THE POPULATION AND FEEDING ECOLOGY OF TORTOISES AND FERAL BURROS ON VOLCAN ALCEDO, GALAPAGOS ISLANDS

By

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Chairman: John H. Kaufmann
Major Department: Zoology

Feral burros (Equus asinus) were introduced to the Galapagos Archipelago in the 1830s. Volcan Alcedo, Isabela Island, harbours 500 to 700 burros in addition to the largest remaining population of Galapagos tortoises, Geochelone elephantopus vandenburghi. Burro and tortoise population and feeding ecologies were studied on Alcedo to investigate the possible impact of burros on tortoises.

There is no permanent source of fresh water on Alcedo; during the wet season (January to June) rain water collected in pools and was readily available. Peak burro natality coincided with the rainy season, as did tortoise breeding.

During the dry season water was occasionally available in drip-puddles along the southeastern crater rim. Temporary water availability influenced distributions and behavior of burros and tortoises. Both species showed a tendency to congregate along the moist southeastern section in the dry season.

Apparently water shortages result in an unusually high level of mortality among young, sexually mature burros. Forty percent of 136 burro carcasses and skeletons were of animals between three and six years old. Water shortages probably limit burro population growth.

Burro and tortoise diets were investigated using direct observation of feeding animals and fecal analysis techniques. Seventy-two percent of 92 plant species consumed by burros and/or tortoises were eaten by both animals. Burro and tortoise wet season and early dry season diets were different, but in the late dry season both animals consumed *Sida* and competition for food is a possibility.

An investigation of seasonal tortoise feeding behavior demonstrated, however, that in late dry season months tortoises spent little time feeding. Late in the dry season feeding occupied only nine percent of tortoise daily activity time. In wet and early dry season months tortoises fed during 40 percent of their active hours. Even during the dry season competition for food may be insignificant because tortoises scarcely feed.

Burros trampled some tortoise nests; eighteen percent of 88 monitored nests were damaged by burros. Entire clutches were destroyed in 4.5 percent of the nests. Natural emergence success for *Geochelone elephantopus vandenburghi* was 64.9 percent.

CHAPTER ONE

INTRODUCTION

About twelve thousand years ago man began to domesticate selected animal species. As he spread across the globe, he took his domesticated animals with him. In time, domestic animals escaped or were abandoned. Some successfully established feral breeding populations in their new homelands.

The problems created by feral mammals are diverse and widespread. Island ecosystems are particularly fragile and vulnerable to the ecological disturbances that are created when domestic animals become feral. Goats, cattle, pigs, and sheep are among the destructive, large herbivores that have been widely introduced onto islands across the world and have been the subject of much research (on goats, Yocom [1967], Sykes [1969], Williams and Rudge [1969], Spatz and Mueller-Dombois [1973, 1975a], Coblentz [1976], Bullock [1977], Rudge and Campbell [1977], Wardel et al. [1978]; on sheep and cattle, Wilson and Orwin [1964], Taylor [1971]; on pigs, Taylor [1971], Spatz and Mueller-Dombois [1975b]).

The Galapagos Islands, 960 kilometers off the coast of Ecuador, are unique in their flora and fauna and in their historical role in the origin of Darwin's theory of evolution by natural selection. As on many of the world's island systems, various endemic Galapagos species are threatened by populations of exotic plants and animals. Feral horses, burros, cattle, goats, pigs, dogs, cats, rats and mice inhabit the Islands. Research projects are being conducted to investigate the ecological impact of these introduced species and recommendations are being made concerning methods of control or eradication.

In an effort to determine the effect that feral burros have on the endangered Galapagos tortoise, _Geochelone elephantopus_, I studied feral burro and tortoise feeding ecologies, population distributions and interactions on Volcan Alcedo, Isabela Island. Research began in October 1979 and was completed in December 1980.

Feral burros occur on all five of the major islands in the Galapagos Archipelago. The exact date of introduction is not known. Colonists first settled on Isla Floreana in the 1830s and brought with them a variety of domestic animals. Since burros are utilized by farmers on the mainland and are preadapted to arid climates, they were probably among the first animals taken to the Galapagos by early settlers. Burros were soon dispersed to even the uninhabited regions by oil seekers (R. H. Beck in Van Denburgh, 1914) who used them to transport kegs of tortoise oil to ships and settlements, and by miners who were in search of sulfur in the deposits around the volcanic craters.

Estimates of the feral burro populations on the major islands are as follows: 300 on San Cristobal, 200-300 on Santa Cruz, 500-700 on Santiago (Lucho Calvopina, pers. comm.), and 2,000-4,000 on Floreana (Tina Beach and Felipe Cruz, pers. comm.). In addition, burros occur on three of the five volcanoes that make up the largest island, Isabela. Volcan Cerro Azul and Sierra Negra on southern Isabela have relatively small burro populations; Volcan Alcedo, to the north, has a population of between 500 and 700 animals (this study).

Feral burros had become established on Isabela by the 1860s (S. Habel, 1868 in Salvin, 1876). By the 1880s, they were very numerous on Isabela as well as on San Cristobal, Floreana and Santa Cruz Islands (T. Wolf in Baur, 1891). Old literature makes no specific mention of exactly how and when burros arrived on Volcan Alcedo. Because Alcedo had both a large tortoise population and sulfur deposits, however, oil seekers and sulfur miners with pack burros surely visited its slopes.

The Charles Darwin Research Station (CDRS) and Galapagos National Park personnel have long feared that feral burros damage the flora and fauna of Alcedo and the other islands where they occur. Thorton (1971), Wiggins and Porter (1971), MacFarland et al. (1974a), and van der Werff (1978) expressed these fears. Prior to this study, however, no investigation of the impact of feral burros in the Galapagos had been undertaken. Similar studies have been completed of feral burros in the southwestern United States and their impact on flora, their competition with bighorn sheep, and their effect on birds and small mammals (Moehlman, 1974, 1979; Woodward, 1976; Woodward and Ohmart, 1976; USDI, 1977; Hanley and Brady, 1977 a, b; Norment and Douglas, 1977; Seegmiller and Ohmart, 1981).

In addition to a large burro population, Volcan Alcedo has the largest remaining population of Galapagos *Geochelone* tortoises. In the past, the Galapagos giant tortoises were heavily exploited; first by pirates, sealers and whalers in the 1600-1800s, then by colonists and oil seekers, and during the early 1900s, by scientific collecting expeditions. Well over 100,000 tortoises were taken from the Galapagos Archipelago (Townsend, 1925).

Of the original fourteen races of *Geochelone elephantopus* only ten races remain; seven of these are severely threatened due to decreased populations and introduced mammalian competitors and predators (MacFarland et al., 1974a, b). Alcedo's *Geochelone elephantopus vandenburghi* population is the least endangered of the tortoise races. However, introduced rats, cats, and burros on Alcedo pose a potential threat from both predation and competition.

CHAPTER TWO

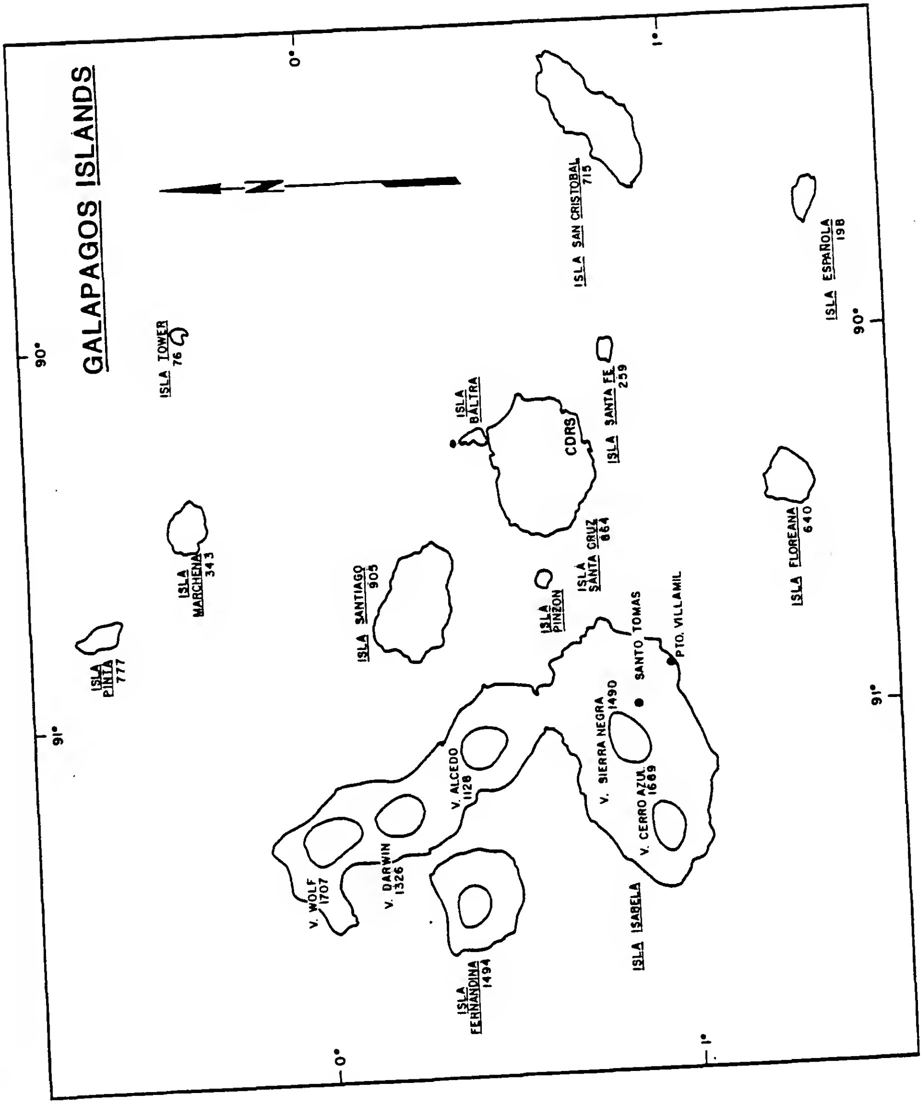
THE STUDY SITE

Volcan Alcedo, Isabela Island

Isabela is by far the largest island in the Galapagos group. Its land surface area of 4,670 square kilometers (Wiggins and Porter, 1971) includes more than half of the total land area of all the islands in the Archipelago combined. Six volcanoes, connected by extensive lava flows, form this J-shaped island (Figure 2-1). Volcan Alcedo, in the middle of Isabela and 1128 meters high, has a large central caldera which is between seven and eight kilometers wide (Banfield et al., 1956 and Parque Nacional Galapagos, 1980).

The Galapagos volcanoes are typical, gently sloping shield volcanoes; several of them are active. Sierra Negra, to the south of Alcedo, erupted as recently as 1979. Volcan Wolf erupted in September, 1982. Alcedo last erupted in 1954, from a small fissure on its outer southeastern flank (Thorton, 1971). There is an active fumarole on the inner southeastern wall of the crater which, until 1969, was surrounded by a bubbling pool of mineral-laden water. The pool has since dried, but the fumarole remains and emits hot sulfur steam

Figure 2-1 Galapagos Islands


GALAPAGOS ISLANDS
N
0°
1°
90°
91°
ISLA TOWER 76
ISLA MARCHENA 343
ISLA PINTA 777
ISLA SANTIAGO 905
ISLA BALTRA
CDRS
ISLA SANTA CRUZ 864
ISLA PINZON
ISLA SANTA FE 259
ISLA SAN CRISTOBAL 715
ISLA ESPAÑOLA 198
ISLA FLOREANA 640
SANTO TOMAS
PTO. VILLAMIL
V. SIERRA NEGRA 1490
V. CERRO AZUL 1689
V. ALCEDO 1128
V. DARWIN 1326
V. WOLF 1707
ISLA ISABELA
ISLA FERNANDINA 1494

continuously. Other small sulfur vents dot the inner south and southwestern slopes of the caldera, testimony to the incessant activity underground.

To reach Alcedo's crater, one lands on a small beach towards the northeastern side of the volcano. From there, a burro/tourist trail leads ten kilometers up its flank to the base of the crater rim. My "Midcamp" study site was located in this area, at the eastern foot of the volcano (Figure 2-2). The rim of Alcedo rises abruptly from its outer slopes. A few hundred meters high and relatively flat-topped in some places and hilly in others, the rim varies greatly in width. My "Rim Camp" study site was approximately five kilometers southeast of the ascent path from outer flanks to rim. Six kilometers further south along the rim was a descent path to the inner wall fumarole. From the fumarole, a path led to the caldera floor and my "South Floor" study site. One of the main tortoise nesting zones was located in this area. During the rainy season several large pools of water formed on the south floor. These were heavily used and of great importance to animals since there is no permanent source of fresh water on Alcedo. The "North Plateau" study site was located on the widest, northern section of the rim. Directly below the North Plateau, on the caldera floor, was the north floor nesting area, where many tortoises nested.

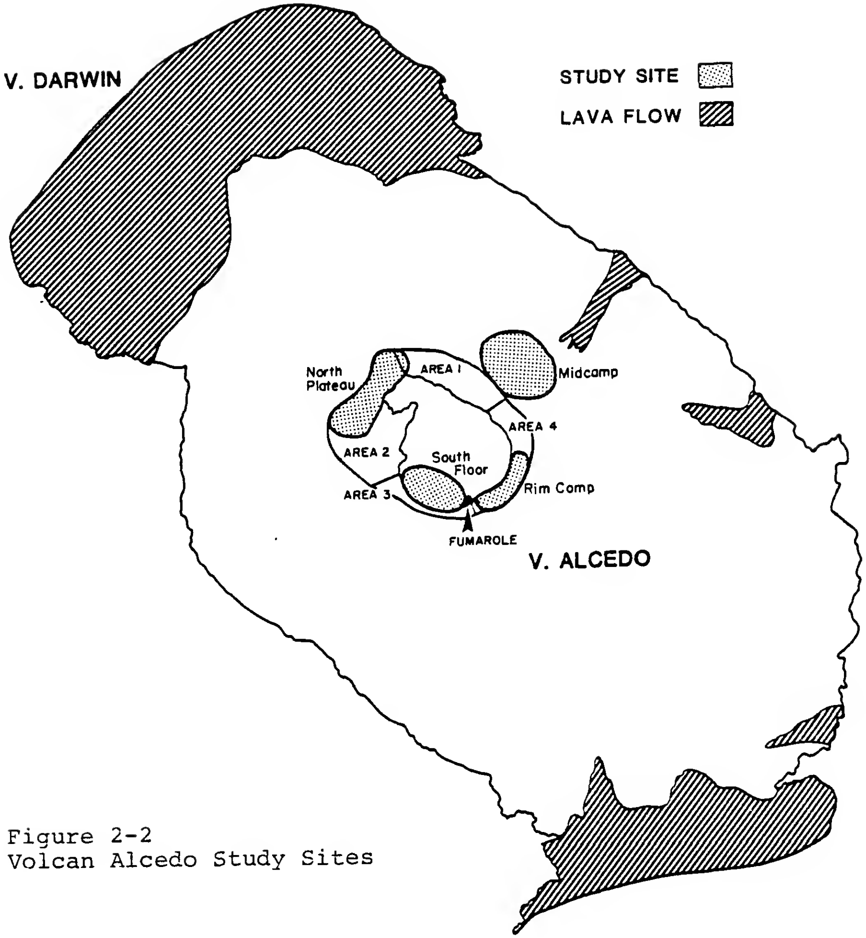


Figure 2-2
Volcan Alcedo Study Sites

To facilitate data collection, I divided the caldera rim into four areas of roughly equal length. Area two encompassed the wide North Plateau and area four included Rim Camp study site. Areas one and three were relatively narrow sections of the rim with vegetation somewhat similar to Midcamp and North Plateau, respectively.

The Climate

The Galapagos Islands, though they straddle the equator, are not typically "tropical" in their climate, which is strongly influenced by the sea surrounding them. The Humboldt current, sweeping up the western coast of South America from Antarctica, turns west at the equator and bathes the Islands in its chilling waters. Sea water temperatures range from 19 to 23 degrees C during the warmer months of January through June and are usually several degrees cooler during the remainder of the year (Wellington, 1975).

There are two seasons in the Galapagos: a "warm season" (also referred to as "wet season") from January through June and a "cool, garua season" (or "dry season") from July through December. Rains, though they primarily fall during the warm, wet season, vary considerably from one location to the next. During the dry season, coastal areas may be several months without precipitation. Highland areas, however, are often blanketed in a fine wet

Table 2-1

Monthly Rainfall, 1980
(Millimeters)

Location	CDRS	Puerto Villamil	Santo Tomas	Media Luna	Volcan Alcedo*
Island	St.Cruz	Isabela	Isabela	St.Cruz	Isabela
Altitude	6 m	6 m	350 m	620 m	1100 m
January	23.4	2.4	62.6	267.0	(18.6)**
February	69.2	20.2	207.8	240.0	178.4
March	0	6.0	8.0	170.0	13.2
April	139.4	54.0	292.1	275.0	360.7
May	0	31.4	103.7	0	(141.9)***
June	1.2	1.0	23.4	-	-
July	4.7	0	68.2	156.0	58.5
August	3.0	11.0	58.9	-	.8
September	3.6	5.3	60.4	-	-
October	5.8	2.9	102.0	108.0	0
November	4.5	5.8	56.4	-	46.0
December	1.0	12.5	58.8	162.0	(54.2)***

*Southeast Rim Camp.
**Data for only the last five days of January.
***Data for only the first one-half of the month.

Table 2-2

Daily Air Temperatures (^{o}C)
Isabela Island, 1980

Location Altitude	Pto.Villamil 6 m		Santo Tomas 350 m		V.Alcedo* 1100 m	
	Max.	Min.	Max.	Min.	Max.	Min.
January	26.4	24.3	27.8	18.6	20.6	15.0
February	29.6	26.5	29.2	19.0	24.2	15.1
March	27.6	24.0	31.4	19.4	26.5	16.1
April	27.6	24.2	30.1	20.1	26.3	17.0
May	26.1	24.0	26.5	19.4	25.0	16.7
June	25.3	23.3	25.0	17.3	-	-
July	24.1	21.1	23.0	16.4	21.9	12.0
August	23.9	19.4	23.2	16.2	26.7	11.4
September	23.7	19.0	23.4	16.0	-	-
October	23.1	19.6	23.2	16.5	24.5	13.0
November	23.1	20.0	24.1	16.5	23.7	12.1
December	23.1	20.8	25.0	16.8	23.3	13.1

*Southeast Rim Camp.

mist, "garua," which condenses on the vegetation. The prevailing winds are from the southeast, hence the southern, windward slopes of islands are wetter than their northern slopes. Wiggins and Porter (1971) and van der Werff (1978) provide more detailed discussions of the climate of the Galapagos Islands.

Meteorological data for 1980 on Volcan Alcedo is presented in Tables 2-1 and 2-2. Monthly rainfall and daily temperatures from Alcedo (Rim Camp) are compared with data from other CDRS weather stations in the Islands. As mentioned previously, rainfall is quite variable and often localized. Areas of higher altitude tend to receive more precipitation, but not necessarily during the same months of the year, or as a result of the same storms. During 1980, rainfall on Alcedo was greatest between January and May; March was unusually dry. From August through early November, very little rain fell. Light rains began again in mid-November. Temperatures at 1100 meters on Alcedo were predictably lower than temperatures recorded on the southern coast of Isabela at Puerto Villamil or on the slope of Sierra Negra at Santo Tomas.

Sporadic rainfall and temperature records from the South Floor and Midcamp study sites indicate that these areas generally received less rainfall than did Rim Camp. Likewise, at both sites, maximum and minimum temperatures were usually several degrees higher than at Rim Camp.

Rim Camp, situated on the southeastern section of Alcedo's rim, was in the path of the wet prevailing winds. Consequently this area received a great deal of precipitation in the form of garua, even during the cool, dry season. Frequently, when the rest of the volcano was dry and warm, and bathed in sunshine, Rim Camp was wet, cold and windy, under a thick blanket of garua. Heavy garua, condensing on the vegetation along the southeastern rim, would often form drip-pools under the moss covered trees. Many of these pools had become quite deep and enlarged after years of tortoise and burro use.

Daily weather profiles were kept for 121 days while I was camped at Rim Camp (Table 2-3). On 92.6 percent of these days there was garua. Rarely was the rim clear at sunrise, and only 7.4 percent of the days were garua-free from sunup to sundown. Most common were days with garua at dawn, followed by some sunshine in the early afternoon. Often, just before sunset, the garua clouds would roll in again.

Seeking to compare the amount of moisture received by the various sections of the volcano, I set up several "garua catches." Four locations along the crater rim were chosen and at each site two wire window-screens cut into squares measuring 50 centimeters by 50 centimeters were erected. Garua condensed on the screens, dripped down into a slanted pipe-trough along the lower edge and was collected in a holding container until measured.

Table 2-3

Monthly Frequency of Garua Days
Rim Camp, Alcedo
1980

	Garua/Rain Entire Day	Garua and Sun	Sun Entire Day
January	3	2	0
February	5	9	0
March	3	5	3
April	3	11	0
May	8	2	0
July	7	6	0
August	0	6	3
October	1	5	1
November	6	14	2
December	11	5	0
Total	47	65	9
Percentage	38.8%	53.7%	7.4%

I positioned the two screens at each rim location at slightly different angles, to insure that at least one would be perpendicular to the direction of the winds for maximum garua collection. Later, where one screen was obviously more correctly oriented to the winds, I discarded the data from the poorly positioned screen. Or, if the two screens collected approximately equal amounts of water and neither was consistently more efficient, I averaged the amounts collected.

It was difficult to suspend containers for water holding more than 3.8 liters, due to their weight when filled, and to the destructive curiosity of tortoises. Tortoises destroyed my garua catch number three. I was forced to attach other screens high or over rockpiles where tortoises could not reach. Unfortunately, because I could only infrequently check the garua catches north and south of Rim Camp, on extremely wet days the 3.8 liter containers overflowed. Therefore the data presented in Table 2-4 are an underestimate of garua precipitation collected by catches number one/two and four. Catches five and seven never overflowed.

As seen from Table 2-4, the amount of garua moisture condensing on the southeastern section of Alcedo was much greater than the amount condensing on the eastern and northeastern rim. I found that differences in amount of moisture strongly influenced the distribution of both

Table 2-4

Average Daily Garua Catch Measurements (Milliliters/Centimeters^2) 1980

Garua Catch Location (Position Number)	SE, Above Descent to Fumerole (1 & 2) n=9 days	SE Rim Camp (4) n=51 days	E, at Tourist Ascent Trail (5) n=16 days	NE, Last Hill Before North Plateau (7) n=8 days
July	.68	1.14	.008	.01
August	1.25	.51	.004	.02
October	1.36	1.14	.12	.02
November	.63	1.22	.06	.10
December	–	1.52	.10	.12
Average ml/cm^2 July-December	.98*	1.11**	.06	.06

*Because this catch had a 1 gallon maximum, it overflowed one-half the time, thus this is an underestimate.

**Two and a half gallon maximum, only rarely overflowed.

tortoises and burros in the dry season. (See Chapter Three.)

The Vegetation

The heterogeneous pattern of soil types and moisture availability on Alcedo has produced a diverse array of vegetational zones. Van der Werff (1978), employing a method of vegetation classification based on physiognomical and structural criteria (after Fosberg, 1967) made a detailed study of the vegetation of Alcedo. He listed the species present in 10 meter by 40 meter quadrants and estimated species abundance using the Tansley and Chipp categories (1926, as cited by van der Werff, 1978). Following are summaries of van der Werff's descriptions of the vegetation types at my four study sites.

Rim Camp Study Site

Alliance Psychotrian rufipedis, association Zanthoxylo-Polystichetum gelidi: an open, mossy evergreen forest. The tree and shrub layers, three to seven meters tall, were dominated by *Zanthoxylum fagara*, *Tournefortia pubescens* and *Tournefortia rufosericea*. The herb layer was nearly closed, with ferns and *Verbena spp*. the most common tall herbs present. The low herb layer was made up of several species which prefer open habitats. These included *Borreria laevis*, *Conyza bonariensis*, *Cyperus brevifolius*, *Dichondra repens*, *Hyptis rhomboidea*, *Mecardonia dianthera*, *Panicum fasciculatum*, *Paspalum conjugatum*, *Plantago major* and *Solanum nodiflorum*. Exposure to winds and garua also contributed to the lowness and openness of the vegetation. Vascular epiphytic plants were very common.

On the upper outer slopes of the southeastern rim was the community of *Pteris quadriaurita* and *Tropidia polystachya*. This community, not placed in an alliance by van der Werff, consisted of two structurally different vegetation types; one, an open evergreen forest dominated by *Scalesia microcephala* and *Croton scouleri* with a shrub layer of *Tournefortia rufosericea* and *Psychotria rufipes*; the second, a closed evergreen scrub vegetation dominated by *Psychotria rufipes* and *Tournefortia rufosericea*. *Ipomea alba*, the most conspicuous herb, grew in dense mats on the shrubs. For a complete list of the plant species which occurred on Alcedo's southeastern rim and upper slope, see van der Werff (1978). A partial species list is included in Chapter Six of this report.

South Floor Study Site

Alliance Burserion graveolentis, association Abutiletum depauperati, subassociation cyperetosum aristati: a low deciduous forest. The most common tree was *Bursera graveolens* and *Walteria ovata* was the most common shrub. The tree layer was often only four meters high; the shrub layer was one to three meters high. The herb layer, with coverage of about 50 percent, was composed of many species including *Cyperus anderssonni*, *C. aristatus*, *C. confertus*, *Cordia revoluta*, *Crotalaria incana*, *Desmodium procumbens*, *Paspalum galapageium*, *Portulaca oleracea*, *Phyllanthus caroliniensis* and *Chrysanthellum pusillum*. Epiphytes (except lichens) were lacking.

Several communities which van der Werff did not place in alliances also occurred on the South caldera floor. The community of *Cyperus ligularis* and *Scoparia dulcis* was a sparse, open evergreen herb vegetation, found around fumaroles and sulfur vents. The community of *Polygola anderssonni* and *Scalesia microcephala*, an open evergreen shrub savanna, was found on the southwestern floor in areas of pumice and obsidian deposits. *Walteria ovata* and several herbs including *Blainvillea dichotoma*, *Cenchrus platyacanthus* and *Ophioglossum reticulatum* were common in this community. Finally, on the bare lava flows of Alcedo, of which there were several in the caldera, the community of *Jasminocereus thouarsii var. sclerocarpus* and *Pilea peploides*, a sparse vegetation dominated by cacti, occurred. See van der Werff and Chapter Six of this report for more detailed species lists.

Midcamp Study Site

Alliance Burserion graveolentis, association Abutiletum depauperati, subassociation sidetosum rupo: an open evergreen shrub community with a closed herb layer. The dominant shrub species was Scalesia microcephala. The most common herbs included Bidens riparia, Blainvillea dichotoma, Cenchrus platyacanthus and Sida rhombifolia. A few trees of Bursera graveolens and Pisonia floribunda were present; epiphytes were absent except for lichens.

Areas of Pennisetum pauperum and Acnistus ellipticus, a more or less closed, evergreen scrub community, were also found at Midcamp. Common shrub species were Zanthoxylum fagara, Psidium galapageium and Tournefortia pubescens. The cover of the herb layer reached 80 percent after rains and common herb species were Heliotropium angiospernum, Pennisetum pauperum and Sida rhombifolia. Epiphytic lichens occurred frequently.

The community of Salvia pseudoserotina and Polypodium tridens, a more or less closed, evergreen scrub community occurred on Alcedo's eastern slope around Midcamp. Common shrubs were Zanthoxylum fagara, Scalesia microcephala and Psidium galapageium. Common wet season herbs included Commelina diffusa, Alternanthera halimifolia and Sida glutinosa. Ferns, bryophytes and lichens were common.

North Plateau Study Site

The community of *Ophioglossum reticulatum* and *Tournefortia pubescens*, an open or closed evergreen scrub, was found on the northeastern, northern and western sections of Alcedo's rim. Trees were absent in this community and common shrubs, growing to three meters, were *Zanthoxylum fagara*, *Tournefortia pubescens*, *Scalesia microcephala* and *Darwiniothamnus tenuifolius var. glabriusculus*. Herbs covered 80 to 100 percent of the ground after the rains and included several ephemeral species. Some of the most common were *Bidens riparia*, *Blainvillea dichotoma*, *Chrysanthellum pusillum*, *Ophioglossum reticulatum* and *Trichoneura lindleyana*. Epiphytic plants were rare.

CHAPTER THREE

BURRO AND TORTOISE POPULATION SIZES AND DISTRIBUTIONS

In the cool dry season when, on most of Alcedo, puddles and ephemeral plants were desiccating and dying, the area around Rim Camp remained green and moist, a consequence of almost daily garua. During this time of the year I suspected that both burros and tortoises converged on the southeastern rim. There they could feed on damp grasses and suck what little water was available from the muddy puddles that formed under dripping trees after a night of heavy garua. To study the seasonal changes in the distributions of burros and tortoises, I made regular bi-monthly around-the-rim censuses. I also made various burro and tortoise counts in my study sites as frequently as was feasible.

Methods

On all of these censuses and counts I tallied the numbers, sexes, and ages of all observed burros, and recorded information on group size and composition when aggregations of animals were seen. An adult burro, of course, could not be aged from afar, but a young animal was classified as either infant (from newborn to five months), juvenile (from six to ten months), or adolescent (from ten to more than twelve months, but not full grown). From information kept on all young animals sighted and from records of all sightings of female burros in their last months of pregnancy, the peak foaling season for burros was obtained.

Since burro population size could not be calculated using the traditional methods of mark and recapture, aerial surveys and the like, I made an estimate of population size utilizing data from my counts and censuses. This estimate was based on the average number of burros seen in a specific type of habitat on Alcedo and the extent of that habitat on the volcano. Tortoise population size was estimated in the same way. A mark and recapture study might provide a more accurate estimate of the Alcedo tortoise population, but I was not authorized to conduct such research.

On the censuses, tortoises were counted and classified into three arbitrary size categories: small (curved carapace length of less than 75 centimeters), medium (curved carapace length between 76 and 105 centimeters), or large (curved carapace length greater than 106 centimeters). I could not reliably sex tortoises, therefore this information was not recorded.

For the purpose of rim censusing, I mentally divided the crater rim into four areas based on parameters such as local climate, moisture and vegetation

(Figure 2-2). Though these four areas were approximately equal in length, their widths were variable; the area which encompassed the North Plateau was by far the largest. The around-the-rim path I followed on rim censuses required between six and eight hours to complete, one and a half to two hours for each area. Because visibility and rim width varied considerably along my census route, the amount of land actually surveyed per area also varied. However, the aim of rim censusing was to monitor seasonal changes in burro and tortoise distribution. Therefore, it was important only that I follow the same path on each census and record all animals seen each time, so that the resulting identically executed censuses could later be compared.

Dense garua occasionally reduced the visibility on censuses. But dense garua rarely occurred on most of Alcedo, except in the early mornings and along the south-eastern rim. Fortunately this section of the rim was sufficiently narrow that animals there were often easy to count in spite of garua. On garua days, slope counts could not be made. In order to reduce the loss of data caused by low visibility due to early morning garua along the same rim sections, I alternated the direction I went around the rim on successive counts.

Rim censuses were made as close to the first and the fifteenth of each month as possible. I began taking censuses in November 1979 and made a total of 26 through

December 1980. Tortoises were not counted on the 1979 censuses, but they were recorded thereafter. Censuses were not made in June or September 1980, as I was absent from Alcedo during those months.

Besides the bi-monthly around-the-rim censuses, various other censuses and counts were made in my study areas (Table 3-1). Censuses were made along established paths and on all of them, excluding the Rim Camp census, I counted both tortoises and burros. Counts were made from distant vantage points overlooking or below areas to be surveyed. From a distance, accurate counts of tortoises could not be made, therefore only burros were recorded on counts. Study site censuses and counts were made so that I could investigate the local changes in tortoise and burro abundances and served to reinforce the distributional patterns elucidated by the around-the-rim censuses.

At Rim Camp study site, censuses were made at least four times each month. These Rim Camp censuses were taken along the rim, from my camping spot to the fumarole descent path, at all hours of the day to test whether burros were observed more often at certain times than at others. A southeast slope census path was established and I made the one and a half hour burro and tortoise census at least twice a month during my year on Alcedo. Lastly, from a spot on the low outer slopes below the southeastern rim, burros could be counted on the upper

Table 3-1

Burro and Tortoise Censuses and Counts

Census/ Count	Species Counted	Study Site/ Area Counted	Frequency of Counts
Around-the-Rim Census	burros & tortoises	Areas 1-4 rim, and slopes if visible	2 per month
Rim Camp Census	burros	Rim Camp/Area 4 rim, and slopes if visible	4-10 per month
SE Slope Census	burros & tortoises	Rim Camp/Area 4 outer slopes	2-3 per month
Slope Count from Outer Floor	burros	Rim Camp/Area 4 outer slopes	4 in a year
South Floor Census	burros & tortoises	South Floor inner caldera floor	2 per month
Sulfur Slopes Count	burros	South Floor inner western slopes	2 per month
Midcamp Census	burros & tortoises	Midcamp	2-3 per month
N. Plateau Count	burros	N. Plateau/ Area 2	5 in a year

slopes. I took the long trip down to the outer southeastern slope only four times, but the resulting burro counts show dramatic differences in numbers of burros on the southeastern slopes at different times of the year.

South Floor censuses of burros and tortoises at study site two were made bi-monthly, concurrently with rim censuses, to study the changing distributions of both species on the floor. Counts of burros on the sulfur slopes of the inner western caldera also were made in conjunction with rim censuses. Midcamp censuses were made at least twice a month; burros and tortoises were tallied along a two hour path on the eastern outer slopes of Alcedo. Finally, five counts of North Plateau burros were made during the year of study.

Rim Census and Count Results

The total number of animals seen on each rim census varied greatly (Figure 3-1). The maximum number of burros counted was 176 animals on July 5, 1980. The smallest number of burros was observed on January 30, 1980, when only 21 were counted on the entire around-the-rim census. Many more tortoises were seen per census than burros; their numbers also fluctuated from census to census. The maximum number of tortoises counted was 640 on July 5, 1980. The minimum number was 169 on October 24, 1980.

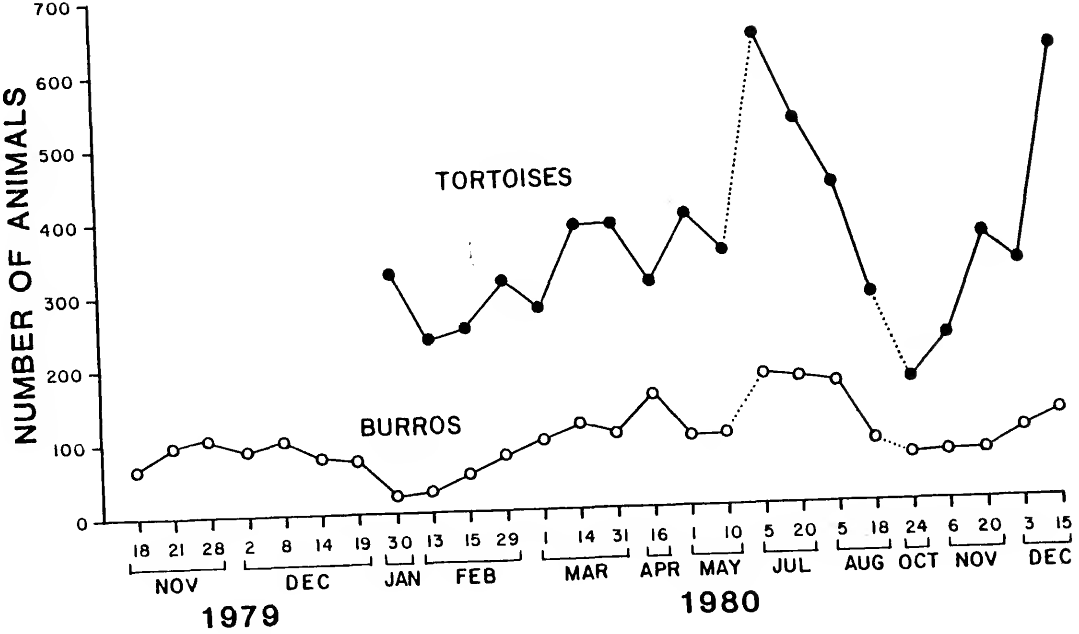


Figure 3-1 Around-the-Rim Censuses of Burros and Tortoises

One apparent cause of the observed fluctuations in the total numbers of burros and tortoises seen on the censuses was the daily weather. For example, on hot sunny days, both tortoises and burros spent much of their time under shade trees and were consequently more difficult to observe and count. The low counts of burros and tortoises made in October and November 1980 were the result of hot weather. On cool, cloudy days, like July 5, burros and tortoises were especially active and easy to count. On some mornings thick garua reduced visibility. On others, however, particularly on an extremely wet garua morning following a dry spell on the southeastern rim, burros and tortoises would be out in large numbers, searching to quench their thirsts in the drip-puddles forming under trees. These animals were often so intent on their quest that they were unaware of my approach, making them especially easy to observe. The lowest total burro count, made on January 30, 1980, was the only entire census made in the rain. Visibility was poor and no doubt animals were less active than normal, due to the weather conditions.

I averaged census data over months and tabulated the sightings by area (Tables 3-2 and 3-3). Chi-square tests on burro and tortoise data showed significant differences between the numbers of animals seen in any given area in different months for all except area one burros (χ^2 values ranged from 33.5 to 384.3 with $P<.001$).

Table 3-2

Average Number of Burros on Rim Censuses
by Month and Area, 1979/80

Area	Nov	Dec	Jan Feb	Mar Apr	May	Jul	Aug	Oct Nov	Dec
1	6.3	9.0	2.5	3.8	65.0	10.0	14.5	11.0	8.5
2	5.0	9.8	22.5	84.0	66.5	124.0	65.5	11.3	23.0
3	33.7	45.8	14.5	24.0	18.5	36.0	24.5	34.3	47.0
4	43.3	20.0	2.0	2.8	4.5	30.5	21.5	9.7	31.0

Table 3-3

Average Number of Tortoises on Rim Censuses
by Month and Area, 1980

Area	Jan Feb	Mar Apr	May	Jul	Aug	Oct Nov	Dec
1	22.5	35.5	32.0	29.0	3.0	5.3	14.5
2	79.5	111.8	97.0	78.0	24.5	12.3	43.5
3	102.0	119.8	152.5	131.0	67.5	51.3	151.0
4	76.0	70.0	91.5	342.5	266.0	184.3	260.0

A few burros were found on area one consistently throughout the year. A summary of the changing burro and tortoise distributions on the rest of the volcano follows.

Burros were more numerous than would be expected in a uniform distribution on area two between March and August, and less common than expected from October to February (Figure 3-2). On area three, burro numbers were less than expected or near the expected value between January and November; more burros were seen than expected only in December 1979 and 1980. Between January and July, burros were rarely seen on area four; in the months of August and December, burros were quite common there.

The changes in tortoise distribution followed a similar pattern (Figure 3-3). Between March and July tortoises were common on area one. In December, January and February, they were seen at the expected rate on censuses. Between August and November there were very few tortoises along the rim section of area one. During March, April, and May, there were many more tortoises than expected on area two; in August through December, there were fewer. On area three, tortoises were abundant in May, July, and December. There were relatively fewer tortoises on area three between August and November. And finally, tortoises were most numerous on area four between July and December, while fewer tortoises were recorded on area four censuses during January to May.

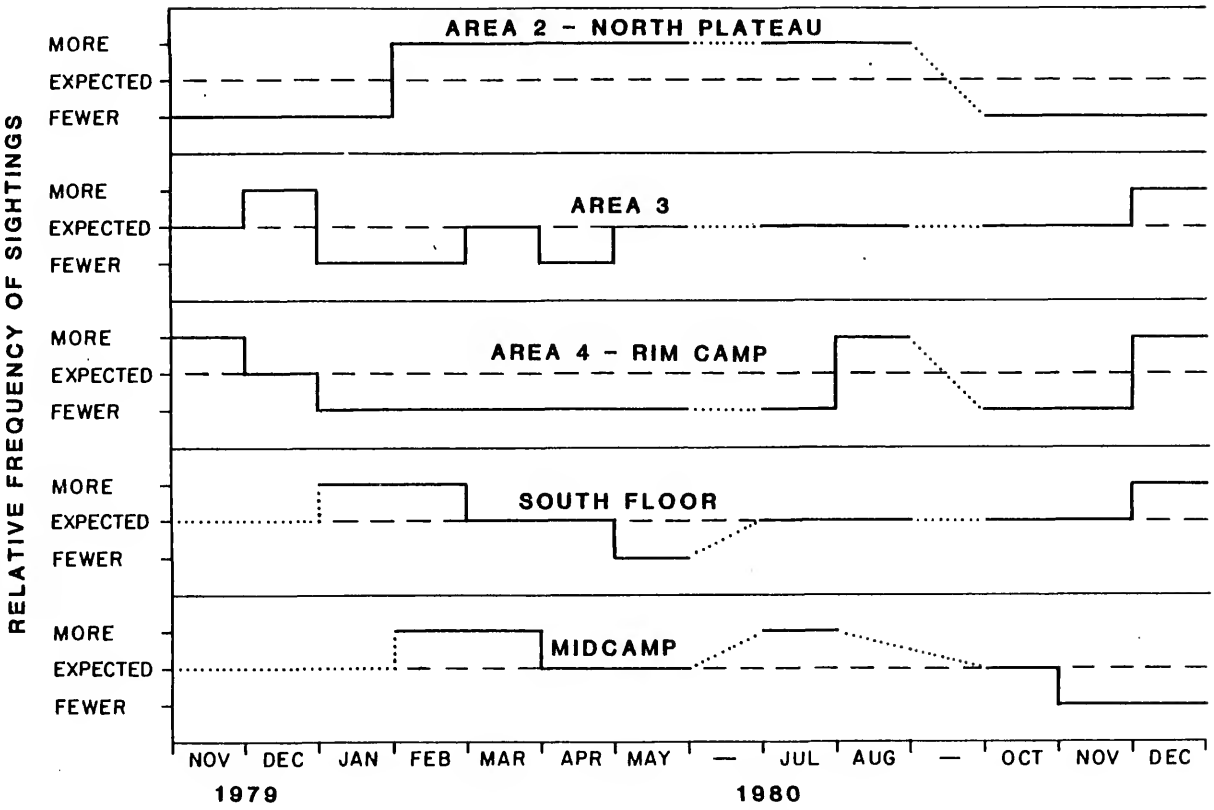


Figure 3-2 Burros on Around-the-Rim,
South Floor and Midcamp Censuses

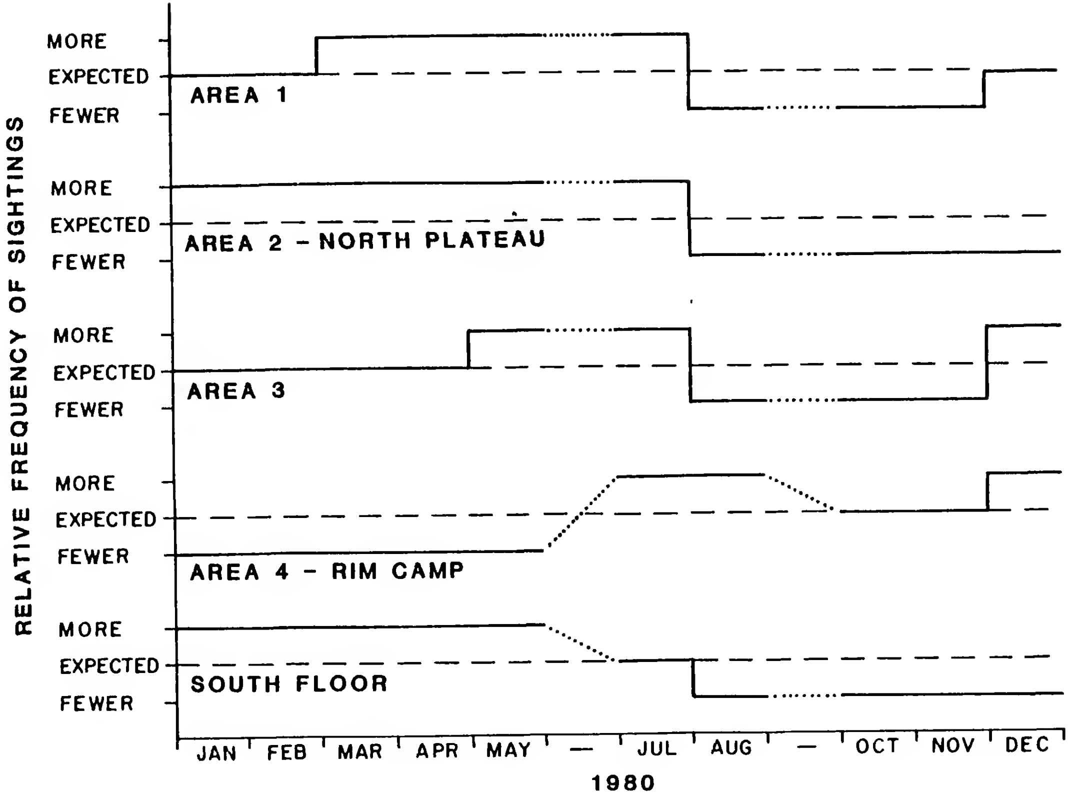


Figure 3-3 Tortoises on Around-the-Rim and South Floor Censuses

To determine whether burros and tortoises were utilizing the same sections of the volcano at the same times of the year, I applied separate chi-square tests to monthly burro and tortoise around-the-rim census data. All tests showed significant differences between the burro and tortoise data (January/February at $\chi^2=15.4$, $P<.01$ and for all others, $\chi^2 = 39.0$ to 263.1, $P<.001$); burros and tortoises were not distributed in the same manner on Alcedo.

Briefly, the results show that in the early wet season months of January to April, there were comparatively more burros than tortoises on area two and comparatively more tortoises than burros on area four. In May and July, the situation had changed, with tortoises now comparatively more abundant on area two and burros more abundant on area four. From August to December, burros were not utilizing area four to the extent that tortoises were; however, burros were common relative to tortoises on areas one, two and three.

The various additional burro and tortoise counts I made at Rim Camp study site included a southeast slope census and a slope count from the outer floor. I made a total of 80 Rim Camp censuses at different hours of the day on which only burros were tallied. A summary of the Rim Camp census data, grouped by month and time of day, is presented in Table 3-4. There was a significant difference in the number of burros seen at different times of the day (chi-square test, $\chi^2 = 18.4$, $P<.01$). More burros were seen than expected in a uniform distribution from 10:00 a.m. to 2 p.m. in November and December 1979, and from dawn to 10:00 a.m. between July and December 1980. Fewer burros were seen than expected in October through December 1980 between 10:00 a.m. and 2:00 p.m. and in November and December 1979 between 2 p.m. and sunset. Generally the Rim Camp census data show the same pattern of burro abundance along the southeast rim that was evident from the around-the-rim census data for area four. Few burros were recorded from January to July, with a substantial increase between August and December.

Fifteen southeast slope censuses were made at intervals throughout 1980 (Table 3-5). Once again these data provide evidence that burros and tortoises migrate into and out of the area along Alcedo's southeastern rim. Between January and April very few burros and tortoises were recorded on slope censuses. However, from August to December many more animals were present on this section of the volcano. Chi-square tests indicated that statistically significant differences existed between the numbers of animals seen on slope censuses during the various months ($\chi^2 = 103.7$ for burros and 77.5 for tortoises, $P<.001$ for both).

Burros on the outer slope also could easily be counted from down below on the outer floor. I made four long hikes down to the outer floor to count slope burros

Table 3-4

Rim Camp Censuses

Month	Year	Time of Day*	No. of Counts**	Average No. Burros on Rim	Average No. Burros on Slope
November and December	79	da-10	6	21.8	33.5
		10- 2	5	30.2	56.6
		2-du	3	11.3	24.0
January to March	80	da-10	5	2.2	0
		10- 2	9	1.0	0.2
		2-du	7	1.9	0.8
April and May	80	da-10	9	0.8	0
		10- 2	6	0.3	1.0
		2-du	2	0	0.5
July and August	80	da-10	8	3.4	3.8
		10- 2	3	1.7	0
		2-du	6	7.3	0
October to December	80	da-10	7	25.7	-
		10- 2	3	10.3	20.5
		2-du	1	11.0	7.0

*da-10 is from dawn to 10 a.m., 10- 2 is from 10 a.m. to 2 p.m., 2-du is from 2 p.m. to dusk.

**On 37 of the 80 counts, burros on the slope could not be counted because of thick garua.

Table 3-5

Southeast Slope Censuses

Month	Year	No. of Counts	Average No. Burros	Average No. Tortoises
January and February	80	3	4.3	-
March	80	2	2.0	7.0
April	80	3	4.3	4.0
August	80	2	27.5	42.0
November	79	3	63.3	-
November	80	3	42.7	50.0
December	79	1	16.0	-
December	80	2	32.0	58.5

and a chi-square test showed statistically significant differences between the total numbers of burros I tallied on each count. In early November 1979, I counted 161 burros on the slope; in late December 1979, I counted 26; in early March 1980, only three were counted; and in mid-October 1980, I counted 118 ($\chi^2 = 218.3$, $P<.001$).

Twice each month South Floor censuses of burros and tortoises, and counts of burros on the inner western sulfur slopes were made (Tables 3-6 and 3-7). I found that both burros and tortoises moved into and out of the caldera; their movements were apparently correlated with changing water and food availability. The greatest numbers of burros on the South Floor were observed between December and February (Figure 3-2). Tortoises likewise showed a definite peak of abundance on the floor, but it occurred a few months later than the burro peak; they were most numerous between February and May (Figure 3-3). On the sulfur slopes (the inner caldera slopes of area three), burros were abundant from March to May and thereafter dwindled to almost zero in December. Chi-square tests showed significant differences in the number of burros and tortoises on South Floor censuses, and of burros on sulfur counts in the different months of 1980 ($\chi^2=16.2$ for floor burros, $P<.02$; $\chi^2=142.0$ for floor tortoises, $P<.001$; $\chi^2=181.8$ for sulfur slope burros, $P<.001$)

Table 3-6

South Floor Censuses, 1980

Month	No. of Counts	Average No. Burros	Average No. Tortoises
February	3	31.7	143.0
March and April	3	17.0	133.7
May	2	14.0	198.5
July	2	17.0	110.3
August	2	21.0	47.5
October and November	3	18.7	51.5
December	2	33.5	61.3

Table 3-7

Sulfur Slope Counts, 1980

Month	No. of Counts	Average No. Burros
February	3	30.0
March and April	4	55.5
May	1	76.0
July	2	21.5
August	2	6.5
October and November	3	1.7
December	2	1.0

To determine whether tortoises of the three different size classes were uniformly distributed on Volcan Alcedo, I applied chi-square tests to tortoise size data from my around-the-rim and South Floor censuses. Figures 3-4, 3-5 and 3-6 graphically illustrate the changing distributions of the tortoise size classes during the different months of the year. Three chi-square tests, each utilizing size and distribution data for a four month period, were used; all showed significant differences among the distributions of different sized tortoises (χ^2=112.8 for January to April, χ^2=88.7 for May to August, χ^2=206.5 for October to December; $P<.001$ for all).

The tortoise size class distribution results are complex and difficult to interpret. These data show that small and medium tortoises seemed to prefer areas one and four during the early wet season months of January to April; small tortoises were also common on the South Floor. Large tortoises preferred area two and were less common than would be expected if their distribution were uniform, on areas one and four.

During May to August, small tortoises were more abundant than predicted by a uniform distribution at the South Floor study site. Medium tortoises were more abundant than predicted on area four and large tortoises were still common on area two. In the months of October to December, small tortoises were more numerous on areas

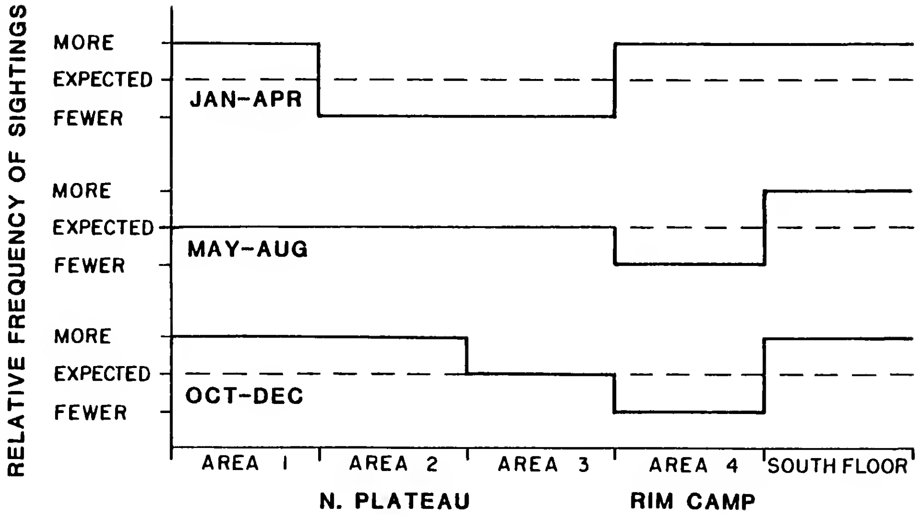


Figure 3-4 Distribution of Small Tortoises on Alcedo, 1980

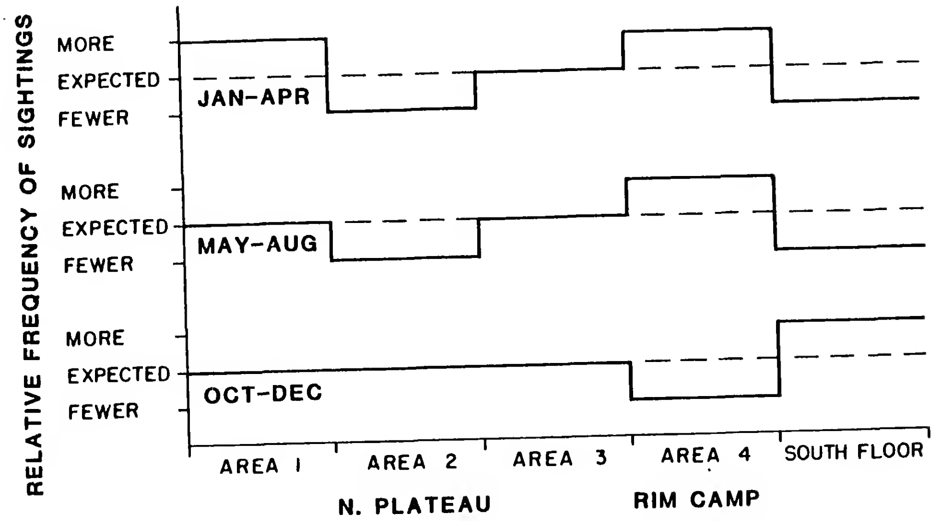


Figure 3-5 Distribution of Medium Tortoises on Alcedo, 1980

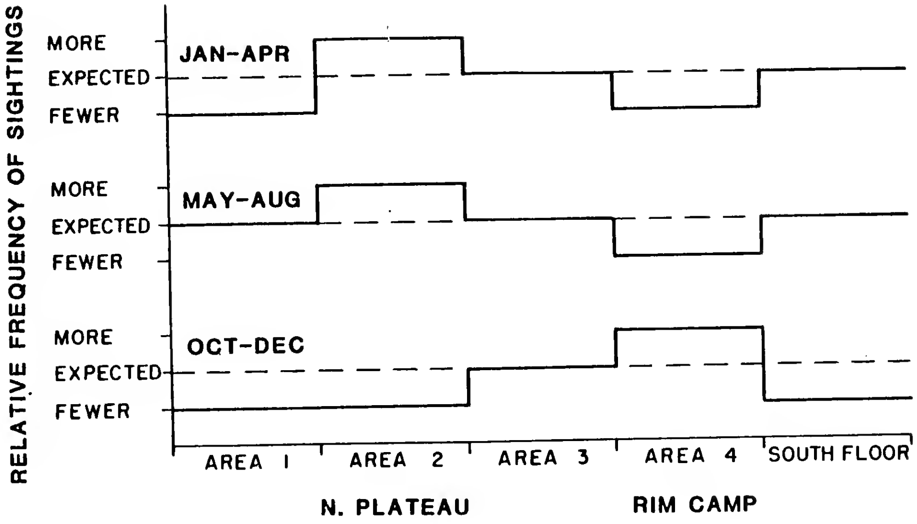


Figure 3-6 Distribution of Large Tortoises on Alcedo, 1980

one and two in addition to the South Floor. Medium tortoises were more abundant than expected at uniform on the South Floor and large tortoises were common on area four.

Counts made at the Midcamp and North Plateau study sites were taken at infrequent intervals, whenever I could travel to these areas (Tables 3-8 and 3-9). Burro numbers were significantly different between months at both Midcamp and North Plateau ($\chi^2=50.2$ for Midcamp burros, $\chi^2=49.5$ for North Plateau burros, $P<.001$ for both). A larger number of burros than expected was tallied at Midcamp in February and July and fewer burros than expected were counted there in November and December (Figure 3-2). Burros on the North Plateau were most numerous in July, and least abundant in November. Tortoise Midcamp census totals did not vary significantly during the months of 1980.

Using data from the various censuses and counts reported above, and knowledge of Volcan Alcedo following a year of extensive hiking and camping there, I estimated the Alcedo feral burro population to be between 500 and 700 animals. I estimated the tortoise population to be around 3,000 animals. MacFarland et al. (1974a) estimated 3,000-5,000 tortoises on Alcedo but I have been unable to find out on what procedures their estimate was based. As mentioned earlier, I based my estimates on the number of burros or tortoises generally observed in a

Table 3-8

Midcamp Censuses, 1980

Month	No. of Counts	Average No. Burros	Average No. Tortoises
February	6	36.0	-
March	2	29.5	9.0
April and May	3	16.0	11.7
July	3	32.3	4.3
October	1	25.0	0
November	3	6.0	2.7
December	1	2.0	6.0

Table 3-9

North Plateau Counts, 1980

Month	No. of Counts	Average No. Burros
May	2	73.5
July	1	106.0
August	1	77.0
November	1	24.0

particular habitat on Alcedo and the extent of that habitat on the volcano.

Burro Foaling Season and Group Size/Composition Results

Very young burros were recorded on Alcedo during all months of 1980. Yet there was a definite peak in the number of births during the rainy season (Figure 3-7). Between March and July, burros from newborn to five months old were observed more often than young animals of other age classes. However, very few newborn to five month olds were seen near the end of the year, in November and December. Graphs of the frequency of sightings of juvenile burros (six to nine months old) and adolescents (ten months to over a year old, but not fullgrown) follow the pattern established in the graph of infant sightings. By August through December, the rainy season infant cohort was classified as juvenile; there was a corresponding increase in sightings of six to nine month old burros during these months.

Further evidence demonstrating that foals were born between February and April or May comes from my record of sightings of pregnant females in their last months before giving birth. I noted the vast majority of these females between January and April.

The distributions of pregnant burros and burros with young were not uniform among areas on Alcedo (Table 3-10). Chi-square tests show significant

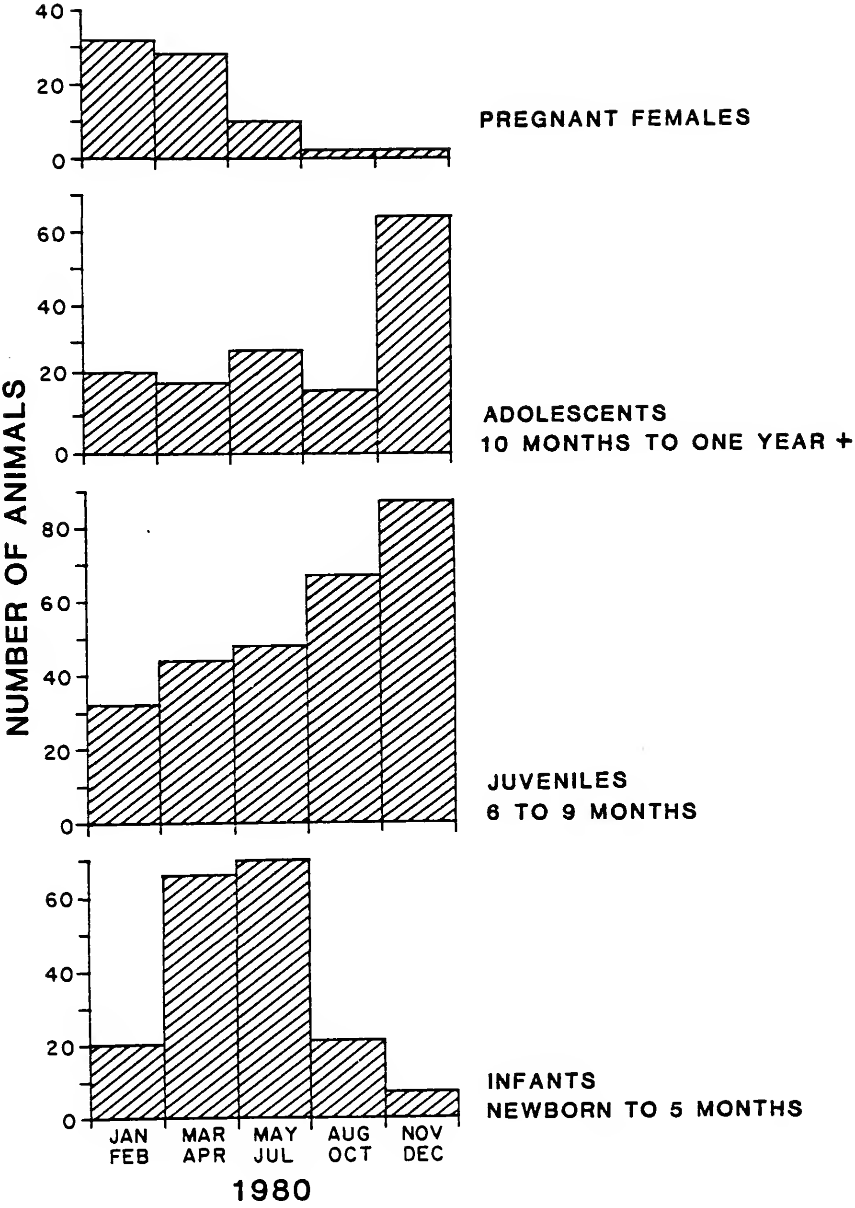


Figure 3-7 Reproductive Periodicity of Burros

differences in the distribution of young burros and pregnant females on Alcedo in the different months ($\chi^2 = 321$, young burros and $\chi^2 = 27.3$, pregnant burros; $P<.001$ for both). Between January and April, females with young were concentrated in the areas of the South Floor and on the eastern outer slopes at Midcamp. Most late term pregnant females were seen at area two, on the South Floor and at Midcamp.

In May, July, and August, burros less than ten months old were abundant at area two, on the North Plateau. Older juveniles were common at Midcamp. Few late term pregnant females were seen during these months. Area four, Rim Camp, supported a majority of the females with offspring from October to December. The only infants recorded during these months were around Rim Camp, where most of the late term pregnant females were also seen. In addition, a fair number of juvenile burros were observed at area three.

Burros were often seen alone or in pairs, and groups of all sizes up to 23 animals were recorded on Alcedo. Three larger groups, each consisting of 29 burros, were also observed. Seventy percent of all burros were found solitary or in groups of two to five animals (Tables 3-11 and 3-12). Twenty percent of the Alcedo burros were observed in groups of two animals. The most frequently observed "group" size was one; solitary burros were sighted on 668 occasions and 34.6 percent of all

Table 3-10

Seasonal Distribution of Young and Pregnant Burros
1980

Month/Area	Infants	Juveniles	Adolescents	Pregnant Females
Jan-Apr/1	5	3	1	0
2	7	8	5	17
3	18	9	5	1
4	11	9	3	2
South Floor	35	26	11	18
Midcamp	10	21	15	12
May-Aug/1	4	8	3	0
2	52	42	9	2
3	16	10	5	3
4	3	14	2	0
South Floor	12	8	2	2
Midcamp	6	11	16	3
Oct-Dec/1	0	4	3	4
2	0	5	2	3
3	0	27	14	1
4	7	70	45	19
South Floor	0	9	10	5
Midcamp	0	3	5	0

Table 3-11

Percent of Burro Groups of Different Sizes by Season

Months Group size	1*	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	29
Jan-Apr	36.7	28.2	16.2	5.5	4.4	3.7	3.0	0.6	0.3	0.2	0.3	0.2	-	0.1	-	0.1	-	-	-	-	-	0.3	-	0.1
May-Aug	33.3	25.2	16.6	10.1	6.2	2.1	2.5	1.3	0.2	0.2	0.6	0.3	0.3	0.5	0.5	-	-	-	-	-	0.1	-	-	-
Oct-Dec	33.7	30.1	13.1	7.8	4.8	2.4	2.0	1.6	0.5	0.5	0.6	0.2	0.2	0.6	0.3	-	0.2	0.2	0.2	0.3	-	0.2	0.5	-
Average	34.6	27.8	15.4	7.8	5.1	2.8	2.5	1.1	0.3	0.3	0.5	0.2	0.1	0.4	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Weighted Average**	12.5	20.1	16.6	11.2	9.3	6.0	6.4	3.3	1.0	0.9	2.1	0.9	0.7	2.1	1.4	0.3	0.3	0.3	0.4	0.8	0.4	1.2	1.3	0.5

*Based on observations of 5,345 burros in 1,929 groups.
**Number of groups x number of individuals.

Table 3-12

Percent of Burro Groups of Different Sizes by Area

Study Site/ Area	Group size 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	29
1	18.9	24.5	22.6	17.0	11.3	3.8	-	1.9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
N. Plateau/ 2	34.6	23.7	16.5	10.7	5.1	2.6	2.8	.9	0.4	-	0.9	0.2	0.4	0.6	0.4	-	-	-	-	-	-	0.2	-	-
3	30.1	31.9	13.9	6.0	3.1	2.4	6.0	2.4	-	-	-	0.6	0.6	-	0.6	0.6	0.6	-	-	-	-	-	1.2	-
Rim Camp/ 4	35.9	34.5	11.5	6.1	4.2	2.0	1.2	1.4	0.6	0.6	0.8	-	-	0.2	0.2	-	-	0.2	0.2	0.2	-	-	0.2	-
South Floor	35.1	22.4	17.6	6.3	6.3	4.4	4.0	0.7	0.2	0.5	0.5	0.5	-	0.7	-	-	-	-	-	0.2	0.2	0.2	-	-
Midcamp	36.9	28.7	16.5	7.3	5.2	2.1	1.2	0.9	-	-	-	-	-	0.3	0.3	-	-	-	-	-	-	0.3	-	0.3

*Based on observations of 5,345 burros in 1,929 groups.

"groups" seen were of single animals. Kolmogorov-Smirnov tests (Siegel, 1956) indicated that burro group sizes did not vary significantly either between areas or with the months of the year.

Complete burro group composition data were difficult to obtain. On approximately half of the occasions when I sighted burro groups I could sex all the adult animals so that complete group composition information could be recorded. In the total of 5,345 burros observed during my year of research on Alcedo, 2,683 were sexed. Five types of burro groups were recognized: 1) all-male; 2) all-female; 3) male and female; 4) female and young; 5) male, female and young. Chi-square tests were used to determine whether the frequency of sightings of the different group types varied between the months and from area to area. Both tests showed highly significant differences between the expected and observed frequencies of group types ($\chi^2=65.1$ for groups compared in different months, $\chi^2=65.1$ for groups compared on different areas, $P<.001$ for both).

All-male groups were seen at approximately equal frequencies in all months of the year (Figure 3-8). More all-female groups than would be expected in a uniform distribution were found during the wettest months of January through April. Fewer all-female groups were observed in October to December.

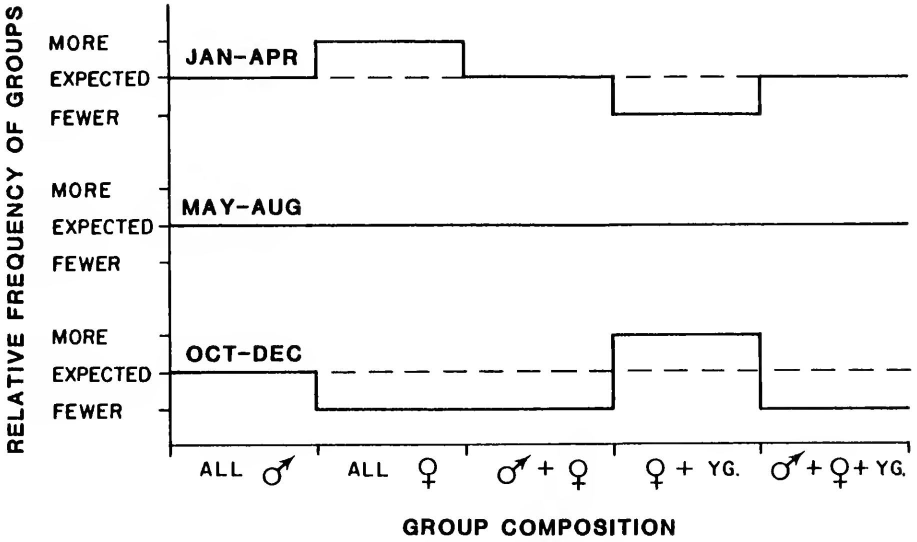


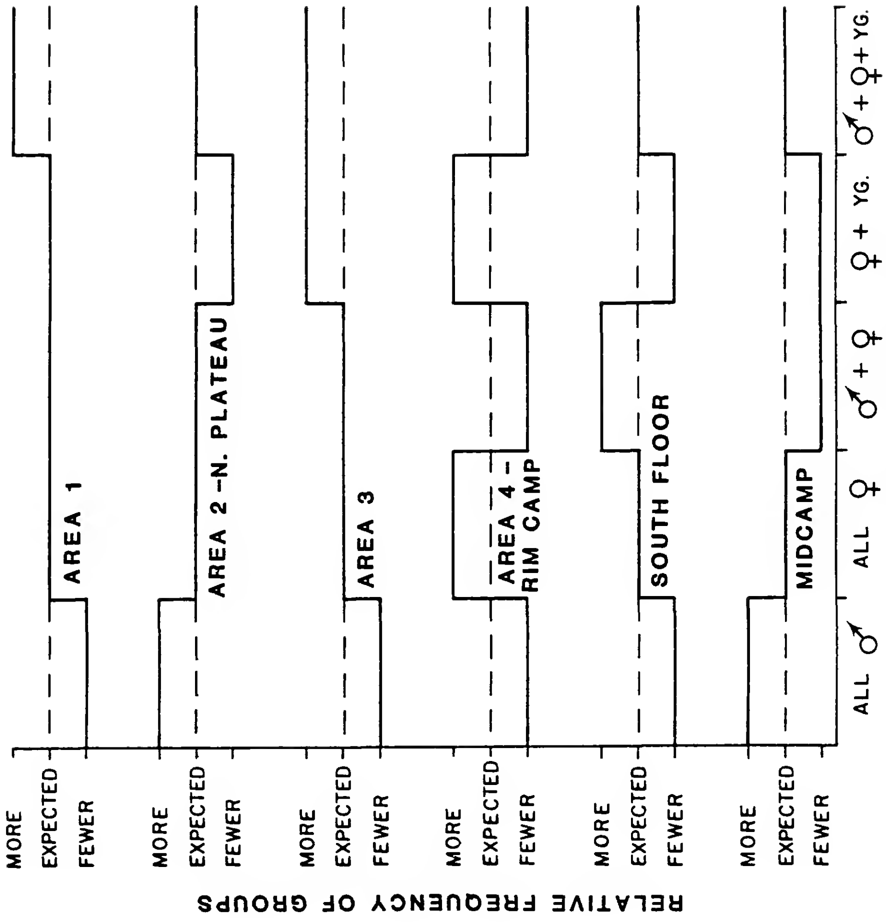
Figure 3-8 Seasonal Changes in Burro Group Composition, 1980

Few male and female groups and male, female and young groups were recorded between October and December. Females with young were seen less frequently than a uniform distribution would predict in the months of January to April and more often than expected in October to December.

Male groups were most frequently recorded on area two (North Plateau) and at Midcamp (Figure 3-9). Fewer all-male groups were seen on the rest of Alcedo. All-female groups apparently preferred area four, around Rim Camp. Male and female groups were most common on the South Floor and least common in the Rim Camp and Midcamp study site areas. Females with young preferred areas three and four and were notably less frequent on area two, the South Floor and at Midcamp. Burro groups containing males, females and young were more common than expected in a uniform distribution on areas one and three, and infrequently recorded on area four at Rim Camp.

All-male groups of up to 16 animals were observed; however, over 50 percent of the males in all-male groups were either solitary or in pairs. Late term pregnant females seemed to have a tendency to be in all-female groups. Twenty-four percent of the female burros in singles, pairs or trios of all-female animals were pregnant. For comparison, only seven percent of the females in male and female groups were noticeably pregnant. No all-female

Figure 3-9 Burro Group Composition on Different Areas


AREA 1
AREA 2 -N. PLATEAU
AREA 3
AREA 4 - RIM CAMP
SOUTH FLOOR
MIDCAMP
MORE
EXPECTED
FEWER
RELATIVE FREQUENCY OF GROUPS
ALL ♂
ALL ♀
♂ + ♀
♀ + YG.
♂ + ♀ + YG.
GROUP COMPOSITION

groups of more than three animals were recorded. Female groups of up to four or five and even more may exist on Alcedo; it was more difficult to quickly sex females than males from afar.

The largest mixed sex and age burro groups observed were of 15 animals, including three young burros. The largest male and female groups were of six animals; one, made up of one male and five females and another of three males and three females. Other larger mixed sex groups no doubt existed but I could never rapidly sex all the animals in the largest groups before they fled. Sixty-four percent of the male and female groups contained either one male and one female or one male and two females. I never saw more than five young burros in a group (a group of one male, five females and five young) and groups of up to seven females with three young were observed. Seventy-five percent of the female with young groups were of a single mother and offspring. Eleven percent were made up of a mother and her offspring plus another female, six percent were of two females with two young and four percent were of three females with one young. All other female and young groups were seen less than one percent of the time.

Discussion

Burro and Tortoise Distribution

Studies of feral burros in North America have shown that burros use a wide range of habitats and frequently have seasonally distinct habitat preferences (Moehlman, 1974; Woodward, 1976; USDI, 1977; O'Farrell, 1978; Seegmiller and Ohmart, 1981). Summer burro distributions in the southwestern United States were found to be strongly influenced by water availability. Burros were generally concentrated within three or four kilometers of water sources during the hottest months of the year. In summer, Moehlman (1974) observed that adult burros watered every 24 hours in Death Valley, while females with young foals watered several times a day. During the cooler winter months, burros ranged up to 10 or 13 kilometers from water. In winter in the Chemehuevi Mountains of California, burros watered every three days (Woodward, 1976).

Water availability apparently also influences the distribution of burros on Alcedo. During the early half of 1980, the puddles which formed after heavy rains provided ample water for both burros and tortoises on all sections of the volcano. At this time of the year, burros were most common on the South Floor, the North Plateau and Midcamp areas. They avoided the Rim Camp area which was often cool and foggy, particularly in the mornings. On Alcedo, unlike the southwestern U.S., the hottest months of the year are also the wettest. Hence, when Alcedo's weather was hot, burros usually had plenty of water available to them. There was abundant forage on all of the volcano during the warm wet season.

In mid-August, burros began leaving the wide North Plateau and Midcamp areas where grasses and ephemeral plant species were desiccating. By late in the year, large numbers of burros were concentrated on the moist Rim Camp section of Alcedo. This was particularly true in November and December of 1979. In 1980, light rains had begun to fall on Alcedo by mid-November but 1979 was dry until late December; this explains the greater number of burros at Rim Camp at the end of that year. There burros could obtain moisture from garua dampened grasses and occasionally find water in garua drip-pools under trees.

Burros are known to travel for several kilometers to reach water (Woodward, 1976). Alcedo burros apparently traveled regularly from other areas in search of water near Rim Camp during the dry season. On wet garua nights, particularly on wet nights following several consecutive dry days on the southeast rim, burros were active and noisy during the night. All night long, caravans of burros would pass my camp. I could hear burros just ten meters from my tent, stomping and slurping in the mud under a tree from which garua dripped and formed a favorite drinking hole. In the mornings, I could hide and watch as single file burro trains passed me, going from one muddy puddle to the next in search of moisture. I once followed a lone male burro for an hour as he investigated over a dozen garua drip-holes, wading and putting his muzzle in the mud. Alcedo burros behave differently around water than do the feral burros of California; Woodward (1976) reports that she never saw a burro so much as put its hoof in the mud or water of the Colorado River. Twice I saw burros licking water droplets off mosses and leaves.

The shortage of water in the dry months of the year on Alcedo also seemingly influenced the distribution of pregnant female burros and females with offspring. By the end of the dry season, in October to December, pregnant females and females with young were concentrated on area four at Rim Camp. Since lactating females provide fluids for themselves and their young, their water requirements are greater than those of the average adult female burro.

The lack of a permanent source of water on Volcan Alcedo is a relatively new situation on that volcano. Until the late 1960s, a pool of water surrounding the southeastern inner caldera wall fumarole provided year round water for burros and tortoises. When the pool mysteriously dried up, several hundred burros died. The current burro population on Alcedo may be much smaller than it once was (MacFarland, pers. comm.)

Burros are well adapted to life in arid environments and are able to withstand a water loss of up to 30 percent of their body weight (Maloiy, 1970). On Alcedo, however, they must be under water stress during the dry season when they may go for several months without the chance to drink fully. Both their behavior at times of some garua-water availability and the changes in their distribution as the dry season progressed provide evidence that water shortages do exist on Alcedo and may strongly influence the feral burro population.

Tortoises can go for months without food or water. This fact led to the over-exploitation of the Galapagos tortoises for oil and meat by pirates, sealers, whalers and other seamen in the seventeenth and eighteenth centuries. Tortoises were stored alive aboard ships for several months. One tortoise, lost aboard the ship Niger out of New Bedford, was found alive in the lower holds after two years (Townsend, 1925).

In spite of their ability to withstand long periods without water, tortoises too seemed to be distributed on Alcedo in response to water, and possibly to food availability. And, like the burros, tortoises were very intent on searching for water under dripping trees following a wet garua night on the southeastern rim. On mornings in the dry season when there was only a very small amount of water in garua drip-puddles, tortoises would spend hours going from puddle to puddle nosing in the mud (see Chapter Seven for details).

Tortoise distribution was actually more straightforwardly related to moisture availability than was burro distribution. This was probably because tortoises, unlike burros, are not capable of rapid mobility. While burros could easily travel several kilometers to reach the southeast rim during a wet night, drink and leave, all in the span of a few hours, tortoises travel too slowly to do this. They apparently had more regular migrations to and from the various sections of Volcan Alcedo.

During the rainy months, many tortoises were concentrated on the South Floor where the largest pools for drinking and wallowing formed. Tortoises were also common on areas one and two along the rim, where food and water were plentiful during the wet season. Rim area four, Rim Camp, with its many rainy season puddles and abundant forage, had few tortoises, again perhaps because of the cool foggy days that were common there yet rare on other sections of Alcedo.

Data on both burro and tortoise use of the Rim Camp area confirm that tortoises moved into that section of the volcano in June or July after the rains had ended and remained there until the end of the dry season. Burros, however, were moving in and out of the Rim Camp area. The two species were not identically distributed on

Alcedo, although their patterns of distributon are similar. Both burro and tortoise distributions may be the result of the combined influences of water and food availability. Food availability on Alcedo will be discussed in Chapter Six.

Burro Foaling Season and Group Size/Composition

A peak in burro natality occurs on Alcedo during the rainy months, when ample food and water resources are available. Infant burros were seen during all months of the year on Alcedo, however. Moehlman (1974) likewise found year round reproduction in the burros of Death Valley, with a peak in births occurring when forage was abundant, between May and July. Foaling in the burro herds of the Grand Canyon was restricted to the months of March to July (USDI, 1977). Woodward (1976) reported no peak foaling season for the Colorado River feral burro herds and proposed that the mild winters there may not exert selective pressures towards the development of a distinct breeding season. Water is available to these burros all year long. Indeed, it seems likely that peak birth seasons are selected for only in populations where foals produced out of season have a decreased chance of survival. This may well be the case on Alcedo; giving birth in the dry season may be selected against since females with foals would be burdened with an added fluid stress.

Studies of the feral Equus asinus populations in North America have revealed that feral burros exhibit a range of social organizations and behaviors. In the southwestern United States, adult male burros are typically solitary and some are territorial. Temporary groups of mixed ages and sexes are common and the basic stable unit is the mother and offspring pair (Woodward, 1979). Koehler (1974) is alone in reporting the occurrence of stable groups in the Southwest of four to six animals existing for several months on the periphery of the feral burro range at Bandelier, New Mexico. However, on the lush humid island of Ossabaw, Georgia, stable burro groups are the rule, rather than the exception (Moehlman, 1979 and McCort, 1979). On Ossabaw, the occurrence of stable harem groups and of high sociability (greeting, mutual grooming, social play in foals, etc.) among these groups may be in response to an environment with near optimal conditions (Moehlman, 1979).

The social organization of the wild African ass (Equus asinus) has been described by Klingel (1972, 1977) as a form of territoriality where the only stable groups are mother and offspring pairs. Fowler et al., (in prep.) found that during the wet season on Alcedo, stable harem burro groups with specific home ranges occurred. During the dry season, when food and water resources are not abundant, these groups may disband and the individuals then disperse. Evidently burro social organization is extremely plastic and is strongly influenced by various environmental factors.

In the Alcedo population, 34.6 percent of all burro sightings were of single animals, mostly males. This falls into the range of percentages of solitary animals recorded in other feral burro studies; 23.9 percent solitary males reported by Moehlman in Death Valley and 50 percent by O'Farrell (1973) in one of his study herds in Nevada-Arizona. For Death Valley burros, 60 percent of all groups contained two to four individuals; 51 percent of the groups were of two to four animals on Alcedo. Larger groups of up to 20-29 burros were reported in most of the studies from the southwestern United States. These large herds were usually associated with a scarce resource such as water or an estrous female. I saw similar herds on Volcan Alcedo; many of the largest were gathered around shade trees and favorite dust-bathing localities. Other large, predominantly male groups were undoubtedly temporarily attracted together by an estrous female. On Alcedo, only four percent of all burro groups contained eight or more animals; similarly in Death Valley, three percent of the burro groups sighted were of 8-21 individuals (Moehlman, 1979). Solitary female burros and all-female groups appear to be more common on Alcedo than in other study areas; other researchers have seldom noted females alone.

Young burros (those still with their mothers and not yet full grown) make up 9.3 percent of the Alcedo burro population. Seegmiller and Ohmart (1981) found that the age structure in the Bill Williams Mountains was 64.4 percent adult, 16.7 percent yearlings and 18.9 percent foals. Woodward (1976) has comparable data from the burro herds in southeastern California. According to her, the Chemehuevi Mountain burros epitomize a successful colonizing exotic species in a habitat without limitations; they show precocious sexual maturity and have a high reproductive rate. Twenty-three percent of that population is made up of young burros. The Alcedo population, by comparison, may be near the carrying capacity of its environment and restricted by some limiting resource (water or food), hence, the relatively low reproductive rate.

CHAPTER FOUR

BURRO MORTALITY

The feral burros on Volcan Alcedo live completely free from predators. The endemic and introduced predators of Alcedo (hawks, owls and cats) are all too small to prey on burros. Packs of feral dogs may hunt young and weak burros elsewhere in the Archipelago, but there are no feral dogs on Alcedo. And, because theirs is an isolated population which never comes into contact with other large mammalian species, the burros of Alcedo rarely encounter disease. Hence I was intrigued, when I arrived on Alcedo in October 1979, to find fresh carcasses of numerous adult and juvenile burros.

Mortality in the herds of feral burros of the southwestern United States has been mentioned by several researchers. In the populations studied, the observed natural adult mortality rates were uniformly low, with juvenile mortality somewhat higher and more variable (Moehlman, 1974; Norment and Douglas, 1977; USDI, 1977; Seegmiller and Ohmart, 1981). To investigate the apparently high level of burro mortality on Volcan Alcedo, I examined burro carcasses and collected teeth from the skulls.

Methods

Recently dead burros were easily located by smell. The bleached bones of older skeletons also could be readily detected, particularly in the dry season when plant growth was minimal. With the bi-monthly around-the-rim censuses, frequent study site censuses and counts, and trips to the landing beach every fifteen days for food supplies, I had ample opportunity to search much of Alcedo for dead burros. There were, of course, sections of the volcano that I did not visit frequently, and some areas that I never explored. I did not discover all the burros that died on Alcedo in 1980. But I certainly found a large percentage of the animals that died along the crater rim and in my four study site areas.

Beginning in January 1980, I searched for all dead burros that were detected by scent. In only four instances was I unable to locate or to reach a carcass. In addition to investigating fresh carcasses, I searched the crater rim and my four study site areas for older skeletons. Dead burros were sexed and aged whenever possible. Young burros could be aged based on knowledge of *Equus* tooth eruption timing and sequence, but adults could not be aged in the field. Young burro carcasses could be sexed but skeletons of juvenile animals could not be. Animals older than four years could always be sexed; males have large canine teeth, while in females the canines are absent or rudimentary (Simpson, 1951). The first incisor, first premolar and first molar of upper and lower jaws were collected from the skulls of adult burros. Based on the extent of decay of carcasses, I estimated the approximate date of death for each animal. Carcasses were examined for clues to the cause of death. Older skeletons were classified as to length of time since death of the animal according to the weathered appearance of the bones. I was later able to use bone weathering information from Behrensmeyer (1978) to translate these classifications into approximate estimates of years since death.

Equus spp. have traditionally been aged based on tooth wear. Wear is related to diet, soil conditions, and in addition, varies from individual to individual. More recently, mammalogists have been using an aging technique in which tooth cementum layers are analyzed. Cementum is produced throughout a mammal's life by cementoblast cells on the outer surface of the tooth roots. Dark cementum bands are formed when there is a change in cementoblast activity. In North American, dark bands are thought to be formed during winter; in the tropics, they apparently coincide with the dry season (Matson, 1981).

Matson's Commercial Microtechniques Lab in Milltown, Montana specializes in tooth sectioning and aging by cementum analysis. I sent incisors from dead burros I had located on Alcedo to Matson's for processing. Decalcified teeth were sectioned longitudinally at 14 microns, stained with Giemsa and permanently mounted on microscope slides for aging (see Humason, 1972 for a description of standard paraffin preparation method). Cementum band patterns vary among species (Matson, 1981). For aging burro teeth, Matson's assumed that tooth eruption occurred before the age of three years; hence the first major dark cememtum band on a tooth section marked the third year of life.

Matson's can only handle burro incisors; premolars and molars are too large to fit into their trimming and sectioning equipment. But as skulls deteriorate in the field, the first teeth to become loose, and therefore lost, are the incisors. Hence for some of the oldest skeletons found on Alcedo, I was unable to collect incisors. Ages of animals for which only premolars and molars were collected were based on wear criteria. Molars were measured according to Joubert (1972) and then, using linear regression, correlated to the molar measurements of animals aged by cementum analysis (correlation coefficient of lower molar length to age = .90 for females, .75 for males and .80 combined).

Results

Thirty recently dead burros were found on Alcedo in 1980. For 22 of these, I made notes in the field concerning the stage of tooth eruption or collected teeth for laboratory aging. Four carcasses of adult burros were too fresh to extract teeth when I first discovered them and I could not locate them later. I could smell but was unable to find or reach another four dead animals.

Over half (56.7%) of the dead burros I discovered had died in January 1980, at the very end of the dry season (Figure 4-1). All the others, except for one which died during the rainy month of March, died between September and December of 1979 or of 1980, which were dry months on Alcedo. Twelve of the 30 burro carcasses were of adults and fourteen were of animals under two years of age.

Table 4-1 summarizes the sexes and ages of the 126 burro skeletons and carcasses examined. Aging was done by the three methods previously described. The adult male to female ratio was 1:.95. Other researchers also have reported sex ratios approaching one-to-one in some of the feral burro populations of the southwestern United States (Moehlman, 1974; Woodward, 1976; USDI, 1977; Norment and Douglas, 1977). Burros in the age classes of three to five years, six to nine years and ten to 14 years were found at almost equal frequencies. Each class comprised between 17 and 23 percent of the total number of dead burros. Fewer dead animals (7.1%) that were older than 15 years were found. More burros of

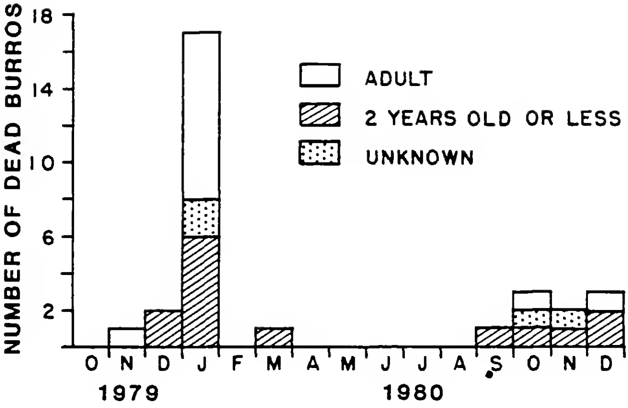


Figure 4-1 Months in Which Burros Died
(n=30)

Table 4-1

Burro Sex and Age at Death
(n=126*)

		Sex and Age in Years											
Aging Method	0-2 Not Sexed	3-5			6-9			10-14			15+		
		♂	♀	?	♂	♀	?	♂	♀	?	♂	♀	?
Tooth Eruption	42	-	-	6	-	-	-	-	-	-	-	-	-
Cementum Analysis	-	7	10	0	10	3	0	13	4	0	5	1	0
Tooth Wear	-	0	4	2	1	7	3	0	4	1	1	2	0
Total	42	29			24			22			9		
Percent	33.3	23.0			19.0			17.5			7.1		

*Based on teeth from 104 skeletons and 22 carcasses.

newborn to two years (33.3%) were found than any other age class.

The 42 skeletons and carcasses of young burros examined could be aged to within a few months (Table 4-2). More than half the dead young animals were less than nine months old, with seven to nine month old individuals the most numerous.

The 30 burro carcasses and 104 skeletons that I located were grouped into categories based on the approximate number of years since death of the animals (Table 4-3). The carcasses, and skeletons to which bits of flesh and hide still clung, belonged to animals that had died within a year. Of these dead animals, 46.2 percent were adults and slightly more, 53.8 percent, were the remains of burros less than two years of age. The skeletons of animals that had died one to three years previously included a similar percentage of adults (47.6%) and juveniles (52.4%). But the older skeletons were predominantly of adult animals (70.6% and 85.7%); fewer skeletons of young burros that had lain exposed to weathering for more than four years were found.

Discussion

Foal mortality rates are variable in the feral burro herds of the southwestern United States. Seegmiller and Ohmart (1981) and Ohmart et al. (1975) found no evidence of foal mortality in Arizona.

Table 4-2

Young Burro Age at Death
(n=42*)

	Less Than 6 Months	7-9 Months	10-12 Months	13-24 Months
Total Number	8	17	7	10
Percent	19.0	40.5	16.7	23.8

*Aged by tooth eruption in 28 old skulls and 14 fresh skulls.

Table 4-3

Years Since Death Based on Weathering of Burro Bones
(n=134*)

Approximate Years Since Death	No. Carcasses Or Skeletons	Percent Adults	Percent Young**
1	30	46.2	53.8
1-3	42	47.6	52.4
4-6	34	70.6	29.4
7-15	28	85.7	14.3

*Based on teeth from 104 skeletons and 30 carcasses.
**Less than two years of age.

Moehlman (1974), working in the Panamint Range of Death Valley, found that foal mortality rates were moderate. She observed one dead foal and three pregnant females who either aborted or lost their foals at an early age. By counting the foals and yearlings in her population between 1970 and 1972, she estimated first year mortality at 20-30 percent. In Grand Canyon, Arizona, USDI (1977) found few burros less than one year of age, and proposed that an even higher level of mortality of the young may occur there.

Natural mortality among burros older than one year is consistently low. Seegmiller and Ohmart (1981) report very low mortality in the Bill Williams Mountains of Arizona; during their year-long study only one case of natural mortality was documented. Other investigators have likewise observed few burro deaths due to disease or predation and state that most yearling to adult mortality is caused by man (Moehlman, 1974; Ohmart et al., 1975; USDI, 1977).

Norment and Douglas (1977), during a 16-month study of approximately 160 burros in the Panamint Mountains, found nine dead burros. At least three of the seven dead adults had been illegally shot. The two foals had apparently died of natural causes. In all of the studies mentioned above, natural mortality among burros older than one year varied from about one to five percent.

The estimated mortality rate on Volcan Alcedo for yearling to adult burros approaches five to seven percent. This calculation assumes an adult burro population of approximately 500 animals and takes into consideration that 13 dead burros, two years of age or older, were found during 1980 on the crater rim and in the four study sites alone (less than 1/3 of the total area of the Volcano). Furthermore, using data on years since death based on bone weathering criteria, the 1980 mortality rate was not unusual. Although yearly adult burro mortality rates can only be approximated from the death tally data, mortality has apparently been consistently high over at least the past ten years.

The 28 skeletons that had been exposed to weathering for seven to 15 years represent only a portion of the animals that died during that time period. Behrensmeyer (1978) reported that bone weathering rates depend on temperature, humidity and soil. Under most conditions, bones will be completely broken down after ten to 15 years of exposure to the elements. In equable environments (swamps and dense woodlands for instance) bone weathering is slow. But the conditions on Alcedo (fluctuating wet and dry periods, hot tropical sun) probably result in the complete disintegration of skeletons well before the 15th year of exposure.

In general, stable mammalian populations (constant size and age structure) in which no more than one offspring is produced per female per year, have mortality profiles that are roughly U-shaped; highest mortality occurs in the very young and the very old (Caughley, 1966; Klein, 1982). In such populations, young, sexually mature adults have a substantially lower mortality rate. Spinage (1972) found that mortality rates for Equus burchelli were similar for the sexes. The mortality profile he obtained closely approximated the U-shaped curve shared by many large mammals.

Not knowing whether the feral burro population is stable makes it impossible to construct a lifetable from the Alcedo burro death tally data. However, it can be tentatively noted that, on Volcan Alcedo, an unusually large number of young sexually mature adults and animals in their prime are dying.

Based on the data from carcasses and skeletons that had lain exposed to weathering for less than three years, Alcedo foal mortality is higher than adult mortality. But foal mortality was certainly underestimated. Spinage (1972) in his studies of African ungulates found that the youngest age classes are usually underrepresented in a death tally. The skeletons of juvenile animals deteriorate more rapidly than do the bones of adults, hence the samples of skeletons that were four to fifteen years old contained increasingly fewer skeletons of young burros. Behrensmeyer (1978) found that the bones of juvenile animals rarely survive more than six to eight years of exposure.

Only one carcass exhibited clues to the cause of death; this individual was found on a steep slope section of the crater rim with a broken neck. Cause of death could not be determined for any of the other 29 burros. I suggest that the high level of burro mortality on Alcedo is the result of a severe water shortage. Almost all (97%) of the observed burro deaths occurred during the latter part of Alcedo's dry season. In particular, 56 percent occurred in January 1980 at the very end of the 1979 dry season.

That the feral burros were under water stress could be deduced from both behavioral and distributional observations. During the dry season when wet garua covered the southeastern rim, burros would travel from other sections of the volcano and spend hours searching for moisture in the muddy puddles that formed beneath Zanthoxylum trees. Burros were even seen to lick water droplets from mosses. During the later months of the dry season, females with very young foals were observed exclusively along the moist southeastern rim and slopes. (See Chapter Three for details of dry season burro distribution and behavior).

Burros are well-adapted to dry habitats and can withstand heat stress and aridity because they are able to tolerate extreme desiccation of the body (water losses of up to 30% total body weight), have an ability to reduce losses of evaporative and fecal water when dehydrated, and can continue to eat for several days when deprived of drinking water (Maloiy, 1970). In laboratory experiments (Maloiy, 1970), burros deprived of water and exposed to temperatures of 22 ± 2 degrees C had depressed their food intake by 80-83 percent by the end of an eight to twelve day period. Daily losses in body weight of .7 to 1.5 percent body weight (1-3 kg) per 24 hours were recorded. The longest period of experimental water deprivation was 12 days. During this period one burro lost 34 kg and another 28 kg body weight (total burro body weight approximately 150 kg). Food intake was reduced from 2.76 and 2.82 to .28 and .36 kg food per 100 kg body weight, respectively.

Adolph and Dill (1938) in a study of water metabolism in the desert, found that a walking burro lost 7.8 percent body weight in one day and required six liters of drinking water per day. Dr. Robert Ohmart, Arizona State University (pers. comm.), who studied burros in the southwestern United States, suspects that burros, even in a cool environment with high relative humidity, can not survive for one month without free water. In a dry season on Alcedo there might not be rain for up to six months. Occasional wet garua nights may not provide enough water to sustain the entire feral burro population between rains.

CHAPTER FIVE

THE EMERGENCE SUCCESS OF TORTOISE NESTS AND THE EFFECT OF BURROS ON NEST SUCCESS

The female tortoises of Alcedo begin nesting at the end of the rainy season. Many tortoises dig their egg chambers in one of two caldera floor sites. Others nest along the crater rim, on the outer crater slopes and in spots on the inner floor where the dirt is dense and deep, and of the appropriate consistency for nest building (see MacFarland et al., 1974b for details on nest site characteristics). Prior to this study, the natural hatching success of Geochelone elephantopus vandenburghi was not known. However, MacFarland et al. (1974a) have obtained natural hatching success data for two other races of Geochelone in the Galapagos. Studies of the giant land tortoises of Aldabra Atoll by Swingland and Coe (1978, 1979) provide comparable hatching success values for Geochelone gigantea.

Because the two major nesting sites on Alcedo are regularly frequented by feral burros, Charles Darwin Research Station and National Park personnel have long suspected that burros damage incubating nests. In this phase of my study, I recorded the natural hatching and emergence success of 1979/1980 tortoise nests. Then, in

July 1980, I began monitoring newly-laid clutches to observe the effect of trampling by burros on nest success.

Methods

In February 1980, I visited the north caldera floor nesting area and located nests which had been constructed during the 1979 nesting season, and from which young had emerged. These nests were easily found by spotting the exit hole in the hard sun-baked mud cap which had once protected the incubating eggs. Several additional unopened nests were discovered in which the young had hatched, moved up the nest column, and were ready to emerge. These nests were located via their rounded nest cap. Because most nests were already empty by February, I broke into them.

The north floor nests were excavated and the number of egg shells, dead embryos, dead and live young, and undeveloped eggs in each was recorded. Although the egg shells were torn, it was still possible to estimate the original clutch size from these tattered shells (see Fowler, 1979 for egg shell counting method and accuracy).

In late December 1979, and again in early 1980, I located vacated nests on the south floor nesting area. These nests also were excavated and their contents examined and recorded.

For the above 1979/1980 nests, no estimation of burro damage to nests could be made because nest research was begun after most of the incubation period was over. However, in July 1980, I began marking newly established nests, and these were monitored at irregular intervals until December. Each time the nests were checked, the caps were inspected for any sign of disturbance. If a nest had been disturbed or damaged, or the young had emerged, I dug until eggs or shells were reached. I did not remove or tamper with unopened eggs but any broken ones were removed, counted and discarded. The contents of vacated nests were recorded and disturbed nests were resealed so that remaining eggs might go on incubating. No attempt was made to build a new mud cap for disturbed nests, the eggs were simply reburied. But many of these nests had one-half to three-fourths of their mud caps still intact.

Many of my marked nests were situated in active burro paths or tortoise sleeping forms. A few of these nests were impossible to relocate, and were deleted from my analysis. Due to the endangered status of the Galapagos tortoise, I did not disturb active nests to count eggs, check nest progress, and the like. When I left Alcedo in December 1980, many of the marked nests were still incubating; hence my data for these nests are incomplete.

Results

Emergence Success of 1979-1980 Nests

By mid-December 1979, hatchling tortoises had begun to emerge from nests in both the north and south nesting areas. Fourteen nests were excavated and examined on four separate visits to the south nesting area (Table 5-1). Clutch sizes ranged from six to 14 eggs, with an average of 11 eggs ± 2.3 S.D. per nest. Undeveloped eggs, eggs that were infertile and those in which the embryo died before it attained a visible size, averaged 2.8 eggs ± 2.8 S.D. per nest and were found in all but three (78%) of the 14 nests. Eleven dead embryos, and one dead twin embryo, were found. From the total of 153 eggs, 99 hatchlings emerged; thus the overall emergence success for the south caldera floor nests was 64.7 percent.

In February 1980, I located 28 nests that had been constructed in the north nesting area during the previous year's nesting season (Table 5-2). The clutch sizes of these nests ranged from seven to 26 eggs, with an average of 14.5 eggs ± 5.0 S.D. per nest. Again, most nests (75%) contained one or more undeveloped eggs. Stranded live young were found in the columns of three nests, and there were 59 dead embryos in a total of 406 eggs and shells examined. The emergence success of these nests, including the young in four unopened nests that were hatched and ready to emerge, was 65 percent.

Table 5-1

Success of South Caldera Floor Nests
1979/1980

Nest Number	Date Examined	Total Eggs	Undev. Eggs	Dead Embryos	Live Young	Dead Young	Emerged Young
5	Dec 79	11*	6				3
6	Dec 79	11	2		1		8
7	Dec 79	13	2			1	10
8	Dec 79	6	1				5
9	Dec 79	12		twin			11
10	Dec 79	11	3				8
11	Dec 79	8	1	3			4
12	Dec 79	9	1				8
13	Jan 80	10		2			8
14	Jan 80	14	7	4			3
1	Feb 80	14					14
2	Feb 80	10	3				7
3	Mar 80	11	6				5
4	Mar 80	13	8				5
Total:	14 nests	153	40	10	1	1	99
Average per nest:		10.9	2.8	.7	-	-	7.1
Standard Deviation:		2.3	2.8	-	-	-	3.2

*This included two broken eggs which may have been broken by burros or by the nesting female.

Table 5-2

Success of North Caldera Floor 1979/1980 Nests
(Examined February 1980)

Nest Number	Total Eggs	Undev. Eggs	Dead Embryos	Live Young	Dead Young	Emerged Young
1	7	2			1	4
2	23	12	9			2
3	8		4			4
4	11	1	3			7
5*	10	1	1		2	(6)
6	20	5	6			9
7	14		10	3		1
8	8		2			6
9	15					15
10	15	1				14
11*	18	2	1			(15)
12*	16	2	1			(13)
13	16		2			14
14	8	1				7
15	19	2	5	1	1	10
16	10					10
17	11	2	3	2		4
18	14	2			3	9
19	26	6				20
20*	10		2			(8)
21	12	1	1			10
22	16	6	2		1	7
23	12	1				11
24	22	1	2			19
25	10	1				9
26	19	11	2			6
27	16	1	1			14
28	20	8	2			10
Total: 28 nests	406	69	59	6	8	264
Average per nest:	14.5	2.5	2.1	0.2	0.3	9.4
Standard Deviation:	5.0	3.3	2.6	-	-	4.8

*Nests in which young had hatched but not yet emerged.

1980 Nesting Results

The 1980 nesting season began in May or June, while I was not on Alcedo, and continued at least into August. The latest freshly established nest, still damp, was discovered on August 4. A few nests were established by tortoises after this date, however, because four new ones were found when the nesting areas were next checked in October. The earliest hatchlings emerged a few days before November 4. Because I monitored nests at irregular intervals and many of my marked nests still had not emerged by mid-December when I last checked them, I was unable to get accurate measurements of incubation periods. However, for the eight nests that produced hatchlings naturally after an undisturbed incubation period, the minimum possible length of incubation was 90 days and the possible maximum was 150 days. Similar incubation periods of 110-250, 85-120 and 98-148 days have been reported by MacFarland et al. (1974b) for *Geochelone elephantopus porteri* and *G. e. ephippium* and by Swingland and Coe (1979) for *G. gigantea*, respectively.

On the south caldera floor nesting area, 19 nests were found and monitored regularly. An additional nine nests were located late in their incubation cycle and monitored thereafter. Of the total 28 south floor nests (Table 5-3), nine (32.1%) were broken into by burros (i.e., the hard protective mud cap was punctured by a

Table 5-3

Fates of South Caldera Floor Nests
1980

Total Nests	Undisturbed, Incubating Nests(%)	Naturally Emerged Nests(%)	Nests Destroyed by Burros(%)	Nests Damaged by Burros(%)
28	13(46.4)	6(21.4)	2(7.1)	7*(25)

*Five produced some hatchlings, two left to incubate.

Table 5-4

Fate of Eggs in Burro Damaged Nests
South Caldera Floor, 1980

Total Nests	Total Eggs	Minimum Broken Eggs	Undev. Eggs	Dead Embryos	Live Young	Dead Young	Emerged Young
5	58	12	9	2	6	8	21
Average per Nest:	11.6	2.4	1.8	0.4	1.2	1.6	4.2

burro hoof) at various stages of incubation. All of the embryos in two of these nine nests appeared to have been killed by early burro damage. Five other nests produced some young, but had an emergence success of only 36.2 percent (Table 5-4). In the damaged nests, an average of 2.4 eggs were broken per nest. Six nests hatched naturally and without disturbance, with an emergence success of 66.2 percent. Thirteen nests were undisturbed and still incubating when they were last checked.

Sixty north caldera floor nests were located between July and October 1980 (Table 5-5). Many of these nests were undisturbed and still incubating when I left Alcedo. Only two had emerged; the overall emergence success for these two north floor nests combined with the six emerged south floor nests, was 61.1 percent (Table 5-6). Seven nests (11.7%) were damaged by burros; two of these were completely destroyed and at least eight eggs were broken in the remaining five nests. I was unable to document the extent of damage to these five nests; I did not disturb them further and they had not emerged before I left Alcedo. Three marked nests were lost because tortoises built their sleeping forms in the area where the females had nested. I doubt these nests were disturbed by the tortoise beds, but since I could not locate the nests after several searches, they were excluded from analysis.

Table 5-5

Fates of North Caldera Floor Nests 1980

Total Nests	Undisturbed Incubating Nests(%)	Naturally Emerged Nests(%)	Nests Destroyed by Burros(%)	Nests Damaged** by Burros(%)
60*	48(80)	2(3.3)	2(3.3)	5(8.3)

*Included three nests which were hidden by tortoise beds.

**Unbroken eggs left to incubate, though possibly some or all were dead.

Table 5-6

Success of Undisturbed Nests South and North Floor, 1980

Total Nests	Total Eggs	Undev. Eggs	Dead Embryos	Live Young	Dead Young	Emerged Young
8	90*	22	12	0	0	55
Average per Nest:	11.2	2.8	1.5	-	-	6.9

*One egg broken by the nesting female.

Discussion

Emergence Success

Natural hatching and emergence success for *Geochelone* is poorly known for the races of *G. elephantopus* on the Galapagos Archipelago. More is known of the reproductive potential of *Geochelone gigantea* on Aldabra Atoll in the Indian Ocean.

MacFarland et al. (1974a) studied the success of undisturbed, natural nests of two of the races of Galapagos *Geochelone*. They reported fertility and hatching rates for *G. e. porteri* (Santa Cruz Island) and *G. e. ephippium* (Pinzon Island) which are similar to the values presented in Tables 5-1 and 5-2 of this chapter. Table 5-7 presents a comparison of the data of MacFarland et al. on *G. e. poteri* and *ephippium* with a summary of my data for *G. e. vandenburghi*. Clutch size averages and ranges varied among the three races. This is consistent with the findings of Swingland and Coe (1978, 1979) on Aldabra. In their study, populations of *G. gigantea* on different islands with dissimilar environments, also produced clutches of variable sizes. Evidently the giant land *Geochelone* are very plastic in their capabilities of egg production.

The trend found on Aldabra of increasing clutch size with decreasing population density was not evident in the Galapagos. Population densities have not been calculated for any of the races of Galapagos tortoises.

Table 5-7

A Comparison of Fertility, Hatching and Emergence Success of Undisturbed Natural Nests of *Geochelone elephantopus porteri*, *ephippium*, and *vandenburghi*

Race Source	Total Nests	Total Eggs	Clutch size		Undev. Eggs (%)	Broken Eggs (%)	Dead Embryos (%)	Hatched Young (%)	Stranded Young (%)	Emerged Young** (%)
			Aver.	Range						
porteri MacFarland et al., 1974a	55	520	9.4	3-16	19.4	1.3	4.0	75.2	7.3*	66.0
ephippium MacFarland et al., 1974a	26	133	5.1	2- 8	13.5	6.0	3.0	77.4	6.0*	72.4
vandenburghi This Study	42	559	13.3	6-26	19.5	0.4	12.3	67.8	2.9	64.9

*These data included several nests in which the entire group was entombed.

***porteri* data for emergence success based on 49 nests, *ephippium* data based on 23 nests.

But it is known that the total population of *G. e. ephippium* on Pinzon Island is very small (150-200; MacFarland et al., 1974a) and that Alcedo's *vandenburghi* population, because it is by far the largest (3,000-5,000; MacFarland et al., 1974a) seems to be the most dense tortoise population in the Galapagos. Hence, *ephippium* with an average clutch size of 5.1 eggs and *vandenburghi* with the much larger average clutch of 13.3, tentatively appear to contradict the clutch size trend found on Aldabra.

The percentages of undeveloped eggs found in *G. elephantopus* nests are comparable to those reported by Swingland and Coe (1978, 1979). They recorded an estimated infertility of between 10 and 20 percent for all the Aldabra populations studied. No correlation between egg infertility and tortoise density was found. The values for infertility obtained by MacFarland et al. (1974a) and those in this study were in the same 10 to 20 percent range.

MacFarland et al. (1974a) found a much lower percentage of dead embryos in emerged *porteri* and *ephippium* nests than I did in *vandenburghi* nests. It is possible that the *vandenburghi* nests contained unusually large numbers of dead embryos as a result of burro disturbance to incubating nests. Breaking the nest cap may increase desiccation. For the group of 1979/80 nests, burro damage was not estimated because I arrived on Alcedo late in the nest incubation period. All nests that I located via hatchling emergence holes or intact nest mud caps were dug up and examined. Hence, nests that had been broken into by burros at an early stage of incubation, but still produced some emerging young, were indistinguishable from completely undisturbed nests. The low hatching success values from disturbed nests were incorporated with the higher success values of undisturbed nests to obtain the overall value of 67.8 percent hatching success. Several vandenburghi nests (Tables 5-1 and 5-2) had large numbers of undeveloped eggs and/or dead embryos and produced only a few emerging hatchlings (notably south floor nests 3, 4, 5, and 14 and north floor nests 2, 7, and 26). These high percentages of unsuccessful eggs may have been caused by burro disturbance early in the incubation period, or may be due to the high elevation or other ecological factors of the Alcedo nesting areas.

Often, when the young emerge, one or several hatchlings are left behind. These may be weak or deformed individuals, or young that simply hatched late and were unable to exit alone. MacFarland et al. found that 6.0 to 7.3 percent of the total hatchlings were stranded in porteri and ephippium nests. These numbers included eight nests in which entire groups of hatchlings were entombed. I found four nests (Table 5-2) in which the hatchlings were apparently ready to emerge but had not yet done so. I released these young and included them among my count of successful emergers. It is possible that one or more of those four hatchling groups in the still closed nests were doomed, and that by intervening I allowed them to escape entombment. If I had not interfered, my value for the percent of young left stranded in emerged nests on Alcedo would more closely approximate that of MacFarland et al. It is also possible that other doomed nests were overlooked since the majority of the nests were located via the emergence holes and non-emerged nests were slightly more difficult to discover.

The overall values for emergence success of 66 percent for porteri, 72.4 percent for ephippium and 64.9 percent for vandenburghi are quite similar. Again, they are within the ranges of emergence success reported by Swingland and Coe for the Aldabra Geochelone. Swingland and Coe (1978, 1979) comparing the hatching success of eggs from an area of dense tortoise population (27.0 tortoises per hectare on Grand Terre Island) with that from a less dense population (7.0 tortoises per hectare on Ile Malabar) found a "positive correlation" between tortoise density and hatching success. On Aldabra, nearly 80 percent of the Grande Terre Island eggs produced hatchlings, while only 60 percent of the Ile Malabar eggs were successful. If one assumes a rank order of density for the three races of Galapagos tortoises, from sparsest to the most dense, of ephippium

(Pinzon Island), porteri (Santa Cruz Island) and vandenburghi (Volcan Alcedo, Isabela Island), then the trend of greatest hatching success on islands with the highest population density, as observed on Aldabra, is not followed in the Galapagos. However, as stated previously, Galapagos tortoise population densities are not known accurately and the above is based on estimates. It may be that the lower hatching success of vandenburghi nests is a result of burro disturbances causing an increased number of eggs to fail to develop and embryos to die, or the result of ecological differences between the races of Geochelone.

The nesting situation on Aldabra is not as simple as it appears. Although on densely populated Grande Terre Island eggs hatch at a higher rate than do eggs on Ile Malabar, the mean number of live hatchlings produced per clutch on Grande Terre is half the number produced on Malabar. Grande Terre tortoises lay smaller clutches than do Malabar tortoises; hence the low number of live hatchlings produced per clutch. The lower overall hatching success of Malabar eggs is in part a consequence of the limited number of suitable nest sites on that island. This results in a great deal of nest destruction by nesting females, a condition not found on Grande Terre (Swingland and Coe, 1979). Data on nest site availability, egg mass, and population density in Galapagos

Geochelone are needed before an accurate comparison can be made with Aldabra Geochelone.

Other information concerning the reproduction and hatching success of Galapagos Geochelone is available from breeding programs in the Galapagos Islands and at zoos. Since 1965, the Charles Darwin Research Station (CDRS) on Isla Santa Cruz, Galapagos, has been involved in efforts to incubate wild-collected tortoise eggs from several of the endangered populations. Additionally, adult tortoises from the most endangered species are being captively bred. Tortoises raised from these incubated eggs are later reintroduced to the islands of their origins. Because handling of young reptile eggs may result in damage to the embryo growing within (Ewert, 1979), CDRS and Galapagos National Park personnel transport eggs only late in their incubation period. In spite of these efforts, CDRS has traditionally had hatching success of between 9.4 and 66.7 percent (32.7% average); slightly lower than the success values for natural nests (Reynolds, pers. comm.).

The hatching success of zoo Geochelone eggs is even lower. Thorp in 1972 reported that only 31.1 percent of the eggs laid by Geochelone at the Honolulu Zoo hatched (MacFarland et al., 1974b). Over a five-year period at the San Diego Zoo, 6.97 percent of the 258 eggs laid produced viable young (Shaw, 1967).

The depressed hatching success of tortoise eggs at CDRS and zoological parks is, no doubt, the result of handling, imperfect incubation techniques and temperatures. Still, artificial restocking of the greatly depleted island populations is essential in the Galapagos, and incubation and rearing techniques are being perfected with experience. We now know that, in undisturbed nests in the wild, between 60 and 80 percent of the eggs produce viable young; this is the goal toward which breeding programs should strive.

Burro Damage to Nests

Volcan Alcedo has the largest remaining population of giant tortoises in the Galapagos Archipelago. Additionally, Alcedo harbors one of the largest populations of feral burros, an estimated 500-700, in the Islands. The fears of those concerned with the conservation of the endangered Galapagos *Geochelone*, that burros trample and damage tortoise nests, have proved to be well-founded.

The south caldera floor nesting area is always occupied by burros. Bi-monthly counts of south floor burros ranged from two to 39 animals per count. A burro population of this size results in substantial burro traffic through the tortoise nesting zone. Burros broke into 32.1 percent of the 28 south floor nests monitored in 1980. Two were completely destroyed and five others produced young at a lowered emergence success. The north nesting area is less frequently visited by burros, and is more heavily used by nesting female tortoises. Fewer nests were damaged there by burro trampling, 11.7 percent of 60 nests. Therefore, of 88 vandenburghi nests monitored on Alcedo, 18.2 percent were damaged by feral burros. Of these disturbed nests, the clutches of 4.5 percent were completely destroyed and the remaining 13.7 percent produced some young at the lowered emergence success of 36.2 percent or were left incubating, the extent of damage unknown.

Both MacFarland et al. (1974a) and Swingland and Coe (1978, 1979) investigated mortality of hatchling tortoises in the wild. High mortality occurred in the Galapagos Islands even in areas devoid of feral mammalian predators. MacFarland et al. found a 50 percent hatchling mortality rate on Isla Santa Cruz in a year of plentiful rain and 95 to 100 percent mortality within four months of emergence in a dry year. Swingland and Coe reported hatchling mortality due to predators and food stress of 80 percent on Ile Malabar and of 94 percent on Grand Terre Island.

With "normal" hatchling mortality so high, the additional deaths and damage to nests caused by the feral burros on Alcedo may well lower annual recruitment into the G. e. vandenburghi population. Hatchling mortality and recruitment rates on Alcedo need to be investigated. Then we might determine whether the extent of burro damage to which the G. e. vandenburghi population is presently subjected is greater than the population can withstand.

CHAPTER SIX

BURRO AND TORTOISE DIETS

Because both the burros and the endangered giant tortoises are herbivores, and there are large populations of each on Volcan Alcedo, an investigation of their plant food preferences was undertaken. Evidence of an extensive dietary overlap between the burros and tortoises would provide some support for the fears of CDRS and Galapagos National Park personnel that the burros may be competing with the tortoises for food.

Feral burros in the southwestern United States are primarily browsers. Moehlman (1974), Woodward and Ohmart (1976), USDI (1977), and Norment and Douglas (1977) found that between 50 and 60 percent of burro diets consisted of woody browse species. Hansen and Martin (1973), in a study of the burros in the lower Grand Canyon, found that burros ate more grasses and forbs than browse species. Woodward and Ohmart (1976) suggest that burros prefer forbs and grasses to browse species and will select them if available.

Moehlman (1979) found that on the lush, humid island of Ossabaw, off the coast of Georgia, feral burros were primarily grazers. Grazing on Ossabaw occupied

38 percent of burro diurnal activity time. In the southwestern United States, 51 percent of burro activity time was spent browsing.

Giant tortoise foraging has been studied on Aldabra Atoll. Grubb (1971) listed food plant species and discussed the impact of tortoises on Aldabra's vegetation. Merton et al. (1976) and Hnatiuk et al. (1976) also studied tortoise and vegetation interactions on Aldabra. More recent research by Hamilton and Coe (1982) discusses feeding, digestion and assimilation in Geochelone gigantea. No detailed studies of the diet of the Galapagos Geochelone have been made.

The various techniques available for quantification of diets, notably microhistological analysis of esophageal, rumen (or stomach) and fecal samples, and bite counts and other direct observation/utilization methods, have been compared and contrasted repeatedly (Free et al., 1971; Anthony and Smith, 1974; Vavra et al., 1978; Smith and Shandruk, 1979; Johnson and Pearson, 1981). The results of these and other studies are varied; each technique has advantages and disadvantages. Although microscopic analysis of plant fragments in fecal material may underestimate some highly digestible food items (flowers, fruits, fungus), it is a particularly useful technique for studying the diets of endangered species.

In this phase of my research, fecal sample collection was combined with direct observation of feeding animals to investigate feral burro and giant tortoise diets on Volcan Alcedo. By observing feeding animals, I was able to obtain dietary data for the wet season (when feces were not collected) and also a list of the plant species that were consumed. The list was essential for collection of plant specimens to be used as reference material.

Methods

In February 1980, during the hot rainy season, I began gathering data on burro and tortoise feeding by direct observations. Neither species is especially alert on Alcedo, so I was able to approach the grazing animals. Tortoises are less wary than burros and could always be approached to within a couple of meters. Burros, particularly those feeding in groups, had to be watched from distances of two to ten meters, depending on the circumstances.

I watched an individual animal feed until it either became frightened or left the immediate area. A one meter square plot was staked around the grazed area. For each of these feeding plots, a list of the plant species present, the relative percentages of the plot occupied by each species, and a list of the species that had been consumed, was recorded. Only during the dry season was it occasionally difficult to ascertain which plant species had been eaten by burros in a plot. Due to the dry conditions in some of the study sites, plants were easily uprooted and thus evidence of grazing was hard to observe. However, by watching the burros while they fed and periodically lifted their heads, the plants dangling from their mouths could readily be identified.

Table 6-1 lists the numbers and locations of the feeding plots examined for burros and tortoises. I attempted to make observations on 20 feeding plots for each species in each of the three main study sites (Midcamp, South Floor and Rim Camp) during four different months. Because of seasonal changes in distribution however, it was sometimes impossible to locate sufficient grazing animals and so fewer than 20 plots were examined. In July, due to a scarcity of burros at both Rim Camp and South Floor study sites, burro feeding was observed at North Plateau.

During the rainy season fecal samples were not collected because of the weather conditions; they could not be dried for preservation. However, in July 1980, fecal collection began (Table 6-2). Samples were taken at the beginning and at the end of the dry season and collected from each of three study site localities, Rim Camp, Midcamp and South Floor. In addition, burro fecal material was collected from North Plateau. Only very fresh feces were collected, those that had been deposited

Table 6-1

Number of Burro and Tortoise Feeding Plots Examined
1980

	Rim Camp		Midcamp		South Floor		North Plateau		Month Totals	
	B	T	B	T	B	T	B	T	B	T
Feb	23	20	20	20	22	20	-	-	65	60
Apr	8	20	20	15	10	15	-	-	38	50
Jul-Aug	-	23	20	13	10	16	20	-	50	52
Oct-Nov	30	30	3	-	15	2	-	-	48	32
Area Totals	61	93	63	48	57	53	20	-	201	194

Table 6-2

Numbers of Burro and Tortoise Fecal Samples Collected
1980

						South		North	
Rim Camp		Midcamp		Floor		Plateau			
	B	T	B	T	B	T	B	T	
Jul-Aug	15	15	13	6	13	8	15	-	
Nov-Dec	16	16	10	4	21	8	10	-	
Area Totals	31	31	23	10	34	16	25	-	
Grand Total 170*									

*An additional 25 burro and 15 tortoise samples were lost in US Customs upon entering the country.

within a few days prior to collection. Because of the difficulty of backpacking a large number of samples to the landing beach, only a small number were gathered.

Samples were sun-dried in the field and later oven-dried at a temperature of 60 degrees C for 16 to 20 hours. They were then ground in a Wiley Mill through a 1.0 mm screen. Samples were decolorized in household bleach and mounted on slides with Hoyer's solution according to techniques outlined by Johnson and Pearson (1981). A series of slides made from 87 known burro food plant species from Alcedo provided a reference collection from which the diagnostic features of forage species could be learned.

Quantification of plant species amounts and diversity in burro and tortoise feces was performed by Dr. Mark K. Johnson, Louisiana State University, using frequency sampling techniques as described by Johnson (1982). Data were expressed as estimates of dry weight proportions in the diet samples. Diets of burros and tortoises were statistically compared using a procedure proposed by Watson (1956) and later expanded by Stephens (1982).

Results

Table 6-3 summarizes the data obtained via direct observations of feeding burros. Plants were classified as "common species," those occurring in more than ten

Table 6-3

Plant Species Eaten by Burros in Feeding Plots
1980 (n=201 plots)

	Feb-Apr		Jul		Nov	
	%Plots	%Time Eaten	%Plots	%Time Eaten	%Plots	%Time Eaten
Common Species*						
Gramineae & Cyperaceae	96.1	96.0	90.0	95.6	68.8	90.9
Sida spp.	84.5	1.1	66.0	24.2	75.0	52.8
Blainvillea dichotoma	48.5	6.0	0	-	0	-
Borreria laevis	26.2	7.4	(<10%)	-	37.5	11.1
Hyptis rhomboidea	21.4	0	0	-	37.5	27.8
Crotalaria incana	33.0	14.7	(<10%)	-	0	-
Polypodiaceae	15.5	25.0	(<10%)	-	33.3	25.0
Ipomea triloba	27.2	3.6	(<10%)	-	0	-
Hypoxis decumbens	12.6	46.2	(<10%)	-	20.8	40.0
Oxalis corniculata	13.6	14.3	0	-	14.6	28.6
Portulaca oleracea	17.5	11.1	(<10%)	-	0	-
Physalis pubescens	10.7	27.3	(<10%)	-	(<10%)	-
Sonchus oleraceus	(<10%)	-	16.0	37.5	(<10%)	-
Uncommon Preferred Species**						
Fimbristylis dichotoma	5.8	83.3	10.0	80.0	0	-
Ipomea alba	-	(<25%)	6.0	66.7	8.3	75.0
Sonchus oleraceus	2.9	100	(>10%)	See above	2.1	100
Amaranthus quitensis	9.7	50.0	-	(<25%)	0	-
Solanum nodiflorum	2.9	66.7	0	-	4.2	50.0
Plantago major	5.8	50.0	0	-	6.3	33.3
Mollugo snodgrassii	1.9	50.0	0	-	0	-
Fleurya aestuans	7.8	25.0	0	-	0	-
Commelina diffusa	3.9	25.0	-	(<25%)	10.0	60.0
Crotalaria spp.	-	(<25%)	6.0	33.3	0	-

*Species present in more than 10 percent of the feeding plots.

**Species present in less than 10 percent of the feeding plots, but eaten in more than 25 percent of the plots where they were available.

percent of the feeding plots, or "uncommon but preferred species," those that occurred in less than ten percent of the plots but were eaten in more than 25 percent of the plots where they were available. From observations, it was evident that species abundance changed over the seasons; hence some species that were common during one sampling period were uncommon or even absent during another. Analogous tortoise feeding plot data are presented in Tables 6-4 and 6-5. All plant species that burros and tortoises consumed, including those they only occasionally ate, are listed in Table 6-6.

Throughout the year burros selected grasses and sedges from 90 percent or more of the plots in which they were observed feeding. *Sida*, common year round in the plots, was selected by feeding burros during July and November. Several common forb species, with seasonal changes in abundances, also were frequently consumed by burros: *Borreria* and *Hyptis* were selected in November, *Crotolaria* was selected in February/April and November and *Hypoxis* and *Oxalis* were selected in February/April and November.

Tortoises selected grasses and sedges, *Sida*, *Borreria* and *Hyptis* the year round. *Ipomea*, *Sonchus*, *Mecardonia*, *Plantago* and *Mollugo* were not common in tortoise feeding plots but were readily eaten by tortoises when available.

Table 6-4

Common Plant Species Eaten by Tortoises in Feeding Plots
1980 (n=194 plots)

	Feb-Apr		Jul		Nov	
	%Plots	%Time Eaten	%Plots	%Time Eaten	%Plots	%Time Eaten
Common Species*						
Gramineae & Cyperaceae	99.1	89.9	92.3	70.8	93.8	86.7
Sida spp.	82.7	75.8	92.3	54.2	62.5	80.0
Scoparia dulcis	24.5	7.4	46.2	0	25.0	0
Blainvillea dichotoma	40.9	20.0	(<10%)	-	0	-
Borreria laevis	32.7	72.2	34.6	55.6	43.8	57.1
Hyptis rhomboidea	16.4	55.6	23.1	50.0	43.8	35.7
Crotalaria incana	20.0	27.3	(<10%)	-	0	-
Verbena spp.	14.5	1.8	23.1	16.7	40.6	0
Hypoxis decumbens	15.5	52.9	21.9	14.3	(<10%)	-
Portulaca oleracea	40.0	50.0	(<10%)	-	0	-
Chrysanthellum pusillum	30.0	39.4	0	-	0	-
Amaranthus quitensis	16.4	27.8	0	-	0	-
Synedrella nodiflora	18.2	60.0	(<10%)	-	0	-
Mecardonia dianthera	(<10%)	-	23.1	16.7	(<10%)	-
Ipomea alba	(<10%)	-	19.6	44.7	(<10%)	-
Salvia occidentalis	(<10%)	-	13.5	28.6	0	-
Oxalis corniculata	(<10%)	-	0	-	12.5	25.0
Conyza bonariensis	0	-	11.5	16.7	(<10%)	-

*Species present in more than 10 percent of the feeding plots.

Table 6-5

Uncommon Plant Species Eaten by Tortoises in Feeding Plots
1980 (n=194 plots)

	Feb-Apr		Jul		Nov	
	%Plots	%time Eaten	%Plots	%time Eaten	%Plots	%time Eaten
Uncommon Preferred Species*						
Ipomea alba	6.8	100	(>10%)	***	3.1	100
Sonchus oleraceus	1.0	100	0	-	-	(<25%)
Mercardonia dianthera	1.0	100	(>10%)	***	-	(<25%)
Plantago major	3.6	100	9.6	60.0	-	(<25%)
Mollugo snodgrassii	1.0	100	0	-	0	-
Fleurya aestuans	5.5	33.3	-	(<25%)	0	-
Solanum nodiflorum	0	-	7.7	50.0	-	(<25%)
Commelina diffusa	1.8	50.0	9.6	40.0	-	(<25%)
Crotalaria pumila	1.8	50.0	0	-	0	-
Salvia occidentalis	8.2	44.4	(>10%)	***	0	-
Oxalis corniculata	7.3	37.5	0	-	0	-
Bidens spp.	5.5	33.3	0	-	0	-
Stylosanthes sympodialis/ *Tephrosia decumbens***	1.8	100	5.8	66.7	0	-
Elaterium carthagenense	-	(<25%)	1.9	100	0	-
Datura stramonium	1.8	100	0	-	0	-
Acalypha parvula	-	(<25%)	1.9	100	0	-
Conyza bonariensis	0	-	(>10%)	***	9.4	33.3

*Species present in less than 10 percent of the feeding plots, but eaten in more than 25 percent of the plots where they were available.

**Did not distinguish between the two species in the field.

***See Table 6-4.

Table 6-6

Plant Species Eaten by Burros and Tortoises, Volcan Alcedo, 1980
(Based on fecal analysis and direct observation of feeding animals)

Species	Burros	Tortoises
Polypodiaceae		
Adiantum concinnum	X	X
Asplenium praemorsum		X
Blechnum occidentale	X	
Dennstaedtia cicutaria	X	X
Nephrolepis cordifolia	X	
Amaranthaceae		
Alternathera echinocephala	X	
Amaranthus quitensis	X	X
Molluginaceae *Mollugo snodgrassii*	X	X
Nyctaginaceae		
Commicarpus tuberosus	X	
Pisonia floribunda	X	
Urticaceae *Fleurya aestuans*	X	X
Viscaceae *Phoradendron henslovii*	X	
Boraginaceae		
Heliotropium angiospermum	X	
Tournefortia psilostachya	X	
T. pubescens	X	
T. rufo-sericea	X	
Compositae		
Baccharis gnidiifolia	X	
Bidens pilosa	X	X
B. riparia	X	X
Blainvillea dichotoma	X	X
Chrysanthellum pusillum		X
Conyza bonariensis	X	X
Darwiniothamnus lancifolius	X	
Sonchus oleraceus	X	X
Synedrella nodiflora	X	X
Convolvulaceae		
Evolvulus glaber	X	
Ipomea alba	X	X
I. triloba	X	X
Cucurbitaceae *Elaterium carthagenense*		X

Table 6-6-continued

Species	Burros	Tortoises
Labiatae		
Hyptis rhomboidea	X	X
Salvia occidentalis		X
S. pseudoserotina		X
Plantaginaceae *Plantago major*	X	X
Rubiaceae		
Borreria laevis	X	X
Psychotria rufipes	X	
Scrophulariaceae		
Mecardonia dianthera		X
Scoparia dulcis		X
Solanaceae		
Datura stramonium		X
Physalis pubescens	X	
Solanum nodiflorum	X	X
Verbenaceae *Verbena townsendii*	X	X
Burseraceae *Bursera graveolens*	X	
Caryophyllaceae *Drymaria cordata*	X	
Euphorbiaceae *Acalypha parvula*	X	X
Leguminosae		
Crotolaria incana	X	X
C. pumila	X	X
Stylosanthes sympodialis	X	X
Tephrosia decumbens	X	X
Zorina piurensis	X	
Malvaceae		
Sida rhombifolia	X	X
S. salviifolia	X	X
S. rupo		X
S. glutinosa		X
Myrtaceae *Psidium galapageium* (fruit of)	X	X
Oxalidaceae *Oxalis corniculata*	X	X
Portulacaceae *Portulaca oleracea*	X	X

Table 6-6–continued

Species	Burros	Tortoises
Sterculiaceae *Walteria ovata*	X	
Commelinaceae *Commelina diffusa*	X	X
Hypoxidaceae *Hypoxis decumbens*	X	X
Cyperaceae		
Bulbostylis hirtella	X	
Cyperus brevifolius	X	X
C. esculentus	X	X
Fimbristylis dichotoma	X	X
Gramineae		
Antephora hermaphrodita	X	X
Cenchrus platyacanthus	X	X
Digitaria adscendens	X	X
Eragrostic cilianensis	X	X
Panicum hirticaule	X	X
Paspalum conjugatum	X	X
P. galapageium	X	X
Sporobolus indicus	X	X
Trichoneura lindleyana	X	X

Statistical analyses, using analysis of proportions with disproportionate numbers (Snedecor and Cochran, 1967), were performed to compare burro and tortoise consumption of grasses and sedges and *Sida*. Significant results were those in which Z values were greater than 1.96 and $\alpha = .05$. Analysis of feeding plot data showed that burros consistently selected significantly more grasses and sedges than did tortoises. Tortoises selected grasses significantly more often in February/April and November than in July. *Sida*, on the other hand, was selected by tortoises significantly more often than by burros throughout the year. Tortoise *Sida* consumption was highest in February/April and November. Burros *Sida* consumption was lowest in February/April, moderate in July and highest in November.

Because fecal samples for quantification of diets could be collected solely during the dry season, only feeding plot data were available to investigate rainy season burro and tortoise diets. Apparently during February/April both burros and tortoises ate a great deal of grasses and sedges. Tortoises also consumed a large amount of *Sida*, while burros ate little *Sida* in February/April. Both animals also ate a variety of other forb species.

July and November burro and tortoise diets, as obtained via fecal analysis, are compared in Table 6-7. The plant species that occurred at densities of more than

Table 6-7

Percent Relative Density of Plant Fragments in Burro and Tortoise Feces, Volcan Alcedo, 1980

Species	Burro		Tortoise	
	Jul n=56	Nov n=57	Jul n=29	Nov n=28
Grasses				
Panicum spp.	34.4	7.5	5.1	1.3
Papsalum spp.	6.7	5.3	4.1	0.3
Sporobolus indicus	14.2	1.7	1.5	0.2
Digitaria adscendens	9.2	1.1	2.9	-
Antephora hermaphrodita	-	0.6	4.3	-
Trichoneura lindleyana	0.4	-	0.7	-
Eragrostis spp.	6.2	0.6	1.3	-
Cenchrus platyacanthus	1.1	0.3	-	-
Unidentified grasses	0.1	0.5	-	0.3
Total grasses	72.3	17.6	19.9	2.1
Sedges				
Cyperus spp.	-	-	13.8	3.3
Unidentified sedges	1.7	1.3	2.6	-
Total sedges	1.7	1.3	16.4	3.3
Browse				
Sida spp.	12.1	66.5	45.8	61.6
Polypodiaceae	1.4	0.1	0.9	7.1
Phoradendron henslovii	0.7	1.8	-	-
Unidentified browse	-	0.1	0.8	3.6
Misc. browse*	0.1	0.7	0.2	-
Total browse	14.3	69.2	47.7	72.3
Forbs				
Synedrella nodiflora	0.2	-	2.0	-
Borreria laevis	-	-	3.1	-
Solanum nodiflora	1.2	-	-	-
Acalypha parvula	1.4	0.2	0.1	-
Tephrosia decumbens	1.3	0.2	2.8	-
Commelina diffusa	-	-	2.0	-
Hypoxis decumbens	1.6	4.2	0.4	-
Unidentified forbs	4.7	3.1	4.9	3.6
Misc. forbs*	1.2	3.4	0.7	0.6
Total forbs	11.6	11.1	16.0	4.2
Fruit of Psidium galapageium	-	0.8	-	18.1

*Identifiable species that occurred at densities of less that 1%.

one precent in feces are listed. Species that were identifiable, but an insignificant component of the diets (miscellaneous forbs, miscellaneous browse), are included in Table 6-6. Seventy-two percent of the plants in this list of all species known to be eaten by burros and/or tortoises were at least occasionally consumed by both animal species.

In July, burro diets consisted of 72.3 percent grasses, 1.7 percent sedges, 14.3 percent browse and 11.6 percent forbs. In November, burros shifted to a heavier dependence on browse and diets consisted of 17.6 percent grasses, 1.3 percent sedges, 69.2 percent browse and 11.1 percent forbs. Browse species were the major component of tortoise diets for both months. July tortoise diets were composed of 19.9 percent grasses, 16.4 percent sedges, 47.7 percent browse and 16 percent forbs. In November, 18.1 percent of tortoise diets were _Psidium galapageium_ fruits and 72.3 percent was browse, with the balance of 2.1 percent grasses, 3.3 percent sedges and 4.2 percent forbs.

Panicum spp., _Paspalum spp._, _Sporobolus indicus_ and _Digitaria adscendens_ were the most abundant grasses in both burro and tortoise diets. _Antephora hermaphrodita_ was a major component of tortoise grass consumption in July. _Cenchrus platyacanthus_, an abundant grass on Alcedo during the rainy season but dead and dying by July, was not frequent in the July or November fecal samples. This species was frequently consumed, however, during the rainy season by burros and to a lesser extent by tortoises.

Six species of *Sida* were identified on Alcedo: *S. salviifolia*, *S. rhombifolia*, *S. acuta*, *S. spinosa*, *S. rupo* and *S. glutinosa*. *Sida rhombifolia* was the most abundant species of *Sida* on Alcedo, and the primary one upon which burros and tortoises fed. By the end of the dry season, all *S. rhombifolia* plants on Alcedo's south-eastern rim and slopes had been heavily browsed. Tortoises congregated along this section of the crater during the dry season and burros traveled to the area for water (See Chapter Three), hence the density of animals was highest there. In contrast, *Sida* plants on the North Plateau and at Midcamp, areas where fewer burros and tortoises remained in the dry season, were often 20 to 25 centimeters high and few plants showed signs of heavy browsing.

On the extremely dry South Floor, where few food plants were available besides *Sida* after the rains had ended, all *Sida* plants were cropped at ground level. *Phoradendron henslovii*, a shrubby parasite growing in *Croton scouleria* trees, was a favorite burro food item on the crater floor. *Phoradendron* showed a distinct browse line at burro reach height and most *Croton* trees had branches broken as a result of burros pulling at the parasitic *Phoradendron* plants.

Statistical analyses comparing burro diets in July and November, tortoise diets in July and November, and finally burro and tortoise diets were performed according to Stephens (1982). For analysis, food plants were grouped as "grasses," "sedges," "*Sida*," "*Psidium* fruit" and "others" so that the most important food items could be compared.

The comparison of percentage compositions of burro diets in July and November yielded an F value of greater than 95, a highly significant result ($\alpha = .001$). It is obvious from the burro data that the importance of grasses and *Sida* in the diets were reversed between July and November.

A similar comparison of tortoise diet data also established that significant differences exist between July and November tortoise diets (df = 4, F = 5.75, $\alpha = .01$). The difference appeared to be due to changes in all four of the major dietary components: grasses, sedges, *Sida* and *Psidium*. *Sida* was the most important food species in both months, and *Sida* consumption was higher in November than in July. *Psidium* fruits were an important item in the November diet, while sedges and grasses were reduced in importance in that month.

A comparison between tortoise and burro diets, with each month compared separately, showed that the component percentages of monthly diets were significantly different. For July, the differences were due to grasses being consumed more by burros than by tortoises; tortoises consumed more sedges and _Sida_. In November, burros again ate more grasses, and _Psidium_ became an important item in tortoise diets.

The quantified diet results obtained from fecal analysis can be compared to the feeding plot data for the months of July and November. Feeding plot results closely resemble fecal data for burro and tortoise consumption of _Sida_ in both months, and for grass and sedge consumption in July. However, November feeding plot grass and sedge consumption was inconsistently high when compared to the percentage composition of grasses and sedges in November feces. In accordance with the reduced amount of grasses and sedges in November feces, I would have expected a decrease in the selection of grasses and sedges in feeding plots by both animal species. The discrepancy may be related to the fact that by the last months of the dry season, grasses were uniformly cropped short. Although animals still frequently selected grasses, perhaps because of previous grazing pressure less grass was obtained per unit of time.

Discussion

Burros are opportunistic in their diets and will change from grazing to browsing depending on locality and food plant availability (Hansen and Martin, 1973; Woodward and Ohmart, 1976; Moehlman, 1979; Seegmiller and

Ohmart, 1981). On Volcan Alcedo, burros were primarily grazers during the rainy season and early part of the dry season, when green grasses and growing forbs were plentiful. They shifted to a greater dependence on browsing, particularly of Sida, during the latter part of the dry season. Sida was the most important food item in tortoise diets during the entire dry season and probably year round (no quantitative diet data are available for the rainy season, but Sida was selected in 75% of the rainy season feeding plots). Grasses were important in tortoise diets during the rainy season and the early dry months of the year, while Psidium fruits were a major food source in November.

Competition between species may occur when resources, which are in short supply, are shared by sympatric species. Competitive interactions cause a reduction in the overall fitness of the populations involved as a result of the decreased availability of the limiting resources (Pianka, 1978). Researchers have demonstrated dietary and ecological overlap between feral burros and other native and domestic mammals (Hansen and Martin, 1973; Seegmiller and Ohmart, 1981).

On Alcedo, burros and tortoises showed considerable year round overlap in the food plants they consumed. Seventy-two percent of the 92 plant species eaten by burros and/or tortoises were consumed by both animal species. However, the various plant species were consumed in significantly different amounts by burros and tortoises during the wet season and early part of the dry season.

If competition for food between burros and tortoises does occur on Alcedo, it occurs during the latter part of the dry season, in the form of a competition for *Sida*. *Sida* accounted for 66.6 and 61.6 percent of November burro and tortoise diets, respectively. In the dry season *Sida* plants in areas of high tortoise and/or burro density were heavily browsed. By October and November, all *Sida* on the moist southeastern rim and slopes and on the dry crater floor were cropped at ground level.

Based on a short-term study, one can only speculate as to whether or not there is competition for food resources on Volcan Alcedo. To verify that competition exists, one must look at species fitness. Fitness is not easily determined in a field setting and is impossible to measure in a short-term study. The occurrence of burro and tortoise dietary overlap provides some evidence of possible competition. Competition between burros and tortoises may be reduced by differences between their dry season feeding behaviors and distributions. This will be discussed in the Conclusions.

CHAPTER SEVEN

TORTOISE DAILY TIME BUDGETS

During the dry season on Volcan Alcedo, much of the vegetation dries up and tortoises congregate along the moist southeastern rim where green forage exists year round. I noticed, too, that during the drier months, tortoises seemed to be less intent on feeding than they are during the rainy season. It was at this time of the year that they were noticeably more curious about my camp and me; without fail, every day in the dry season a tortoise would try to break through the protective fence surrounding my tent area.

Since tortoises are known to survive for up to two years without eating (Townsend, 1925), I wondered whether, when food was in short supply, tortoises simply spent less time feeding and more time engaged in other activities. To test this hypothesis, I collected data on tortoise daily time budgets during several months of the year.

Methods

To eliminate feeding preferences and behavioral variability due to sex, size or locale, I chose to observe only large male tortoises on the southeastern rim at Rim Camp study site. Three or four tortoises were observed during each of three study periods: the wet season in late April and early May, the transition period between the wet and dry seasons in mid-August, and the end of the dry season, in early December. Individual tortoises were followed for one to four days and eleven different tortoises were studied on the thirty days of observation.

Study tortoises were chosen from among the large males who had bedded down along the rim within a half mile of my camp. A tortoise was selected on the evening before study so that I could be certain to observe a full-day of activity. Tortoises dug into dusty beds, called "tortoise forms," in the late afternoon and rarely moved again until after dawn the next day. I selected a tortoise, noted his approximate position and then made certain I arrived to begin observations before he had moved the next morning. In May and August two tortoises were observed each day; one by my assistant and one by me.

When the tortoise under observation first stirred, data collection began. From that time until he returned to a form and dug in for the night, I recorded his activity at one minute intervals. In addition, behavioral data were taken when he interacted with other tortoises. I kept track of the approximate straight-line distance traveled and whether a tortoise returned to the same bed for the night.

The following categories of behavior were initially recorded; feeding, walking, running, sitting, sprawled-sleeping, puddle-sitting, chasing, mounting, sitting socially (i.e., within a meter of another tortoise and actively aware of it, not sleeping side by side), drinking, extending for finches, defecating and urinating. Later I lumped data into the five classes of feeding, walking/running, resting, social interacting, and maintenance behavior.

Tortoises were easy to follow and could be observed from a distance of just a few meters if the observer took care to move slowly and remain slightly hidden from view. Only occasionally did my presence apparently interfere with a tortoise's natural behavior. In almost every case, when an animal had stopped feeding or walking to look at me, he resumed an activity before time for the next data point to be recorded. Tortoises that I followed for two or more days consecutively became habituated.

Results

A summary of the daily activities of the eleven tortoises studied is presented in Table 7-1. Tortoises began to leave the dusty forms where they had spent the night as early as 5:13 a.m.; the latest riser began activity four hours later, at 9:16 a.m. Activity start times varied between and within individuals and seasons. Start times did not vary significantly with the time of year (one-way analysis of variance test; Snedecor and Cochran, 1967) nor with daily weather conditions (Mann-Whitney U test; Siegel, 1956).

Tortoises began to bed down as early as 12:22 in the afternoon. The latest that any tortoise remained active in the evening was 6:10 p.m. Bedding down times were not related to season or weather conditions. The length of daily activity ranged from 5 hours 27 minutes to 11 hours 58 minutes. The average lengths of daily activity for tortoises in the different seasons were very similar; 8 hours 43 minutes for tortoises in the wet season, 8 hours 25 minutes for tortoises in the transition period from wet to dry season and 9 hours 5 minutes for tortoises in the dry season. The length of daily activity was not significantly affected by either weather conditions or season.

A one-way analysis of variance test showed no statistically significant differences in the distances traveled by tortoises in the different seasons. Nor was the

Table 7-1

Summary of Tortoise Activity

Tortoise	Date	Activity		Minutes Active	Meters Traveled	Hours Active Per Day		Meters Per Day	
		Started	Ended			Mean	Stand. Dev.	Mean	Stand. Dev.
Wet Season									
Alberto	Apr 14	0716	1628	553	190				
	15	0747	1558	491	300				
	16	0623	1643	620	200	9.5	1.0	197.5	81.8
	17	0633	1649	616	100				
Eduardo	May 2	0650	1737	642	90				
	3	0916	1616	421	600	9.1	1.9	430.0	294.4
	4	0654	1635	582	600				
Randell	May 2	0816	1746	451	600				
	3	0850	1810	441	80				
	4	0658	1351	413	120	7.3	.3	266.7	289.4
Transition									
George	Aug 7	0656	1222	327	20	7.4	2.8	410.0	551.5
	8	0622	1547	566	800				
Pedro	Aug 7	0832	1757	565	10	9.3	.2	405.0	558.6
	8	0601	1509	549	800				
Equivocacion	Aug 9	0554	1641	648	30				
	10	0617	1304	408	30	9.0	2.0	30.0	0
	13	0609	1537	568	30				
Jose	Aug 9	0550	1335	466	100				
	10	0545	1352	488	60				
	13	0621	1407	467	50	7.9	.2	70.0	26.5
Dry Season									
George	Dec 1	0532	1615	614	20	-	-	-	-
Carlos	Dec 4	0634	1542	549	80				
	5	0539	1703	685	380	10.3	1.6	230.0	212.1
John	Dec 6	0640	1510	547	15				
	7	0608	1526	559	1700	9.2	.1	857.5	1191.5
Bill	Dec 9	0725	1455	419	150				
	10	0514	1711	718	40				
	11	0611	1345	425	20				
	12	0513	1341	509	150	8.6	2.3	90.0	69.8
Tom	Dec 13	0814	1610	420	30	-	-	-	-
				Wet Season Average		8.7	1.5	288.0	225.0
				Transition Average		8.4	1.6	193.0	320.9
				Dry Season Average		9.1	1.8	258.5	518.7

distance traveled related to weather conditions (Mann-Whitney U test). However, tortoises do show a tendency towards longer daily trips during the wet season, without an accompanying increase in the length of daily activity. This may be a result of the many mating chases that occur during those months.

A comparison of seasonal tortoise daily time budgets is presented in Table 7-2. A chi-square test showed highly significant differences in the amount of time tortoises spent in each type of activity at different times of the year (^{2}=4325.8, p .001).

In the wet season tortoises rested during 20 percent of their wakeful hours, but in the dry season they spent about 59 percent of each day resting. On the other hand, during the wet season and the transition period tortoises spent 41 to 44 percent of their wakeful hours feeding, but only nine percent in the dry month of December. In December, however, a greater amount of time was spent by tortoises in maintenance behaviors. Tortoise maintenance behaviors included drinking and the increase in time spent in these behaviors was due to an increase in the amount of time tortoises spent drinking and searching for water in the dry season. In December, on mornings following a wet garua night, tortoises spent up to five hours traveling from one garua drip-puddle to another, sucking water from the mud. Tortoise George, on December 1, 1980, began activity at 6:56 a.m. and spent

Table 7-2

Seasonal Comparison of Daily Time Budgets of Alcedo Tortoises, 1980 (n=30)

	Resting	Feeding	Maintenance	Walking Running	Social Inter-Acting
April and May - Wet Season	20.74* (1101)**	41.72 (2269)	1.28 (69)	16.87 (821)	16.60 (853)
August-Transition Period	44.16 (2076)	44.02 (2396)	1.66 (87)	9.88 (481)	0.28 (11)
December-Dry Season	59.01 (3155)	9.31 (698)	15.58 (671)	13.87 (848)	2.23 (73)

*Percent of time spent in each activity.
**Number of minutes spent in each activity.

until 1:30 p.m. doing very little besides walking to and from puddles and trying to drink. George did not feed at all that day. December 1, 1980, was the first wet garua day after several consecutive drier ones; that morning all tortoises were intent on searching for water and every muddy puddle had at least three or four tortoises wallowing in it.

In the months of August and December, tortoises regularly extended their necks and limbs in a stance which allows the various species of Geospiza finches to remove ticks from their leathery hides. During the wet season this behavior rarely occurs; in the dry season, especially early in the mornings, it is common.

During the breeding season months of April and May, a large percentage of time, as compared to other months, was spent in social interaction: chasing, mounting and sitting near other tortoises (inspecting them before or just after a chase or mount). All tortoises under observation in the wet season months of April and May mounted one to five different female tortoises each day, except the tortoise Alberto on April 15, 1980. Alberto chased and smelled six tortoises that day but mounted none. However, on the 14th and 16th of April, Alberto indulged in a strange behavior that both of the researchers who watched him independently concluded was a form of masturbation. With penis extended below and legs stretched out in front so that the front of his body was higher than the back, he gently rocked back and forth, his shell rubbing his penis. He made groaning and sputtering noises and continued rocking from 7:19-7:31 a.m. on the first day and from 7:58-8:12 a.m. two days later. After he had left the area, a small amount of blood and more of a mucus-like substance were found. Dr. Auffenberg (personal communication) has never before heard a report of masturbation in giant tortoises.

Discussion

No detailed studies of the activity pattern and time budgets of _Geochelone elephantopus_ in their natural habitat have previously been conducted. Hendrickson (1965) made dawn to dusk watches of two male tortoises on Isla Santa Cruz, Galapagos, but presented no quantitative data. For that matter, there are few precise data on the daily and seasonal activities of most turtle species. Gourley (1979) and Auffenberg and Iverson (1979) discuss some of the recent research into turtle activity patterns but include little concerning the Galapagos _Geochelone_.

The giant _Geochelone_ of Aldabra Atoll have been better studied than their Galapagos relatives, but detailed data on _G. gigantea_ time budgets also are lacking. On Aldabra, tortoises begin grazing at dawn and by 10:00 a.m. on clear days seek shade (Gaymer, 1968; Bourn, 1976, 1977; and Shaffer and Ernst, 1979). In the late afternoons, they resume feeding until dusk; sometimes they feed by moonlight. Tortoises on Aldabra that are unable to find shade in the heat of the day suffer from heat stress and often die. Suitable shelter from the sun is apparently lacking on parts of Aldabra due to the destruction of vegetation by the extremely dense tortoise populations (Merton et al., 1976 and Hnatiuk et al., 1976). Aldabra tortoises copulate during the warm wet season (November to April) and wallow when possible in rain generated pools as they do on Alcedo. During the cool dry months (May to October) the inland pools and lush vegetation produced by earlier rains dry up and little food is available to tortoises (Bourn, 1976).

Along Alcedo's southeastern rim, tortoise activity patterns were not as greatly influenced by the sun and the daily weather conditions as they apparently are on Aldabra. Often the southeastern section of Alcedo is garua covered and even on clear days temperatures are relatively cool (maximum temperature in 1980 was 29°C, average maximum temperature was 24°C).

On Alcedo there is abundant shade and only once was a tortoise seen that was apparently suffering from heat stress. This individual was stumbling, tossing his head and frothing at the mouth one hot morning as he came off a large treeless area of the southern caldera floor; he did reach the shade and recovered. Similar behavioral reactions to overheating are described by Grubb (1971) for Aldabra tortoises. Probably few tortoise deaths on Alcedo are actually caused by overheating.

No significant differences among seasons were found on Volcan Alcedo in relation to tortoise activity start times, bedding down times, length of daily activity or daily distance traveled. It is doubtful that, even with a much larger sample size of tortoises from which to draw data, statistically significant differences would be seen between the seasonal means of start or bedding down times or the resulting length of daily activity. However, by studying a larger number of animals and/or following individuals for longer time periods, one might be able to discern significant seasonal changes in the distances that tortoises traveled. The data presented here show a great deal of variation within seasons but do suggest a tendency towards longer daily trips in the wet season. A larger sample size is needed to clarify these results.

Distinct seasonal variations in tortoise daily time budgets occur on Alcedo. Alcedo tortoises show a marked seasonal change in the amount of time they spend feeding. Tortoises spent much less of their wakeful hours feeding in the dry season than in the wet or transition seasons. There is less tender green forage at this time of the year, more tortoises are crowded together along the southeast rim and undoubtedly tortoises have a large amount of fat stored up from the wet season. They apparently do not need to feed the year round. In the dry season, more of their time is spent searching for water and drinking, extending for finches to remove ticks, and resting.

The tortoises of Aldabra stop growing in the dry season (Bourn and Coe, 1978) but show no ill effects of food shortages unless food is scarce in the months just prior to the nesting season. If food shortages due to an extended dry season or to extremely dense tortoise populations occur one to two months prior to egg laying, female tortoises will often reabsorb preovulatory follicles (Swingland and Coe, 1978). Nesting occurs in May or June on Alcedo; the rainy season normally begins in late December or in January, hence forage is normally abundant during the four months prior to laying. Apparently a normal dry season shortage of food and water is easily coped with by both species of giant Geochelone.

On Alcedo, as on Aldabra, the breeding season coincides with the rainy season. During the months of April and May, Alcedo male tortoises spent, on an average, 16 percent of each day chasing, mounting or inspecting other tortoises. Outside the breeding season, tortoises showed little interest in one another and social interactions were limited to a few aggressive displays.

When mud wallows or pools of water are available, the Geochelone of both Aldabra and Alcedo soak in them. Hendrickson (1965) noticed that Galapagos tortoises will often spend the night in wallows or pools and concluded that the water makes breathing easier for these ponderous reptiles. Others however have suggested that the pools help animals retain their body heat during the night.

CHAPTER EIGHT

CONCLUSIONS

Feral burros, *Equus asinus*, were introduced into the Galapagos Archipelago in the early 1830s. They were apparently released on Volcan Alcedo shortly thereafter by tortoise oil seekers and/or sulfur miners. The burros on Alcedo now number between 500 and 700. The Alcedo tortoise, *Geochelone elephantopus vandenburghi*, one of the ten surviving races of an original 14 endemic *Geochelone* races, number an estimated 3,000 and are the least endangered of the Galapagos *Geochelone*. This study examined burro and tortoise feeding ecologies, distributions and interactions on Alcedo to evaluate the possible impact of the feral burros on the tortoise population. The facets of burro ecology that are most likely to influence tortoises are competition for water and food and destruction of nests by burro trampling.

Fresh water is a scarce resource in the Galapagos Islands; Volcan Alcedo has no permanent source of fresh water. Temporary water availability influenced the distribution of both burros and tortoises. During the rainy season (January to June) when water was readily available in puddles everywhere, burros and tortoises were common on the inner caldera floor and along the northern rim and outer slopes of the crater. They avoided the cool, foggy southeastern rim and slopes. During the dry months of July to December, burros were more abundant along the southeastern section, traveling there in search of the moisture that collected in drip-pools as wet garua condensed on vegetation. Pregnant burros, and especially females with young, tended to remain along the southeastern section during the dry season.

Although tortoises can withstand long periods without water, they too congregated along Alcedo's southeastern rim and slopes after the rains had ended. They remained there longer and in relatively greater numbers than did burros. This may be related to the tortoises' relative lack of mobility; they remain rather than travel to and from the area as burros do. The differences between burro and tortoise dry season distributions may serve to reduce possible competition for food.

On Alcedo, mortality among burros more than one year old is higher than expected based on estimates of mortality obtained from feral burro research in the southwestern United States. An examination of teeth from Alcedo burro carcasses and skeletons revealed that an unusually large number of young, sexually mature animals were dying. The usual U-shaped mortality profile of large mammalian populations predicts high mortality only among the very young or the very old. But on Alcedo, more than 40 percent of the dead animals examined were in their prime of life, between three and six years old. Apparently Alcedo is lacking in some key resource requirement necessary to support a healthy burro population.

Burro carcasses showed no evidence of cause of death, but 97 percent of the recorded burro deaths on Alcedo occurred during the latter part of the dry season. These facts, combined with burro behavioral and distributional data from the dry season, and knowledge of their water requirements, indicate that Alcedo burros are under considerable water stress for part of the year. During the dry season, when no rain falls for four to six months, moisture can only be obtained from forage and garua. Burros probably can not survive for more than one month without free water. Evidently occasional garua moisture is not sufficient to sustain the entire burro population; a water shortage probably limits burro population growth. The deaths, in the late 1960s, of several hundred burros that followed the disappearance of Alcedo's only permanent water source, the fumarole pool, provides additional support for this hypothesis. When a year-round water supply was available the burro population was considerably larger.

Tortoises can survive for many months without water. Although water is a limited resource on Alcedo, it is not limiting to tortoise population growth. Removal of the burro population would slightly increase the amount of water available to tortoises in garua drip-puddles, but would have no overall effect on tortoise fitness. The elimination of the tortoises would result in more garua water available to burros. However, in the dry season, this water increase would be insignificant in light of the fact that the burros might have to endure four to six months without rain.

Seventy-two percent of a recorded 92 burro and/or tortoise food plant species were consumed by both animal species. Wet season diets were not quantified, but based on observations of feeding animals, the wet season diets of both burros and tortoises included a wider variety of forbs than they did in July, at the start of the dry season. Tortoises apparently consumed large quantities of both grasses and *Sida*; burros consumed a great deal of grasses and little *Sida*.

Using fecal analysis, early (July) and late (November) dry season burro and tortoise diets were quantified. Grasses were the most important component of July burro diets. *Sida* accounted for almost half of July tortoise diets, although grasses, sedges and forbs were also consumed. November burro and tortoise diets were more similar; *Sida* was the most important food for both animal species (67% dry weight of *Sida* in burro feces and 62% in tortoise feces). In addition, burros consumed a moderate amount of grasses (17%) and tortoises ate *Psidium* fruits (18%).

If burros and tortoises compete for food on Alcedo, food competition probably occurs only during the late dry season when Sida is a major item in both their diets. There is evidence however, that burro and tortoise dry season feeding behaviors are different. These differences may serve to reduce or avoid possible competition.

To investigate possible seasonal changes in tortoise feeding behavior, tortoise seasonal time budgets were determined and compared. Social interactions occupied 16 percent of wet season activity time and only a small percent of time in the other months. This is as expected, since tortoises breed during the rainy season. Resting occupied 20, 44 and 59 percent of the wet season, transition period and dry season time budgets, respectively. The most significant difference between seasonal time budgets was in amount of time spent feeding. Tortoises fed during more than 40 percent of their daily activity time in the wet season and transition period. Feeding accounted for only 9 percent of daily time budgets in the late dry season. This decrease in feeding time, during the months when food (particularly Sida) might otherwise be limiting, may reduce food competition between burros and tortoises to an insignificant level.

It has been shown on Aldabra that Geochelone stop growing during the dry season, but show no ill effects of food shortages unless food is scarce in the months just prior to the nesting season. Geochelone nest at the end of the rainy season; they are adapted to easily cope with food shortages associated with a normal dry season.

True competition between two species populations denotes a shortage of some shared, limiting resource which results in a lowered population fitness for one or both species. On Alcedo when food is least abundant, tortoises can simply stop feeding and live off the fat they have accumulated during the rainy season. Burros, known to be capable of subsisting on low quality forage, continue feeding but have no effect on tortoise fitness. Some plant ecologists have even suggested that the feral burros may help to open pastureland for the tortoise population.

Feral burros may lower the overall tortoise population productivity, however, by nest destruction. To determine natural hatching and emergence success for G. e. vandenburghi and to investigate the effect of feral burros on nest success, nests were monitored on Alcedo. The average clutch size was 13.3 and an average emergence success of 64.7 was recorded.

The two major tortoise nesting areas are frequented by burros; eighteen percent of 88 monitored vandenburghi nests were damaged as a result of burro trampling. The clutches in 4.5 percent of these nests were completely destroyed. The remaining 13.7 percent produced hatchlings at a lowered success rate or were left incubating, the extent of damage unknown. Because hatchling tortoise mortality is normally high, it may be that additional nest destruction by burros lowers annual recruitment into the *vandenburghi* population. If the Alcedo burro population increased significantly in size, as a result of several wet years in a row, burro destruction of nests might have a serious adverse impact on the tortoise population.

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BIOGRAPHICAL SKETCH

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In 1978-79, Lynn spent a year working as a naturalist guide in the Galapagos Islands. She remained in the Islands and did the research which led to this dissertation.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

John H. Kaufmann

John H. Kaufmann, Chairman
Professor of Zoology

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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This dissertation was submitted to the Graduate Faculty of the Department of Zoology in the College of Liberal Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

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