomane Woodland, CMT - Clerodendrum Thicket, UG - Underutilized Grassland, GL - Grazing Lawn, OF - Open Forb, DWH I/WH I - Dry Water Hole I/Water Hole I, SCPT - Scleria Stand, PSRU - Psychotria Thicket, DL - Dichondra Lawn, DWH II/WH II - Dry Water Hole II/Water Hole II, and Trail.

[b]DL non-existent in HotDry82.

[c]Real %USE of trails. Observations of tortoises on trails were sometimes recorded with the surrounding habitat type, so that %USE was divided between them. These values eliminate the surrounding habitat type from any trail observations, resulting in the true percent of observations of tortoises traveling that were on trails.

[d]Includes Scalesia Stand, Rhynchospora Stand, Rock Mound, Lemon, Trailside, and Water Hole.

Table 6.30. Seasonal averages of the percent of observations of traveling tortoises at La Caseta and El Chato in open habitats and in shaded habitats. Open, treeless habitat types include Underutilized Grasslands, Grazing Lawns, Open Forb, Dichondra Lawns, and Dry Water Holes/Water Holes (type I). Shaded habitat types include Psidium/Zanthoxylum and Hippomane Woodlands, Clerodendrum and Psychotria Thickets, and Dry Water Holes/Water Holes (type II).

	LA CASETA		EL CHATO	
SEASON	OPEN	SHADED	OPEN	SHADED
Dec81	23.7	44.7	33.4	38.9
HotWet82	17.1	53.4	26.4	41.9
HotDry82	7.7	59.1	8.0	68.3
Garúa82	18.3	61.5	25.4	57.7
El Niño	14.2	55.1	11.7	69.9

associated with Psidium/Zanthoxylum Woodlands. Open habitats were little affected by this change.

Average indices of habitat preference for the 13 major habitat types at La Caseta were significantly correlated with those at El Chato in some seasons (Table 6.31). Lower levels of correlation for traveling in relation to those for feeding may result from the unimportance, and therefore more random use, of micro-habitats for traveling. In addition, habitat selectivity for traveling was significantly lower than for feeding, resulting in a relaxation of preference:avoidance patterns for traveling relative to those for feeding.

Few habitat characteristics measured in the vegetation transects were significantly correlated with habitat preferences for traveling. The characteristics measured were related primarily to food availability. Traveling, not necessarily related to food availability, occurred primarily on trails and in the major habitat types, with some dependence on sun:shade patterns dominated by the presence or absence of overstory.

In the Santa Cruz Nesting Zone, tortoises traveled most in the three major woodland types, with very little use of any of the less abundant habitats (Table 6.32). When considering the total study area, tortoises traveled in the two more rocky woodlands at a level nearly equal to their abundance. Only the open woodland with few rocks was preferred.

Table 6.31. Seasonal comparisons of habitat preference indices for traveling (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area) at La Caseta, with those at El Chato. Results list Spearman's rank correlation coefficients (r_s) at P <.05*, .01**, .001***.

SEASON	N	r_s (E_iVT)	r_s (E_iSA)
All	13	0.83***	0.74**
Dec81	12	0.69**	0.65*
HotWet82	12	0.43	0.48
HotDry82	12	0.87***	0.85***
Garúa82	12	0.42	0.67*
El Niño	12	-0.02	0.28

Table 6.32. Average percent of observations of traveling tortoises at the Santa Cruz Nesting Zone during El Niño 1983, in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT , based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area). N = 3.

HABITAT TYPE[a]	%USE	E_iVT	E_iSA
R/PPW	59.6	+.21	-.06
O/R/PPW	18.1	-.25	-.01
O/PPW	13.4	-.22	+.28
PPW	1.3	-.56	-.37
O/R/IPTR	0	-1.0	-1.0
O/R/IPTR/PPW	0	-1.0	-1.0
O/R/EVGL	2.1	-.40	-.35
O/R/EVGL/PPW	0	-1.0	-1.0
O/EVGL/PPW	0	-1.0	-1.0
O/R	1.3	-.47	-.35
CMT	4.2	-.34	-.34

[a]Habitat types include various combinations of the following: R - Rock, O - Open, PPW - Pisonia/Piscidia Woodland, IPTR - Ipomoea trilioba, EVGL - Evolvulus glaber, and CMT - Clerodendrum Thicket.

Tortoises, observed traveling in only 3 of the 6 major habitat types, R/PPW, O/R/PPW, and O/PPW, preferred habitats with higher levels of available shrubs and with less cover by rock and forbs (Table 6.33).

Tortoises on Pinzón also traveled most often in habitats with less rock, particularly in December (Table 6.34). Use of all Opuntia habitats showed a seasonal trend similar to that for feeding and resting (Table 6.35). In the hot-dry season both food and shade were important factors attracting tortoises to Opuntia areas; whereas at the onset of El Niño, both of these factors were abundant in many other habitats as well. In addition, shade was probably less important in the cooler month. In December, Dry Water Holes, Prosopis/ Croton, and Prosopis habitats, all with relatively low percent cover by rock, were each used by more than 10% of the traveling tortoises.

Five of the measured habitat characteristics on Pinzón were thought to be of potential importance to tortoises when traveling, and only they were included in stepwise regression analyses. Abundance of rock was the only significant variable correlated with use of habitats for traveling, the two being inversely related (Table 6.36, Fig. 6.15). The strong relationship between habitat preferences and rocks at the onset of El Niño coincides with the relaxing of limitations of shade and food, allowing tortoises to be more selective in regards to rock:soil surfaces.

Table 6.33. Significant variables explaining habitat preferences for traveling at the Santa Cruz Nesting Zone during El Niño 1983. Results are based on stepwise regressions with preference index values (E_i)[a] versus the following habitat characteristics: percent cover[b] by rock (%ROCK), and by available food, and the total available biomass (g/m^2) of all foods, of forbs (FORB), and of shrubs (SHRUB). Results list statistics for the model with the most variables which were significant. Percent variance explained is indicated beneath each variable, along with its partial correlation coefficient with the habitat preference index value in parentheses. Significance levels at P < .05*, .01**, .001***, .0001****. Significance of partial correlations are not noted beyond .01**.

MODEL				HABITAT CHARACTERISTICS		
E_i[a]	F	df	R^2	SHRUB	%ROCK[b]	FORB
E_iVT	8.40	2,15	0.53**	35.83*** (+.72**)	17.00* (-.51*)	
E_iSA	12.58	3,14	0.73***	20.89** (+.68**)	40.19**** (-.81**)	11.86* (-.55*)

[a]Index of habitat preference based on habitat availability in key tortoise areas (E_iVT) or on habitat availability in the total study area (E_iSA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

[b]Percent data transformed to its arc sine square root, in radians.

Table 6.34. Percent of observations of traveling tortoises on Pinzón in 1982, in each habitat type[a] (%USE), and the corresponding indices of habitat preference (E_iVT, based on habitat availability in the key tortoise areas, and E_iSA, based on habitat availability in the total study area).

HABITAT TYPE[a]	APRIL/MAY			DECEMBER		
	%USE	E_iVT	E_iSA	%USE	E_iVT	E_iSA
DWH/WH	7.5	-.42	+.62	19.6	+.02	+.83
PR/CR/R	0	-1.0	-1.0	3.6	-.61	-.80
PR/CR	8.3	-.17	+.47	13.2	+.06	+.63
PR/R	7.9	+.26	-.52	4.8	+.02	-.68
PR	10.4	-.04	+.44	16.3	+.19	+.61
CR/R	0.8	-.67	-.71	2.4	-.25	-.32
CR	2.1	-.39	+.60	7.8	+.24	+.88
OP/PR/CR	18.3	+.33	+.32	9.6	+.02	0
OP/PR	5.0	+.10	-.26	0	-1.0	-1.0
OP/CR	13.8	+.29	+.93	7.2	-.02	+.86
OPUNTIA	9.6	+.48	+.06	8.4	+.43	-.01
MA/R	7.1	+.25	+.95	1.2	-.56	+.74
OPEN	3.3	+.38	+.46	3.6	+.41	+.49
O/R	5.8	+.97	+1.0	2.4	+.92	+.92

[a]Habitat types include various combinations of the following: DWH/WH - Dry Water Hole/Water Hole, R - Rock, O - Open, PR - Prosopis, CR - Croton, OP - Opuntia, and MA - Maytenus.

Table 6.35. Percent of observations of tortoises feeding, resting, and traveling on Pinzón in 1982, in the four available Opuntia habitat types, that constituted 27.1% of the study area.

	MONTH	
ACTIVITY	APRIL/MAY	DECEMBER
FEEDING	62.1	28.0
RESTING	52.5	27.6
TRAVELING	46.7	25.2

Table 6.36. Significant seasonal relationships between percent cover by rock (arc sine square root, in radians) and habitat preference indices for traveling on Pinzón in 1982. B value = slope of the regression. Results of regression models significant at $P < .05^*, .01^{**}$.

SEASON	E_i[a]	F	df	R^2	B VALUE
Both	VT	11.45	1,24	0.32**	-0.74
	SA	5.49	1,24	0.19*	-0.56
HotDry	VT			NS	
	SA			NS	
El Niño	VT	14.22	1,11	0.56**	-0.98
	SA	3.12	1,11	0.22[b]	-0.61

[a] Index of habitat preference based on habitat availability in key tortoise areas (VT) or on habitat availability in the total study area (SA). Each index was transformed to the rank order of the index (lowest index value = 1) divided by the number of habitat types for each month.

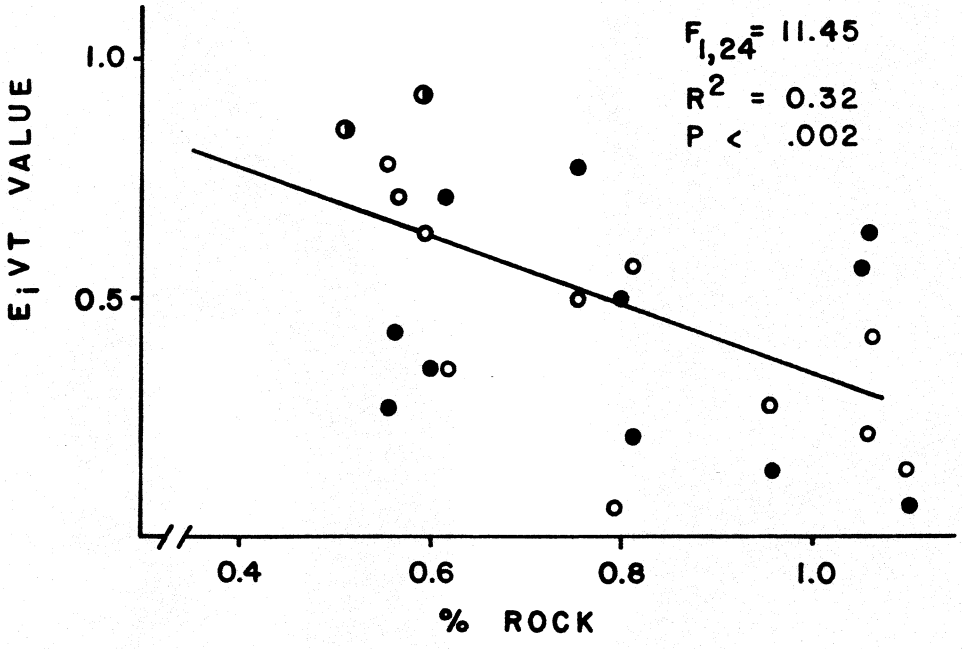
[b] $P < .10$.

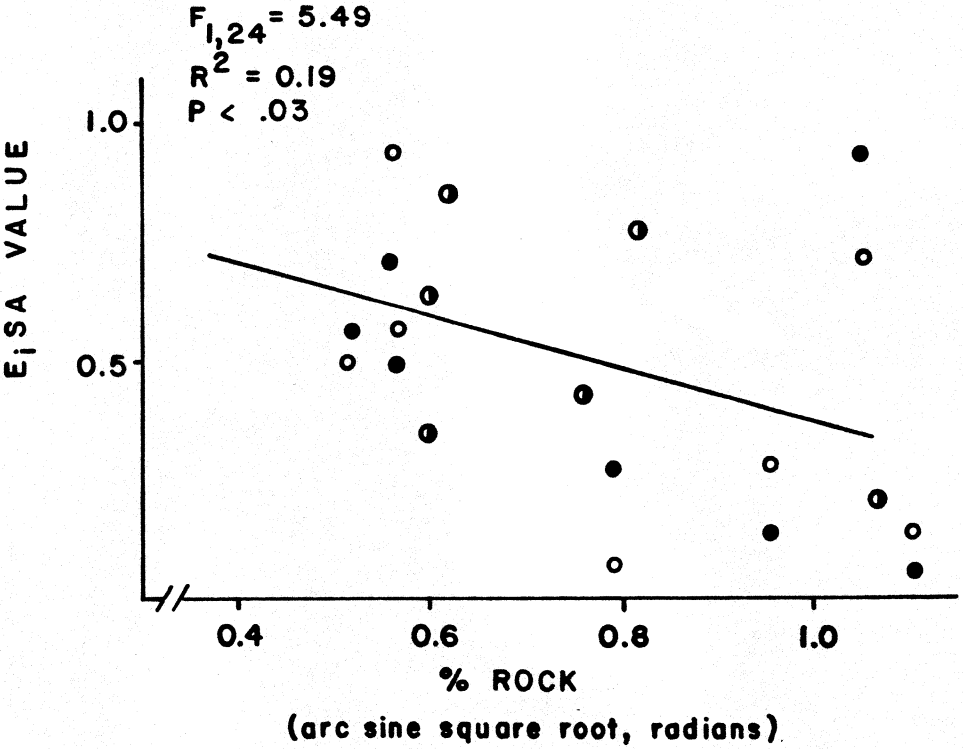
Fig. 6.15. Habitat preferences of tortoises for traveling on Pinzón in 1982, in relation to the percent cover by rock (%ROCK). Preference index values, where E_iVT was based on habitat availability in the key tortoise areas and E_iSA was based on habitat availability in the total study area, equal the rank order of each index (lowest index value = 1) divided by the number of habitat types for each month. Percent rock ranged from 25.1 to 79.9%. Half-open circles indicate data points common to both seasons.

PINZÓN

● HOT-DRY SEASON (APRIL/MAY 1982)

○ EL NIÑO (DECEMBER 1982)





DISCUSSION

The hierarchy of selection exhibited by giant tortoises in the Galápagos Islands includes habitat selection. The heterogeneity of the four study areas results in environmental mosaics, with habitat patches that vary in quality. Within the regions where tortoises choose to concentrate, they demonstrate a higher order of selection by choosing habitats for specific activities, appearing to select habitats of higher quality as predicted. Habitat quality differed for the different activities. Tortoises do not appear to be differentially distributed because of an external agent, such as predation. When conditions are favorable, tortoises move easily among most habitat types. Only when conditions are stressful, as under drought conditions, do tortoises severely reduce their activity, and thus limit the possibility of habitat selection.

Habitat selectivity for feeding was significantly higher than for resting or traveling, especially during drought conditions when tortoises were relatively inactive. At those times, a compromise in habitat use was made in favor of habitats of higher quality for feeding, suggesting that food and its water content were the major limiting factors. In addition, the range in habitat quality may be greatest for feeding relative to other activities. The increase in habitat selectivity for resting when conditions improved suggests that habitat qualities do differ relative to resting, and that these differences are acted upon when other limitations are relaxed.

Both dome-shaped and saddle-backed tortoises concentrated their feeding in habitats that provided an abundance, either in amount or proportion, of preferred foods. Thus, the abundance of preferred food items appears to be the environmental characteristic most closely associated with habitat quality for feeding. Less significant relationships at the Santa Cruz Nesting Zone and on Pinzón may be a result of less well-delineated habitat types. The lack of habitat delineation may result from the less advanced stage of soil development relative to the uplands of Santa Cruz, or it may simply be due to the inability of the observer to distinguish among habitats experienced by tortoises. At all study areas, when conditions were favorable, tortoises preferred areas with high levels of herbaceous vegetation, either grasses or forbs. In the hot-dry season, tortoises tended to feed on specific food items (fruits at La Caseta and El Chato, and cactus on Pinzón), and thus to occur in specific habitat types. Both the concentration of tortoises and the scarcity of food could account for the increase in agonistic interactions in this season on both islands. This period also coincides with the annual peak in breeding activity.

Micro-habitats, often very pointedly preferred or avoided by tortoises when feeding, were seldom used for other activities.

Sun:shade patterns were a dominant factor in determining habitat preferences for resting and traveling on both islands. In the cooler seasons, tortoises preferred the

more open habitats, while in hot seasons they used shaded areas more throughout the day. Although shade is an important factor in determining habitat quality in the Galápagos, it does not play as crucial a role in tortoise survival as it does for Aldabran tortoises. A majority of tortoise mortality on Aldabra is caused by overheating when tortoises are unable to return to shaded areas in sufficient time to to cool (Swingland and Frazier 1979, Coe and Swingland 1984). In the Galápagos, open and shaded habitats are much more interspersed, and shade is relatively close to all feeding areas. In addition, the cool season when the Galápagos are surrounded by cold water is the longer of the two seasons, whereas it is non-existent on Aldabra.

The fact that sun:shade patterns appear to be the major factor in determining habitat quality for resting and traveling may be a partial cause for generally lower levels of habitat selectivity for those activities relative to feeding. Distinguishing habitats based solely on sun:shade patterns would result in fewer total habitat types, spreading use more evenly over those that provide similar, high quality conditions. Whereas, habitats with similar sun:shade patterns may vary significantly in regards to quality for feeding.

The four study areas, all in regions where tortoises concentrate, have similarities in water flow and collection patterns. Tortoises may concentrate in these areas due to the environmental conditions created by these water flow

patterns. Examination of the habitat maps of La Caseta and El Chato reveals that the mosaic of habitats at the center is more complex and provides greater habitat diversity than does that along the outer edges. This mosaic of habitat types within the larger landscape represents the region most used by tortoises. Indeed, the study area boundaries were set because tortoises were infrequently encountered beyond them. Cayot (1985) discussed the importance of water flow in the establishment and maintenance of specific habitat types. Soil movement associated with water flow may also play a key role. Much soil is moved during flood periods, some being carried to the lowlands, while some settles out in ponds or other areas in the uplands where water movement is slowed. Soil deposition, along with water flow, may affect the productivity of the vegetation and habitat structure of the area, and may improve its suitability for tortoises.

The importance of drainages to tortoises cannot be overemphasized. Not only do they provide an ecological mosaic of habitats that is preferentially used by tortoises, they provide corridors for movement among regions. Darwin (1860) noted that the early Spanish visitors followed tortoise trails from the lowlands inland to locate freshwater ponds. It is probable that the tortoises that first arrived in the Galápagos found the same ponds by following the drainages, and then maintained their trails along them. The fact that many tortoise trails coincide with drainages becomes obvious

during periods of extremely high precipitation as occurred in El Niño 1983.

By their use of the drainages as corridors, tortoises may have been instrumental in the establishment of some of the habitat types in the uplands. Hippomane mancinella, a tree generally associated with coastal regions (Ridley 1930, Wiggins and Porter 1971), also has a curious inland distribution in the Galápagos (Stewart 1911, Svenson 1946, Reeder and Riechert 1975, Colinvaux and Schofield 1976, Hamann 1981), as exemplified by the habitat type at La Caseta and El Chato. The species requires or at least tolerates water-saturated soils (Hamann 1981), and its occurrence in the uplands of Santa Cruz is well correlated with river and pond distributions (Cayot 1985). Tortoises have been suggested as a dispersal agent for Hippomane (Ridley 1930, Rodhouse et al. 1975), and it is likely that its original occurrence in the uplands was due to seed dispersal by tortoises migrating inland from the coastal areas (Cayot 1985). Their use of drainages as corridors increased the probability of Hippomane seeds being deposited in suitable locations for establishment and survival. Other plant species may also have increased their range inland through dispersal by tortoises.

Although not along major drainages for the most part, both the Santa Cruz Nesting Zone and South Crater on Pinzon have conditions similar to La Caseta and El Chato in terms of water flow and collection and soil deposition. The key tortoise areas at each site are located in the lower por-

tions of the site, where water collects periodically and much soil is deposited. Both regions have little soil development and are extremely rocky. Soil of any significant depth is primarily a result of being carried and deposited there by water movement. Some of this soil has likely been brought from the uplands where soil development is more advanced. Tortoises avoid the more rocky areas, preferentially using the more open, low areas, where soil deposition is substantial, for all of their activities.

Tortoises select specific habitat patches within the areas of tortoise concentration. Their habitat preferences change both seasonally and by activity, with greatest selectivity for feeding. The most preferred environments for tortoises on both Santa Cruz and Pinzón appear to be those that provide a high diversity of habitat types associated with areas of substantial soil development or deposition relative to the surrounding region. These areas of concentration appear to be related to water flow and collection patterns whether or not surface water is currently available.

CHAPTER SEVEN - CONCLUSION

Giant tortoises in the Galápagos Islands exhibit many behavioral adaptations that are adjusted seasonally to environmental conditions. These behavioral adaptations enable them to survive and reproduce in the arid and unpredictable climate of the archipelago. Precipitation appears to be the dominant controlling factor effecting changes in tortoise behavior. These changes are related to the availability of both food and water. Temperature plays a secondary role in effecting changes in tortoise behavior.

Activity of giant tortoises, both time budgets and daily patterns of activity, are closely related to seasonal changes in temperature and precipitation. Galápagos tortoises, like most tortoises in xeric habitats, show a peak in total time active during rainy seasons when food is abundant. Total active time decreases as conditions decline and the dry season progresses.

Within a given time budget, dependent upon rainfall and food availability, daily patterns of activity change relative to seasonal changes in ambient temperature. During the cool garúa season, when mid-day temperatures are moderate, tortoises exhibit a unimodal pattern of activity with their active period mid-day. Tortoises remain inactive in the early morning and late afternoon when temperatures are cool. During the hot season, when mid-day temperatures are very high, tortoises show a bimodal pattern of activity, remain-

ing inactive during the mid-day hours. Their active periods occur primarily in the early morning and the late afternoon when temperatures are moderate.

The total daily active time of tortoises, ectotherms with the ability to live for long periods of time without food or water, is positively correlated with precipitation and subsequent food availability. Tortoises may remain completely inactive for days when conditions are extremely dry. However, with a given amount of time active, their patterns of daily activity are related primarily to ambient temperature.

Galápagos tortoises have a feeding strategy of flexible selectivity, enabling them to respond to environmental conditions determined primarily by precipitation. They feed on a wide variety of food types, with forbs, grasses, fruit, and cactus predominant in their diet. As the dry season progresses and the amount of time spent feeding declines, tortoises become more and more selective when feeding. Food preferences, especially in drier periods, are primarily related to water content of the food. Nitrogen content of food items is not related to food preferences except when conditions are extremely favorable and free water is plentiful. Calcium may be an important factor in food preferences and should be examined.

Beyond selecting regions of seasonal concentration, tortoises show a higher level of selection by choosing specific habitats. The available habitats vary in quality relative

to different activities and tortoises appear to prefer those of higher quality. Habitat selection for feeding is significantly higher than for other activities, suggesting that food may be limiting or that feeding is the most important activity of tortoises. This difference in habitat selectivity by activity may also be due to a greater range in quality among habitats relative to feeding in comparison with other activities, with preferred foods being more habitat specific than preferred resting or traveling sites.

Preferred habitats for feeding have greater abundance of preferred-significant foods (by proportion or amount). Seasonal changes in habitat preferences reflect seasonal changes in food preferences.

Habitat preferences for resting and traveling are closely related to sun:shade patterns. In the cool garúa season, tortoises prefer more open areas where they can receive direct sunlight. In the hot season, tortoises prefer the more shaded habitats to avoid direct sunlight. In addition, in regions with greater ground cover by lava, typical of the Arid Zone of most of the islands, tortoises prefer habitats with less rock.

Dome-shaped tortoises, characteristic of the higher, humid islands, generally exhibit behavioral adaptations similar to those of the saddle-backed tortoises that are characteristic of the lower, more arid islands. Daily time budgets and activity patterns of both tortoise types are similarly related to seasonal changes in precipitation, food

availability, and ambient temperature. Habitat preferences for feeding are related to food availability, while those for resting and traveling are related primarily to sun:shade patterns. Saddle-backed tortoises on Pinzón avoid more rocky areas, but this is also true of dome-shaped tortoises when inhabiting the Arid Zone of Santa Cruz.

Food habits of the two types of tortoises reflect differences in food availability between Pinzón and Santa Cruz. Tortoises on Pinzón feed primarily on cactus in the dry season, and forbs and shrubs in the wet season. Tortoises in the highlands of Santa Cruz feed primarily on grasses and forbs, and show a high preference for fallen fruit when available. The importance of the tree-like cactus and taller shrubs in the diet of saddle-backed tortoises on Pinzón suggests that a greater capacity to extend their vertical reach would be highly advantageous. The importance of vertical reach for Pinzón tortoises in terms of obtaining food, especially during the harsh dry season, and their capability of doing so as a result of the saddle-backed morphology, support the major current hypothesis for the evolution of the saddle-backed trait on the arid islands of the archipelago. With grasses, forbs, and fallen fruit, the major foods of Santa Cruz tortoises, any increase in vertical feeding range would be of little importance to these large dome-shaped animals, and might be disadvantageous if it also resulted in an upraised carapace morphology that could restrict their movement among the dense vegetation of the higher island.

Galápagos tortoises, both dome-shaped and saddle-backed, exhibit a pulse-reserve pattern of behavior as predicted for organisms in arid environments. The major pulse input into the system is precipitation, and it is the dominant controlling factor. Precipitation plays a major role not only in terms of the availability of both food and water, but also in terms of available habitats. Tortoises on both Santa Cruz and Pinzón tend to concentrate in regions of high habitat diversity associated with areas of water flow or collection. Water flow patterns effect soil distribution and subsequent development of the vegetation, in effect creating the conditions for those habitats most conducive to tortoises.

Galápagos tortoises not only exhibit characteristics that are conducive to dispersal to the islands, but also flexible behavior patterns that, along with their physiological adaptations, provide them with the necessary life strategies for continued survival in the archipelago.

LITERATURE CITED

1. Agassiz, A. 1892. General sketch of the expedition of the 'Albatross' from February to May 1891. The Galápagos Islands. Bulletin of the Museum of Comparative Zoology of Harvard 23:56-74.
2. Alpert, L. 1963. The climate of the Galápagos Islands. Occasional Papers of the California Academy of Sciences 44:21-44.
3. Altmann, J. 1974. Observational study on behavior: sampling methods. Behaviour 49:227-267.
4. Anderson, D. M., and M. M. Kothman. 1982. A two-step sampling technique for estimating standing crop of herbaceous vegetation. Journal of Range Management 35:675-677.
5. Arp, G. K. 1973. The Galápagos Opuntias: another interpretation. Noticias de Galápagos 21:33-37.
6. Auffenberg, W. 1971. A new fossil tortoise, with remarks on the origin of South American Testudinines. Copeia 1971:106-117.
7. Auffenberg, W., and J. B. Iverson. 1979. Demography of terrestrial turtles. Pages 541-569 in Harless, M., and H. Morlock, editors. Turtles, perspectives and research. Wiley & Sons, New York.
8. Bally, P. R. O. 1946. Tortoises eating bones. East African Natural History Society Journal 18:163.
9. Baur, G. 1889. The gigantic land tortoises of the Galápagos Islands. American Naturalist 23:1039-1057.

10. Beck, R. H. 1903. In the home of the giant tortoise. Annual Report of the New York Zoological Society 7:160-174.

11. Black, J. 1973. Galápagos archipielago del Ecuador. Quito. 138pp.

12. Bourn, D. 1977. Reproductive study of giant tortoises on Aldabra. Journal of Zoology 182:27-38.

13. Bourn, D., and M. Coe. 1978. The size, structure and distribution of the giant tortoise population of Aldabra. Philosophical Transactions of the Royal Society of London B 282:139-175.

14. Bourn, D., and M. J. Coe. 1979. Features of tortoise mortality and decomposition on Aldabra. Philosophical Transactions of the Royal Society of London B 286:189-193.

15. Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos finches. University of California Publications in Zoology, Volume 58. 326pp.

16. Brosset, A. 1963. Statut actuel de la faune aux Iles Galápagos. Noticias de Galápagos 1:5-9.

17. Carlquist, S. 1974. Island biology. Columbia University Press, New York, London. 660pp.

18. Carpenter, C. C. 1966. Notes on the behavior and ecology of the Galápagos tortoise on Santa Cruz Island. Proceedings of the Oklahoma Academy of Sciences 46:28-32.

19. Cayot, L. J. 1985. Effects of El Niño on giant tortoises and their environment. Pages 363-398 in Robinson, G., and E. M. del Pino, editors. El Niño en las Islas Galápagos: el evento de 1982-1983. Fundación Charles Darwin para las Islas Galápagos, Quito, Ecuador.

20. Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-215.

21. Chew, R. M. 1974. Consumers as regulators of ecosystems: an alternative to energetics. Ohio Journal of Science 74:359-370.

22. Christian, K. A., C. R. Tracy, and W. P. Porter. 1984. Diet, digestion, and food preferences of Galápagos land iquanas. Herpetologica 40:205-212.

23. Cloudsley-Thompson, J. L. 1971. The temperature and water of reptiles. Merrow Publishing Company, England.

24. Cock, M. J. W. 1978. The assessment of preference. Journal of Animal Ecology 47:805-816.

25. Coe, M., and I. R. Swingland. 1984. Giant tortoises of the Seychelles. Pages 309-330 in Stoddart, D. R., editor. Biogeography and ecology of the Seychelles Islands. Monographiae Biologicae Volume 55, Dr. W. Junk Publishers, The Hague, Boston, Lancaster.

26. Colinvaux, P. A., and E. K. Schofield. 1976. Historical ecology in the Galápagos Islands. I. A holocene pollen record from El Junco Lake, Isla San Cristóbal. Journal of Ecology 64:989-1012.

27. Cook, C. W., L. E. Harris, and L. A. Stoddart. 1948. Measuring the nutritive content of a foraging sheep's diet under range conditions. Journal of Animal Science 7:170-180.

28. Cox, A. 1983. Ages of the Galápagos Islands. Pages 11-23 in Bowman, R. I., M. Berson, and A. E. Leviton, editors. Patterns of evolution in Galápagos organisms. Pacific Division of the American Association for the Advancement of Science, San Francisco.

29. Crawley, M. J. 1983. Herbivory: the dynamics of animal-plant interactions. University of California Press, Studies in Ecology Volume 10, Berkeley, Los Angeles. 437pp.

30. Darwin, C. 1860. The voyage of the Beagle. Natural History Library Edition, 1962. Engle, L., editor. Doubleday Company, Garden City, NY. 524pp.

31. Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science 33:43-64.

32. Dawson, E. Y. 1964. Cacti in the Galápagos Islands. Noticias de Galápagos 4:12-13.

33. Dawson, E. Y. 1965. Further studies of Opuntia in the Galápagos archipelago. Cactus and Succulent Journal 37:135-148.

34. Dawson, E. Y. 1966. Cacti in the Galápagos Islands, with special reference to their relations with tortoises. Pages 209-214 in Bowman, R. I., editor. The Galápagos. Proceedings of the Symposia of the Galápagos

International Scientific Project. University of California Press, Berkeley.

35. Eckhardt, R. C. 1972. Introduced plants and animals in the Galápagos Islands. BioScience 22:585-590.

36. Eliasson, U. 1982. Changes and constancy in the vegetation of the Galápagos Islands. Noticias de Galápagos 36:7-12.

37. Emlen, J. M. 1966. The role of time and energy in food preference. American Naturalist 100:611-617.

38. Emlen, J. M. 1968. Optimal choice in animals. American Naturalist 102:385-389.

39. Enriquez, R. 1982. Aspectos importantes del ciclo de vida de la tortuga de Galápagos Geochelone elephantopus darwinii de la Isla Santiago. Pages 135-137 in Charles Darwin Research Station Annual Report, 1982. Puerto Ayora, Galápagos.

40. Fowler, L. E. 1983. The population and feeding ecology of tortoises and feral burros on Volcán Alcedo, Galápagos Islands. Ph.D Dissertation, University of Florida, Gainesville. 150pp.

41. Fowler de Neira, L. E., and M. K. Johnson. 1985. Diets of giant tortoises and feral burros on Volcán Alcedo, Galápagos. Journal of Wildlife Management 49:165-169.

42. Fowler de Neira, L. E., and J. H. Roe. 1984. Emergence success of tortoise nests and the effect of feral burros on nest success on Volcán Alcedo, Galápagos. Copeia 1984:702-707.

43. Fritts, T. H. 1983. Morphometrics of Galápagos tortoises: evolutionary implications. Pages 107-122 in Bowman, R. I., M. Berson, and A. E. Leviton, editors. Patterns of evolution in Galápagos organisms. Pacific Division of the American Association for the Advancement of Science, San Francisco.

44. Fritts, T. H. 1984. Evolutionary divergence of giant tortoises in Galápagos. Biological Journal of the Linnean Society 21:165-176.

45. Fritts, T. H., and P. R. Fritts, editors. 1982. Race with extinction: herpetological notes of J. R. Slevin's journey to the Galápagos 1905-1906. Herpetological Monograph 1:1-98.

46. Gaymer, R. 1968. The Indian Ocean giant tortoise, Testudo gigantea, on Aldabra. Journal of Zoology 154:341-363.

47. Gerald, J. W. 1966. Food habits of the longnose dace, Rhinichthys cataractae. Copeia 1966:478-485.

48. Gibson, C. W. D., and J. Hamilton. 1983. Feeding ecology and seasonal movements of giant tortoises on Aldabra atoll. Oecologia 56:84-92.

49. Gill, A. E., and E. M. Rasmusson. 1983. The 1982-83 climate anomaly in the equatorial Pacific. Nature 306:229-234.

50. Glasser, J. W. 1984. Is conventional foraging theory optimal? American Naturalist 124:900-905.

51. Gould, M. S., and I. R. Swingland. 1980. The tortoise and the goat: interactions on Aldabra Island. Biological Conservation 17:267-279.

52. Grubb, P. 1971. The growth, ecology and population structure of giant tortoises on Aldabra. Philosophical Transactions of the Royal Society of London B 260:327-372.

53. Hamann, O. 1975. Vegetational changes in the Galápagos Islands during the period 1966-1973. Biological Conservation 7:37-59.

54. Hamann, O. 1979. On climatic conditions, vegetation types, and leaf size in the Galápagos Islands. Biotropica 11:101-122.

55. Hamann, O. 1981. Plant communities of the Galápagos Islands. Dansk Botanisk Arkiv 34:1-163.

56. Hamilton, J., and M. Coe. 1982. Feeding, digestion and assimilation of a population of giant tortoises (Geochelone gigantea (Schweigger)) on Aldabra atoll. Journal of Arid Environments 5:127-144.

57. Haro, M. 1974. Grado de distribución de las plantas introducidas en los caminos antiguo y nuevo de la Isla Santa Cruz - Galápagos. Thesis, Universidad Católica, Quito, Ecuador. 103pp.

58. Haro, M. 1975. Grado de distribucion de las plantas introducidas en la Isla Santa Cruz - Galapagos. Revista Universidad Católica Año III, Numero 8:243-258.

59. Heller, E. 1903. Papers from the Hopkins Stanford Galápagos expedition, 1898-1899. XIV. Reptiles. Proceedings of the Washington Academy of Sciences 5:39-98.

60. Hemsley, W. B. 1895. Cactaceae in the Galápagos Islands. Nature 53:31.

61. Hendrickson, J. R. 1965. Reptiles of the Galápagos. Pacific Discovery 18:28-36.

62. Hendrickson, J. R. 1966. The Galápagos tortoises, Geochelone Fitzinger 1855 (Testudo Linnaeus 1758 in part). Pages 252-257 in Bowman, R. I., editor. The Galápagos. Proceedings of the Symposia of the Galápagos International Scientific Project. University of California Press, Berkeley.

63. Herbers, J. M. 1981. Time resources and laziness in animals. Oecologia 49:252-262.

64. Hickman, C. S., and J. H. Lipps. 1985. Geologic youth of Galápagos Islands confirmed by marine stratigraphy and paleontology. Science 227:1578-1580.

65. Hickman, J. 1985. The Enchanted Islands: The Galápagos discovered. Tanager Books, Dover, New Hampshire. 169pp.

66. Hintz, H. F. [1972?]. Observations on the nutrition of Galápagos tortoises. Equine Research Program, Cornell University, manuscript, 21pp.

67. Hnatiuk, S. H. 1978. Plant dispersal by the Aldabran giant tortoise, Geochelone gigantea (Schweigger). Oecologia 36:345-350.

68. Humphrey, L. D. 1985. Use of biomass predicted by regression from cover estimates to compare vegetational similarity of sagebrush-grass sites. Great Basin Naturalist 45:94-98.

69. Hutchison, V. H. 1979. Thermoregulation. Pages 207-228 in Harless, M., and H. Morlock, editors. Turtles, perspectives and research. Wiley & Sons, New York.

70. Itow, S. 1965. Preliminary note on the vegetation of the Galápagos Islands, Ecuador. Hikobia 4:318-324.

71. Itow, S., and D. Weber. 1974. Fens and bogs in the Galápagos Islands. Hikobia 7:39-52.

72. Ivlev, V. S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut. 302pp.

73. Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65-71.

74. Katz, P. L. 1974. A long-term approach to foraging optimization. American Naturalist 108:758-782.

75. Laruelle, J. 1966. Study of a soil sequence on Indefatigable Island. Pages 87-92 in Bowman, R. I., editor. The Galápagos. Proceedings of the Symposia of the Galápagos International Scientific Project, University of California Press, Berkeley, Los Angeles.

76. Lauenroth, W. K. 1979. Grassland primary production: North American grasslands in perspective. Pages 3-24

in French, N. R., editor. Perspectives in grassland ecology. Springer-Verlag, New York.

77. Lechowicz, M. J. 1982. The sampling characteristics of electivity indices. Oecologia 52:22-30.

78. Loveridge, A. 1945. Reptiles of the Pacific world. Macmillan, New York.

79. MacArthur, R. 1971. Patterns of terrestrial bird communities. Pages 189-221 in Farner, D. S., J. R. King, and K. C. Parkes, editors. Avian biology, Volume 1. Academic Press, New York, London.

80. MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603-609.

81. MacFarland, C. 1972. Goliaths of the Galápagos. National Geographic 142:632-649.

82. MacFarland, C. G., and W. G. Reeder. 1974. Cleaning symbiosis involving Galápagos tortoises and two species of Darwin's finches. Zeitshrift fur Tierpsychologie 34:464-483.

83. MacFarland, C. G., and W. G. Reeder. 1975. Breeding, raising and restocking of giant tortoises (Geochelone elephantopus) in the Galápagos Islands. Pages 13-37 in Martin, R. D., editor. Breeding endangered species in captivity. Academic Press, London, New York, San Francisco.

84. MacFarland, C. G., J. Villa, and B. Toro. 1974a. The Galápagos giant tortoises (Geochelone elephantopus)

part I: status of the surviving populations. Biological Conservation 6:118-133.

85. MacFarland, C. G., J. Villa, and B. Toro. 1974b. The Galápagos giant tortoises (Geochelone elephantopus) part II: conservation methods. Biological Conservation 6:198-212.

86. Mackay, R. S. 1964. Galápagos tortoise and marine iguana core body temperature measured by radiotelemetry. Nature 204:355-358.

87. Mahmoud, I. Y., and J. Klicka. 1979. Feeding, drinking, and excretion. Pages 229-243 in Harless, M., and H. Morlock, editors. Turtles, perspectives and research. Wiley & Sons, New York.

88. Marlow, R. W., and J. L. Patton. 1981. Biochemical relationships of the Galápagos giant tortoises (Geochelone elephantopus). Journal of Zoology 195:413-422.

89. Marlow, R. W., and K. Tollestrup. 1982. Mining and exploitation of natural deposits by the desert tortoise, Gopherus agassizii. Animal Behavior 30:475-478.

90. Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Review of Ecology and Systematics 11:119-161.

91. McNaughton, S. J. 1978. Serengeti ungulates: feeding selectivity influences the effectiveness of plant defense guilds. Science 199:806-807.

92. McNaughton, S. J. 1984. Grazing lawns: animals in herds, plant form, and coevolution. American Naturalist 124:863-886.

93. McNaughton, S. J. 1985a. Ecology of a grazing ecosystem: the Serengeti. Ecological Monographs 55:259-294.

94. McNaughton, S. J. 1985b. Interactive regulation of grass yield and chemical properties, by defoliation, a salivary chemical, and inorganic nutrition. Oecologia 65:478-486.

95. Merton, L. F. H., D. M. Bourn, and R. J. Hnatiuk. 1976. Giant tortoise and vegetation interactions on Aldabra atoll - part I: inland. Biological Conservation 9:293-304.

96. Moll, E. O. 1979. Reproductive cycles and adaptations. Pages 305-331 in Harless, M., and H. Morlock. Turtles, perspectives and research. Wiley & Sons, New York.

97. Nagy, K. A., and P. A. Medica. 1986. Physiological ecology of desert tortoises in southern Nevada. Herpetologica 42:73-92.

98. Naranjo, P. 1985. El fenómeno El Niño y sus efectos en el clima del Ecuador. Pages 3-27 in Robinson, G., and E. M. del Pino, editors. El Niño en las Islas Galápagos: el evento 1982-1983. Fundación Charles Darwin para las Islas Galapagos, Quito, Ecuador.

99. Noy-Meir, I. 1973. Desert ecosytems: environment and producers. Annual Review of Ecology and Systematics 4:25-51.

100. Noy-Meir, I. 1974. Desert ecosystems: higher trophic levels. Annual Review of Ecology and Systematics 5:195-214.

101. Palmer, C. E., and R. L. Pyle. 1966. The climatological setting of the Galápagos. Pages 93-99 in Bowman, R. I., editor. The Galápagos. Proceedings of the Symposia of the Galápagos International Scientific Project, University of California Press, Berkeley, Los Angeles.

102. Payne, G. F. 1974. Cover-weight relationships. Journal of Range Management 27:403-404.

103. Perry, R. 1964. Santa Cruz tortoise reserve. Noticias de Galápagos 4:19-20.

104. Philander, S. G. H. 1983. El Niño southern oscillation phenomena. Nature 302:295-301.

105. Porter, D. 1822. Journal of a cruise made to the Pacific Ocean by Captain David Porter in the United States Frigate Essex in the years 1812, 1813, and 1814. 2 Volumes. Republished in 1970, The Gregg Press, Upper Saddle River, New Jersey. 502pp.

106. Porter, D. M. 1979. Endemism and evolution in Galápagos Islands vascular plants. Pages 225-256 in Bramwell, D., editor. Plants and islands. Academic Press, London, New York.

107. Porter, D. M. 1983. Vascular plants of the Galápagos: origins and dispersal. Pages 33-96 in Bowman, R. I., M. Berson, and A. E. Leviton, editors. Patterns of evolution in Galápagos organisms. Pacific Division of the American Association for the Advancement of Science, San Francisco.

108. Pritchard, P. C. H. 1971. A further report on Galápagos tortoises. Herpetological Review 3:25-27.

109. Pritchard, P. C. H. 1977. Three, two, one tortoise. Natural History 86:90-100.

110. Pritchard, P. C. H. 1979a. Encyclopedia of turtles. T. F. H. Publications, New Jersey. 895pp.

111. Pritchard, P. C. H. 1979b. Taxonomy, evolution and zoogeography. Pages 1-42 in Harless, M., and H. Morlock. Turtles, perspectives and research. Wiley & Sons, New York.

112. Racine, C. H., and J. F. Downhower. 1974. Vegetative and reproductive strategies of Opuntia (Cactaceae) in the Galápagos Islands. Biotropica 6:175-186.

113. Ramage, C. S. 1986. El Niño. Scientific American 254:76-83.

114. Reeder, W. G., and C. G. MacFarland. 1978. The ecology, behavior, and conservation of the Galápagos tortoises. Pages 497-513 in National Geographic Society Research Reports, 1969 Projects.

115. Reeder, W. G., and S. E. Riechert. 1975. Vegetation change along an altitudinal gradient, Santa Cruz Island, Galápagos. Biotropica 7:162-175.

116. Reynolds, R. P. 1982. Some observations on the captive management of Galápagos tortoises and land iguanas at the Darwin Station and suggestions for the future. Pages 115-119 in Charles Darwin Research Station Annual Report, 1982. Puerto Ayora, Galápagos.

117. Rick, C. M., and R. I. Bowman. 1961. Galápagos tomatoes and tortoises. Evolution 15:407-417.

118. Ridley, H. N. 1930. The dispersal of plants throughout the world. L. Reeve & Company, Ashford, Kent. 744pp.

119. Robinson, G., and E. M. del Pino, editors. 1985. El Niño en las Islas Galápagos: el evento de 1982-1983. Fundación Charles Darwin para las Islas Galápagos, Quito, Ecuador. 534pp.

120. Rodhouse, P., R. W. A. Barling, W. I. C. Clark, A. Kinmonth, E. M. Mark, D. Roberts, L. E. Armitage, P. R. Austin, S. P. Baldwin, A. d'A. Bellairs, and P. J. Nightingale. 1975. The feeding and ranging behaviour of Galápagos giant tortoises (Geochelone elephantopus). The Cambridge and London University Galápagos expeditions, 1972 and 1973. Journal of Zoology 176:297-310.

121. Schafer, S. F., and C. O'Neil Krekorian. 1983. Agonistic behavior of the Galápagos tortoise, Geochelone elephantopus, with emphasis on its relationship to saddle-backed shell shape. Herpetologica 39:448-456.

122. Schluter, D. 1981. Does the theory of optimal diets apply in complex environments? American Naturalist 118:139-147.

123. Schoener, T. W. 1971. Theories of feeding strategies. Annual Review of Ecology and Systematics 2:369-404.

124. Sedgwick, C. J., and M. E. Fowler. 1972-1973. Methods of feeding mammals. Annual Proceedings of the American Association of Zoo Veterinarians 1972-1973:177-221.

125. Simkin, T. 1984. Geology of Galápagos. Biological Journal of the Linnean Society 21:61-75.

126. Simpson, G. G. 1942. A Miocene tortoise from Patagonia. American Museum Novitates 1209:1-6.

127. Sinclair, A. R. E. 1975. The resource limitation of trophic levels in tropic grassland ecosystems. Journal of Animal Ecology 44:497-519.

128. Slevin, J. R. 1931. Log of the schooner Academy on a voyage of scientific research to the Galápagos Islands, 1905-1906. Occasional Papers of the California Academy of Sciences 17:1-162.

129. Slevin, J. R. 1935. An account of the reptiles inhabiting the Galápagos Islands. Bulletin of the New York Zoological Society 38:3-24.

130. Slevin, J. R. 1959. The Galápagos Islands: a history of their exploration. Occasional Papers of the California Academy of Sciences, Number 25. 150pp.

131. Smith, D. 1969. Removing and analyzing total nonstructural carbohydrates from plant tissue. Research Report 41. Research Division of the College of Agriculture and Life Sciences, University of Wisconsin. 11pp.

132. Snedecor, G. W., and W. G. Cochran. 1973. Statistical methods, 6th ed. Iowa State University Press, Ames, Iowa. 593pp.

133. Snow, D. W. 1964. The giant tortoises of the Galápagos Islands: their present status and future chances. Oryx 7:277-290.

134. Snow, D. W. 1966. Giant tortoises. Animals 9:140-142.

135. Sokol, O. M. 1971. Lithophagy and geophagy in reptiles. Journal of Herpetology 5:69-70.

136. Staedeli, J. H. 1972. Concern for the Galápagos tortoises. Zoonooz 45:5-10.

137. Stevenson, R. D. 1985. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. American Naturalist 126:362-386.

138. Stewart, A. 1911. A botanical survey of the Galápagos Islands. Proceedings of the California Academy of Sciences, 4th Series 1:7-288.

139. Stewart, A. 1915. Some observations concerning the botanical conditions on the Galápagos Islands. Transactions of the Wisconsin Academy of Sciences, Arts and Letters 18:272-340.

140. Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. Transactions of the American Fisheries Society 108:344-352.

141. Svenson, H. K. 1946. Vegetation of the coast of Ecuador and Peru and its relation to the Galápagos Islands. I. Geographical relations of the flora. American Journal of Botany 33:394-426.

142. Swain, T. 1976. Angiosperm-reptile coevolution. Pages 107-122 in Bellairs, A. d'A., and C. B. Cox, editors. Morphology and biology of reptiles. Linnean Society Symposium Number 3:107-122.

143. Swingland, I. R., and M. Coe. 1978. The natural regulation of giant tortoise populations on Aldabra atoll: reproduction. Journal of Zoology 186:285-309.

144. Swingland, I. R., and M. J. Coe. 1979. The natural regulation of giant tortoise populations on Aldabra atoll: recruitment. Philosophical Transactions of the Royal Society of London B 286:177-188.

145. Swingland, I. R., and J. G. Frazier. 1979. The conflict between feeding and overheating in the Aldabran giant tortoise. Pages 611-615 in Amlaner, C. J., Jr., and D. W. MacDonald, editors. A handbook on biotelemetry and radio tracking. Pergamon Press, Oxford and New York.

146. Swingland, I. R., and C. M. Lessells. 1979. The natural regulation of giant tortoise populations on Aldabra atoll: movement, polymorphism, reproductive success and mortality. Journal of Animal Ecology 48:639-654.

147. Thornton, I. 1971. Darwin's islands: a natural history of the Galápagos. Natural History Press, Garden City, NY. 322pp.

148. Tierney, J. 1985. Lonesome George of the Galápagos. Science 85 6:50-61.

149. Townsend, C. H. 1925. The Galápagos tortoises in their relation to the whaling industry: a study of old logbooks. Zoologica 4:55-135.

150. Townsend, C. H. 1931. Giant tortoises. Scientific American 144:42-44.

151. Van Denburgh, J. 1914. The gigantic land tortoises of the Galápagos archipelago. Proceedings of the California Academy of Sciences, 4th Series 2:203-374.

152. Vanderploeg, H. A., and D. Scavia. 1979a. Calculation and use of selectivity coefficients of feeding: zooplankton grazing. Ecological Modelling 7:135-149.

153. Vanderploeg, H. A., and D. Scavia. 1979b. Two electivity indices for feeding with special reference to zooplankton grazing. Journal of the Fisheries Research Board of Canada 36:362-365.

154. van der Werff, H. H. 1978. The vegetation of the Galápagos Islands. Zierikzee, Holland. 102pp.

155. van der Werff, H. H. 1979. Conservation and vegetation of the Galápagos Islands. Pages 391-404 in Bramwell, D., editor. Plants and islands. Academic Press, London.

156. van der Werff, H. H. 1983. Species number, area and habitat diversity in the Galápagos Islands. Vegetatio 54:167-175.

157. Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. American Naturalist 108:290-304.

158. White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia 33:71-86.

159. Whittaker, R. H. 1970. Communities and ecosystems. Macmillan Co., Toronto. 162pp.

160. Wiens, J. A. 1976. Population responses to patchy environments. Annual Review of Ecology and Systematics 7:81-120.

161. Wiggins, I. L., and D. M. Porter. 1971. Flora of the Galápagos Islands. Stanford University Press, Stanford, California. 998pp.

162. Woodbury, A. M., and R. Hardy. 1948. Studies of the desert tortoise, Gopherus agassizii. Ecological Monographs 18:145-200.

BIOGRAPHICAL DATA

Name: Linda Jean Cayot

Date and Place of Birth: October 13, 1951
Berkeley, California

Elementary School: Cragmont School
Berkeley, California
Graduated 1962

Junior High School: Garfield Junior High School
Berkeley, California
Graduated 1964

High School: Berkeley High School
Berkeley, California
Graduated 1968

College: Univeristy of California
Berkeley, California
1969-1972

Colorado State University
Fort Collins, Colorado
B.S. 1975

Graduate Work: Colorado State University
Fort Collins, Colorado
Research Assistant 1975-1976
Teaching Assistant, Summer 1977
Hill Fellowship 1977-1978
M.S. 1978

Syracuse University
Syracuse, New York
Teaching Assistant 1979-1980, 1984
Research Assistant 1981-1983, 1985-1986
University Fellowship 1984-1985