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**BEHAVIORAL ECOLOGY OF FERAL HOUSE CATS IN THE GALAPAGOS
ISLANDS, ECUADOR**

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BEHAVIORAL ECOLOGY OF FERAL HOUSE CATS IN THE
GALAPAGOS ISLANDS, ECUADOR

By

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Abstract of Dissertation Presented to the Graduate Council of the
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BEHAVIORAL ECOLOGY OF FERAL HOUSE CATS IN THE
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Michael J. Konecny

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Chairman: Dr. John H. Kaufmann
Department: Zoology

Feral house cats (Felis catus) were studied at two sites in the Galapagos Islands. Visual observations, fecal collections, and radio telemetry data were gathered to elucidate their ecology and social organization. Sixty-eight percent of all cats trapped were adults; the adult sex ratio was 2.62 males per female. The density of adult cats at both sites was approximately two cats per square kilometer, although the habitat at each site differed in structure and quality.

Transect analyses revealed that there were temporal fluctuations in prey abundance, while the numbers consumed were often different. There were seasonal differences in diet breadth; the diet was broader in the dry season. A posteriori attempts to determine prey preferences indicated that rats, small birds, lava lizards, and grasshoppers were consumed most frequently. A comparison of estimated daily energy intake and daily energy requirements for males and females indicated

that males and pregnant and lactating females probably face energy stresses. The energy stress on pregnant and lactating females may be severe, contributing to their apparent greater mortality.

The plotted movements of radio-collared cats revealed large differences in home range size between sexes and sites. At Cerro Colorado the home ranges were larger and more overlapping than those at Tagus Cove. In the qualitatively richer habitat of Cerro Colorado locations were concentrated near the coast, while those at Tagus Cove were more diffuse. Plots of daily movements revealed that foraging paths at Cerro Colorado crisscrossed frequently, while paths are essentially straight at Tagus Cove. The activity cycle was bimodally crepuscular with the lowest activity in the early afternoon.

Little aggression was seen during dominance interactions at Cerro Colorado, while no interactions were observed at Tagus Cove. From all the collected data it was hypothesized that feral cats are solitary, opportunistic predators with broad diets. Differences in habitat quality between sites resulted in different social organizations, with a dominance hierarchy at Cerro Colorado and olfactory-mediated territoriality at Tagus Cove.

CHAPTER I. INTRODUCTION

Literature Review and Introduction

Feral house cats (Felis catus) have been studied for more than four decades, although their existence in different parts of the world was recorded much earlier. Salvin (1876) reported finding a well-established feral cat population at Tagus Cove in the Galapagos Islands in 1869. Early scientific studies of feral cats concentrated on their food habits and potential wildlife impact (McMurry and Sperry 1941, McKnight 1964, Pearson 1964, 1966). In Germany, Leyhausen and Wolff (1959) attempted to follow one or more farmyard feral cats for 24 hours, initiating the first field behavioral studies.

Little further work was done with feral cats until the 1970's when there was renewed interest in the environmental impacts of introduced animals. Studies were begun to examine the food habits of feral cats in different areas to assess their impact on endangered species (George 1974, Iverson 1978, Fitzgerald and Karl 1979). Once again behavioral studies were begun on semi-dependent feral cats (MacDonald and Apps 1978, Dards 1978, Liberg 1980), and the first studies were begun on free-living populations, principally on remote subantarctic islands. These studies focused on natality, mortality, population structure, and

food habits (Derenne 1976, Derenne and Mougín 1976, van Aarde 1978, 1979, 1980, 1983, Pascal 1980). Recently, other investigators have begun to examine the behavioral ecology of free-living feral cats on continents and islands. Jones and Coman (1981, 1982a, 1982b) have examined several facets of the behavioral ecology of feral cats in arid southwestern Australia. Peter Apps (unpubl.) has recently examined the behavioral ecology of feral cats on arid Dassen Island in the Indian Ocean.

My project examined the behavioral ecology and social organization of isolated feral cat populations in the Galapagos Islands. Islands provide an interesting study because, in general, the ecosystem is simpler with fewer total species and competitors than comparable continental areas, allowing species interactions to be elucidated more clearly. Survival in the restricted environment of an island can lead to interesting behavioral and morphological modifications. I gathered data on population structure, food habits, movements, and behavior in order to describe how cats survive in the Galapagos environment and how they interact with each other.

Study Areas

The Archipelago of Colon (Galapagos Islands) sits astride the Equator between 1°40'N and 1°25'S latitude and between 89°15' and 92°W longitude (Fig. 1). The land mass encompasses approximately 7855 km², of which more than half is contained in Isla Isabela. The rest is divided among 44 other islands, islets, and rocks resting on the

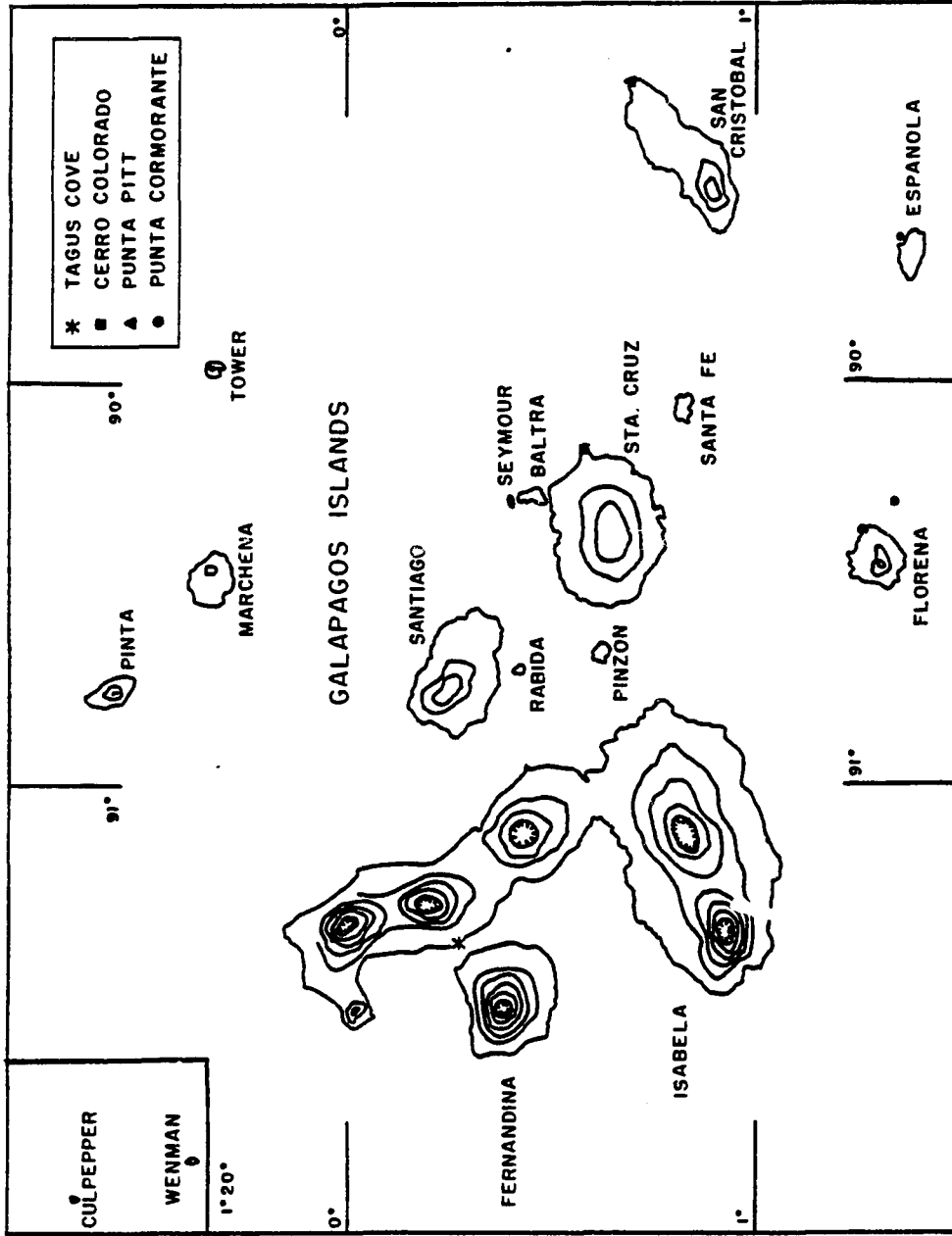


Figure 1. Island outline of the Galapagos Islands with study site locations.

basaltic Galapagos platform. The islands are volcanic, oceanic islands composed predominantly of basalts high in iron and magnesium. The archipelago was probably created by a lithospheric fault or "hot spot" near the East Pacific ridge and the junction of the Nazca and Cocos seafloor plates (NazCoPac triple junction). The Galapagos Platform sits on the Nazca plate which is being forced eastward by the East Pacific spreading center at the rate of approximately 5 cm/year. The construction of individual islands varies according to the climatic factors and magmatic composition present during their emergence. The eastern, and oldest, islands are composed primarily of subaerial marine flows and are estimated to be less than 5 million years old. The western islands, younger and volcanically more active, are characterized by high, shield volcanos. Isla Isabela contains six volcanos which are still intermittently active.

Most of my work was performed at two locations; supplementary food habit data were collected at three additional locations.

Cerro Colorado (0°34'45" S lat., 90°9'42" W long.) is situated on the coast in the northeast quadrant of Isla Santa Cruz and is separated from North and South Plazas Islands by a channel approximately 200 m wide. This area is considered to be the oldest portion of Isla Santa Cruz and consists of uplifted submarine, non-porphyrific basalts which have been interbedded with marine sedimentary rocks and tuff lavas. The substrate of the highly uplifted area immediately north of Cerro Colorado, which is itself an eroded tuff cone, is composed of a finely powdered red soil created by the chemical degradation of the lavas

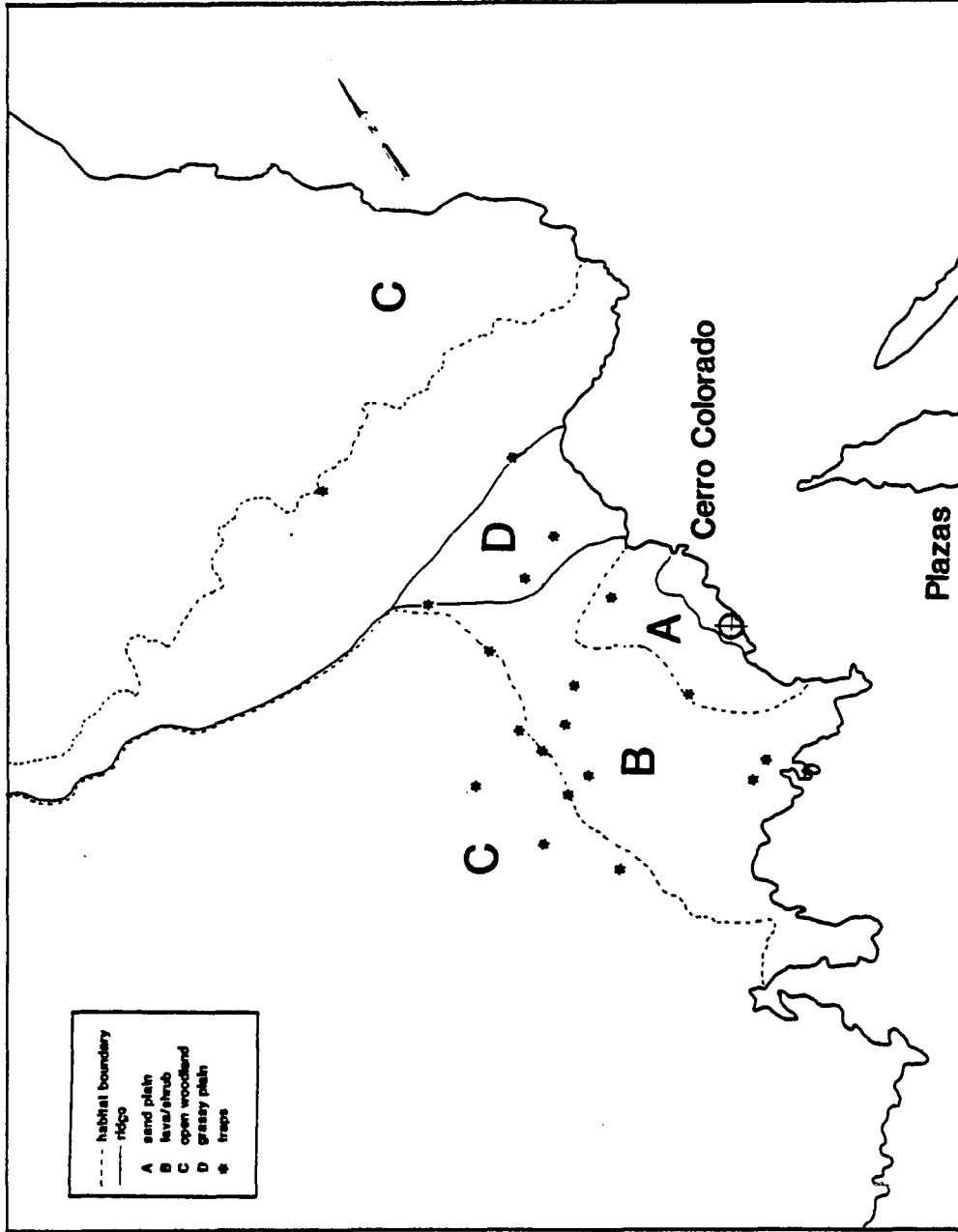


Figure 2. Habitat patch types and trap locations at Cerro Colorado, Santa Cruz Island.

(Fig. 2). The vegetation here is predominantly grasses and widely spaced bushes such as Cordia lutea. Surrounding the base of Cerro Colorado is a tuff sand plain approximately 400 x 75 m. The vegetation is typical of the littoral zone: Sesuvium, Portulaca, Cacabus, Coldenia, Cryptocarpus, and some Scutea. Further to the west and south is a series of broken lava plates and klinker lava soil. This area is covered by an open woodland with a woody, thorny shrub understory. The plant community is typical of Galapagos arid zones, dominated by palo santo (Bursera graveolens), prickly pear (Opuntia echios), and Acacia nilotica. The understory is composed of Castela, Scutea, Lycium, Grabowskia, Parkinsonia, Prosopis, Cordia, and Croton.

The observed faunal community included 27 species of birds, 7 species of mammals, and 6 species of reptiles (Appendix 1). Although four species of mammals are too large to be killed by house cats, their carcasses are undoubtedly scavenged. Among the birds only two of the sea birds, the swallow-tailed gull (Creagus furcatus) and the red-billed tropic bird (Phaethon aethreus), breed near Cerro Colorado, but several other species may roost there. One of the few potential predators of feral cats, the Galapagos hawk (Buteo galapagoensis), has been extirpated from the Isla Santa Cruz. Many species of arthropods are present but relatively few are eaten regularly by cats: grasshoppers (Schistocerca sp.), a centipede (Scolopendra galapagoensis), a crab (Grapsus grapsus), and several tennebrionid beetles.

Tagus Cove (0°15'34" S lat., 91°22'20" W long.) is actually a series of nested tuff cones located on the western coast of Isla

Isabela, the largest island. The crater floor of the largest cone was covered with sea water when the outer wall collapsed establishing the present cove. Tuff is composed of fine pyroclastic particles which are ejected in the presence of water, causing them to become cemented together to form a sandstone-like rock, though not as hard. At the eastern edge of the cone complex are three small lava cones which were created by a transverse fault in the base of Vulcan Darwin (1325 m), one of the six volcanos on the island, and which lies to the east of Tagus Cove. Tagus Cove is surrounded to the north, east, and south by a geologically recent aa lava flow from a lateral vent on Vulcan Darwin (Fig. 3). The flow is recent enough so that few life forms have been able to colonize it, and the hardened, viscous aa lava contains many razor-sharp crystals which impede animal movements. This created a virtually sterile boundary around the cove, essentially isolating it from other portions of the island. The substrate within the cove complex is basically layered tuff, though the floor of the northeasternmost cone was covered with ejecta from the three parasitic cones. The vegetation is similar to that of Cerro Colorado with two major exceptions: the prickly pear cactus is absent and the understory is more open. The open understory is composed of several species of burr-bearing grasses (Graminae), while the woody shrubs are Waltheria, Lantana, Croton, and Macraea. In addition, Tagus Cove contains some of the less common endemic plant species: Gossypium darwinii, Darwiniothamnus tenuifolius, and Lycopersicon cheesmani (Wiggins and Porter 1971).

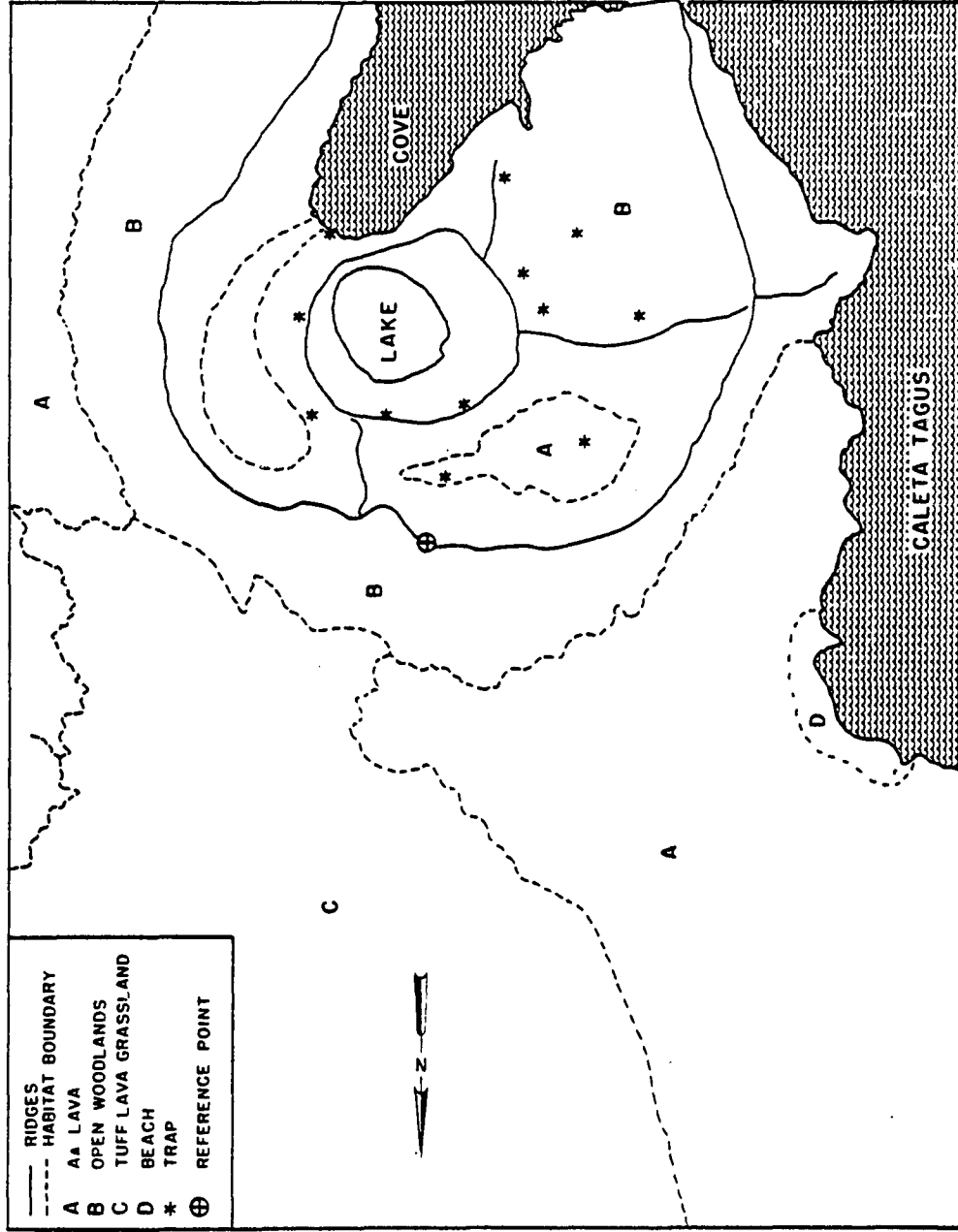


Figure 3. Habitat patch types and trap locations at Tagus Cove, Isabela Island.

The faunal community has many similarities to that of Cerro Colorado. Marine iguanas (Amblyrhynchus cristatus) occur at both sites but breed only at Cerro Colorado. The land iguana (Conolophus subcristatus), which formerly occurred in large numbers (H. Snell, pers. comm.), still occurs in very limited numbers at Tagus Cove but not Cerro Colorado. Galapagos hawks live and breed in Tagus Cove in moderate numbers. The steep-sided cove with deep near-shore water prevents many wading birds from living near Tagus Cove, but the rich waters created by the offshore upwelling of the Cromwell current attract large numbers of seabirds. The brown pelican (Pelecanus occidentalis) and blue-footed booby (Sula nebouxii) breed here in relatively large numbers. Two rare and vulnerable endemic birds, the flightless cormorant (Phalacrocorax harrisi) and Galapagos penguin (Spheniscus mendicula), are also found here in limited numbers. A complete species list may be found in Appendix 2.

Three other locations were visited for varying lengths of time to obtain food habit data for comparison with the two long-term sites. Punta Pitt (0°42'30" S lat., 89°15' W long.) is the easternmost point of Isla San Cristobal and the archipelago. Although there are two tuff peaks (300 m) there, it is basically an open plain of arid zone vegetation. Punta Cormorante (1°13' S lat., 90°25'42" W long.) is a palo santo woodland with open understory on Isla Floreana. Caleta Tortuga Negra (0°29'40" S lat., 90°19'30" W long.) is a palo santo woodland with brushy understory on northwestern Isla Santa Cruz.

Climate

The usual climate of the archipelago results from its geological construction and geographical location. The waters surrounding the central islands are generally less than 300 m deep, whereas outside the platform the depth quickly exceeds 2500 m. Positioned across the Equator 1000 km from the coast of Ecuador, the Galapagos are located near the Intertropical Convergent Zone of the northeast and southeast trade winds and the North and South Equatorial Currents. The combination of shallow waters and wind and current convergence virtually eliminates tropical oceanic storms and places the archipelago in the "dry zone" of the Pacific, with only two seasons (Wiggins and Porter 1971).

The yearly precipitation was concentrated principally in four months during 1980 (Fig. 4). In the months of January through April 220 mm of rain fell while less than 5 mm of rain fell in May and December. No measurable precipitation was recorded in any other month at either site. Daily temperatures fluctuated throughout the year with the highest temperatures found in the months with highest rainfall (Fig. 4). The highest daily temperature recorded was 42° C while the lowest was 12° C. Surface temperatures frequently reached 50° C or greater. Day length varied little throughout the year, from 12 hours 9 minutes to 12 hours 6 minutes.

From approximately December until May the northeast trade winds and North Equatorial Current become stronger relocating the convergent

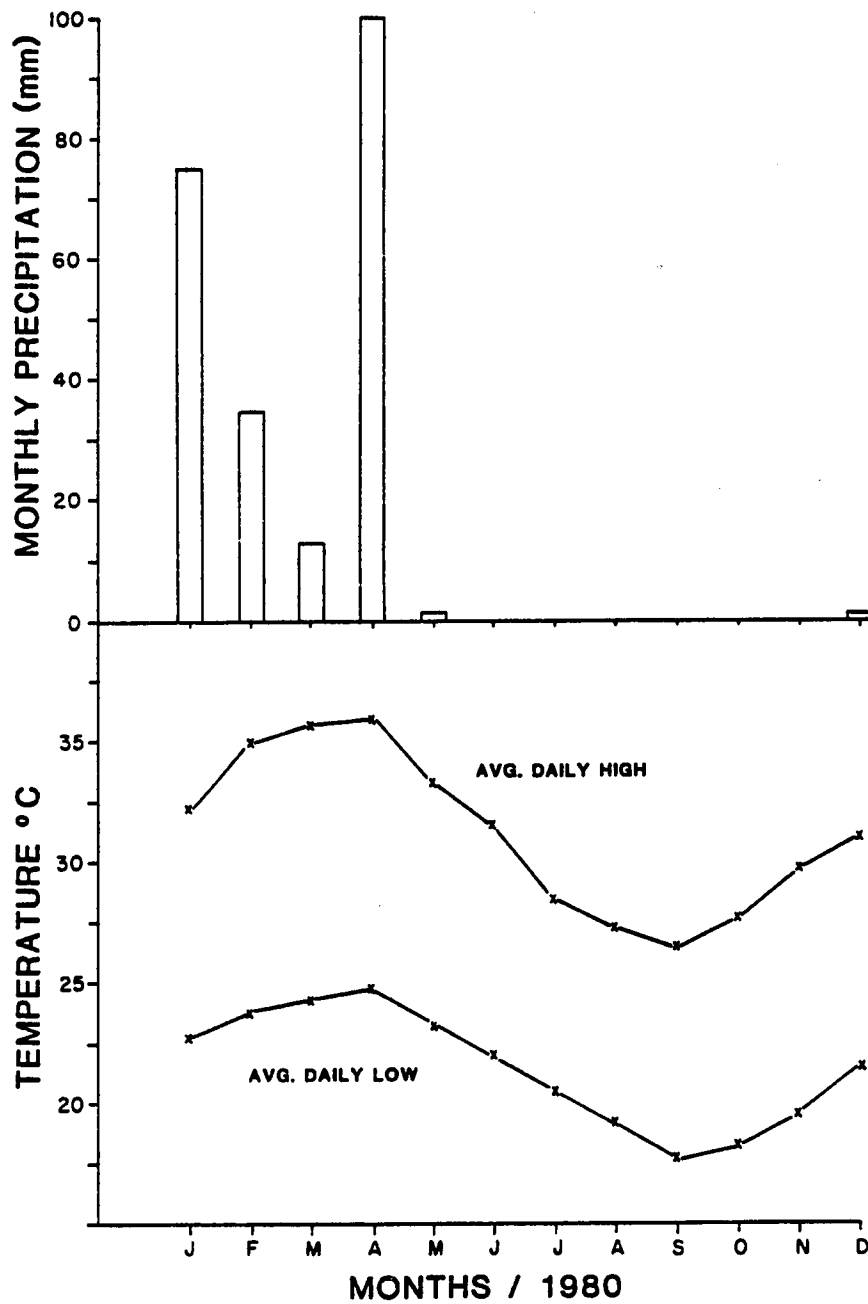


Figure 4. Precipitation by month and monthly average high and low temperatures for 1980 in the Galapagos Islands.

zone further south and over the archipelago, creating windless conditions within the archipelago. Warm surface waters are pushed southward from the Bight of Panama. Surface evaporation is increased and locally heavy thunder showers occur. Between locations the amount of precipitation is highly variable. During the week of 24 February to 1 March 1980, Cerro Colorado received an average of 34.4 mm of rain per day while Daphne Major, a low-lying island 29 km to the northwest, received an average of 2 mm of rainfall. During this period surface accumulations of rain water may persist for short periods. Many plants leaf and flower, causing many islands to become bright green and appear very lush. Insects breed and larger bursts of insect numbers are observed. Many species of passerine birds breed during the rainy season, presumably in response to increased availability of insects or flowers and fruit.

From approximately May through November, the southeast trade winds gain ascendancy and the South Equatorial Current brings to the Galapagos the cold surface waters of the Humboldt Current which upwells near Peru. A combination of cool surface temperatures, strong winds, and high solar incidence creates masses of cool, moist air which gather around the tops of some of the higher islands, but this persistent "fog-mist" or "garua" rarely deposits any measurable moisture on the ground. This "dry" season is characterized by cool temperatures, and many xeric-adapted plants either drop their leaves or mask the chlorophyll with anthocyanin to restrict photosynthesis.

CHAPTER II. DEMOGRAPHY

Methods

Traplins were established at each study site using Tomahawk double-end live traps (80 cm x 25 cm x 25 cm). All traps were baited every third day with tuna fish and catnip. Each trap was checked daily between 0600 and 0800 hours. Extreme temperatures approaching 40° C during the wet season necessitated a second check between 1200 and 1400 hours to prevent heat stress deaths among trapped animals. Even so, four animals died in traps.

Captured animals were weighed in the trap with a 30-kg spring scale and transferred to a nylon net bag. The tare weight of the trap was subtracted from the weight of the cat and trap to determine the weight of the individual. This weight was recorded and used to determine the dosage of ketomine hydrochloride to be administered (20 mg/kg BW). Most animals were tractable within a few minutes although several required subsequent injections to maintain immobilization. In addition to weight, the other body parameters recorded were sex, coat color, total body length, tail length, and neck and chest circumference. The pelage and ears were examined for external parasites and conspicuous scars. The mouth was examined for excessive tooth wear, discolorations, or broken teeth. Cats with only

deciduous teeth were termed juveniles; those with mixed deciduous and permanent teeth, subadults; and those with only permanent teeth, adults. Canines were removed from the skulls of seven known adult individuals and sent to Gary Matson in Milltown, Montana, for cementum analysis to determine their ages.

Population densities were calculated only with respect to adult cats because of the uncertain amount of juvenile dispersion and mortality. Two methods were used to calculate densities for each study site. The home ranges of radio collared cats were plotted, and the area of the circumscribed perimeter was calculated. The density was calculated by dividing the number of radio collared individuals by the circumscribed area. The home range outline method is calculated only using adults with radio collars and does not take into account other adults trapped in the same area, and therefore is probably conservative. A second density calculation was made using the adjusted range length method (Stickel 1954). One half the average home range length is used as a radius of attraction around each trap. The total number of adults trapped is divided by the enclosed areas around the traps. This method utilizes all the trapped individuals but is based on an arbitrary attractive distance around each trap which, in reality, is probably extremely variable. Fortunately, it was possible to make a third density calculation for Tagus Cove. Because Tagus Cove is essentially isolated from other potential living areas by relatively severe lava flows, I assumed that all cats trapped at Tagus Cove were resident there and that all cats present had been trapped.

Tagus Cove was visited during August and September 1979 and from June to November 1980. Punta Pitt was visited during September and October 1979. Cerro Colorado was visited from November 1979 to May 1980 and in December 1980. Single visits of one day were made to Punta Cormorante (September 1980) and Caleta Tortuga Negra (May 1980).

Comparisons of intersexual and intrasexual body parameter data gathered in this study were made by using the Student's t-test for sample means. Body parameter data were then compared with similar data gathered in other studies using the Student-Neuman-Kuhl test. This test allows the comparison of sample means not gathered by the same investigator. The formula is

$$LSR = Q(k, v) \sqrt{MS} \sqrt{\frac{n_1 + n_2}{2n_1 n_2}}$$

where LSR is the least significant range, $Q(k, v)$ is the critical value of the level of significance for v degrees of freedom and k number of items, MS is the mean squares and is calculated as

$$MS = \frac{\sum (n_i - 1) S_i^2}{\sum (n_i - 1)}$$

and n_1 and n_2 are the sample sizes of the two adjacent means to be compared, where all means are ordered in either ascending or descending magnitude. Sex ratio data were tested for differences from an expected ratio of 1:1 by a Chi-square test for k independent samples.

Every captured animal was marked with a collar. Selected individuals were given radio collars manufactured by Telonies Inc. All collars were hermetically sealed, and the antenna was built into the

collar strap. Removal of an external magnet activated the transmitter. Collars were bolted into place loosely enough to allow grooming but too tightly to prevent a paw becoming stuck. Each collar was coded with three strips of reflective tape manufactured by the 3M Corporation to identify individuals. Individuals not fitted with radio collars were given a yellow nylon collar and coded reflective tape. Recaptured individuals were weighed and released.

Results

While I was in residence at each study site, 10 traps were employed continuously. At Cerro Colorado, 20 trap sites were used for the 10 traps while 12 trap sites were used at Tagus Cove. A trap site was changed if there had been no activity at that site for one month. Thirty-nine captures of 17 individuals were made in 1540 trap nights (1 trap x 1 night = 1 trap night) at Cerro Colorado, a trapping efficiency of 2.5% (Table 1). Two subadult cats (#1 and #4) were each captured eight times. The female (#4) was captured eight times on consecutive days and died on the eighth capture. The male (#1) was captured eight times over a 10-week period. Four adult cats were each captured three times; however, no adult was captured more than once a month. Thirty-one captures of 25 individuals were made at Tagus Cove in 1360 trap nights, a 2.3% trapping efficiency. Only four individuals, two adults and two subadults, were recaptured. Of the total of 70 captures, 48 (69%) occurred during the same evening the traps were

Table 1. Population composition, adult sex ratios, and capture ratios of feral cats at two sites in the Galapagos Islands.

	Tagus Cove		Cerro Colorado		Combined	
	Male	Female	Male	Female	Male	Female
Adults	9	6	12	2	21	8
Subadults	2	1	2	1	4	2
Juveniles	4	3	-	-	4	3
	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>	<hr/>
	15	10	14	3	29	13

Sex ratio of adult males:females 2.62:1

Capture ratios: Tagus Cove--31/1360 Trap nights
Cerro Colorado--39/1540 trap nights

initially baited. The night following baiting and the second night after baiting each contributed approximately 16% to the total captures. In 13 months only four unmarked individuals were seen, each apparently only once, in the trapping areas of both sites. I assumed that all "resident" individuals had been trapped.

Population density calculations yielded two different values for each study site. At Cerro Colorado the home range outline method estimated 0.8 cats per km², while the adjusted range length estimate was 2.4 cats per km². At Tagus Cove the values for the methods were 1.31 and 2.24 cats per km². The third value calculated for Tagus Cove, based on its geological isolation, was 1.88 cats per km². An estimate of this type was not possible for Cerro Colorado, because there are no barriers to movement on that island. I believe that the third value is representative of field densities. A fourth density calculation was made using the number of cats seen or trapped in arbitrarily assigned quadrats and calculated as a Poisson distribution (Caughley, 1977). The densities of 2.6 cats per km² for Cerro Colorado and 2.2 cats per km² for Tagus Cove appear to further validate other density calculations. But, because of inherent problems with each calculation, it may not be possible to estimate the densities at each site more accurately than approximately 2 cats per km². Cats were trapped only in the arid zone, the largest of the vegetational zones according to Wiggins and Porter (1971). This life zone occupies about 40% of the 7856 km² archipelago. Extrapolations to population sizes in the entire archipelago are inappropriate because no density

estimates are available from any other life zone and because it is not known if cats occur on all islands with arid zones.

Estimates of the population structure of Galapagos cats are based on trapping data (Table 1), visual observation, and cementum analysis. At Cerro Colorado, 14 adults (12 males : 2 females) were trapped along with three subadults (2 males : 1 female). No juveniles were trapped at Cerro Colorado. Fifteen adults (9 males : 6 females), three subadults (2 males : 1 female), and seven juveniles (4 males : 3 females) were captured at Tagus Cove. The combined trapping results are 29 adults, 6 subadults, and 7 juveniles. Of the 42 individuals trapped, 69% were adult while subadults and juveniles constituted 14% and 17% respectively. The canines of seven individuals (4 males : 3 females) were submitted for cementum analysis, which estimated the mean age for males to be 6.8 years (range 4-8 years) and for females 2.5 years (range 1-4 years). Six litters were either observed or captured during the study. There were four litters of two each and single litters of three and four kittens. The average litter size was 2.5 kittens.

The combined trapping results from both sites were used to calculate the following sex ratios: juvenile (kittens)--1.33:1.0 (males:females) (n=7), subadult--2.0:1.0 (n=6), and adult--2.62:1.0 (n=29). Although the sample sizes for the juvenile and subadult classes are very small, they seem to indicate a trend toward male bias, supporting the strong male bias observed in the adult age class. These data were compared to adult sex ratio data from nine other feral cat

studies on six islands and three mainland studies (Table 2). A Chi-square test for k independent samples (Siegel 1956) demonstrates that the island populations were significantly male-biased ($df = 6$, $p < 0.001$), but that the mainland population did not differ statistically from the expected 1:1 ratio ($df = 2$, $p > 0.10$).

Differences between the sexes were also found in body size parameters (Table 3). Adults were compared intersexually at each study site as a combined population using a Student t-test (Siegel 1956). In all cases males were significantly larger than females for all values except tail length ($p < 0.05$). Intrasexual comparisons were made between study sites. Males from Tagus Cove were significantly larger than Cerro Colorado males for only neck and chest circumference ($p < 0.05$), while Tagus Cove females were significantly heavier than Cerro Colorado females ($p < 0.05$). Female comparisons may be of little value due to the extremely small sample size ($n=2$) from Cerro Colorado. The data from the combined adult populations were compared to those of seven other studies from five islands (Derenne 1976, Derenne and Mougins 1976, Jones 1977, van Aarde 1978, van Aarde and Blumenberg 1979, Longquich 1979, Pascal 1980). Because of differences in parameters measured only two were used: body weight and body length. The Student-Neuman-Kuel test for differences between treatment means was used (Sokal and Rohlf 1967). Both Galapagos males and females were significantly smaller ($p < 0.01$) than all other study samples in body weight and body length.

Table 2. Sex ratios, weight, and length measurements of insular and continental feral cat studies.

	Sex Ratio Males:1 Female	Weight (kg)		Length (cm)		Percent (σ/φ)		
		σ	φ	σ	φ	wt	L	n
Galapagos	2.62	2.69	2.08	43.4	41.1	.771	.935	8/21
Macquarie ¹	2.38	4.52	3.33	42.2	47.8	.736	.916	13/31
Helgoland ²	2.13	4.08	3.46	83.2	78.8	.846	.947	8/17
Marion ^{3,4}	1.89	3.76	2.99	--	--	.795	--	103/195
Kerguelen ^{5,6,7}	1.73	3.86	2.86	71.5	65.8	.741	.920	201/747
Catalina ⁸	1.09	4.65	3.17	60.4	58.4	.682	.968	11/12
Cochon ⁵	0.50	4.13	3.03	79.2	69.8	.732	.881	6/3
Tennessee ⁹	0.87	3.30	2.60	56.0	52.0	.788	.929	39/34
Sweden ¹⁰	0.63	--	--	--	--	--	--	67/47
Paris ⁷	1.11	3.55	2.80	75.8	69.8	.789	.928	19/21

1. Jones 1977

6. Derenne 1976

2. Heidemann and Vank 1971

7. Derenne and Mougine 1976

3. van Aarde 1978

8. Longquich 1979

4. van Aarde and Blumenberg 1979

9. Hall and Pelton 1979

5. Pascal 1980

10. Liberg 1980

Table 3. Body measurements of adult cats by sex and site, including intersexual and intrasexual comparisons (means and variances).

	Tagus Cove		Cerro Colorado		Combined	
	Male N = 9	Female N = 6	Male N = 12	Female N = 2	Male N = 21	Female N = 8
Weight	3.000	2.357	2.465	1.417	2.698	2.075
(kg)	.596	.268	.522	.083	.602	.403
Body length	44.450	42.571	43.536	37.667	43.935	41.100
(cm)	6.025	2.286	12.936	14.333	9.734	10.322
Tail length	27.250	26.571	26.692	26.000	27.043	26.400
(cm)	8.619	4.625	3.814	1.000	3.884	6.044
Neck Circum.	19.250	14.929	16.577	14.500	17.739	14.800
(cm)	2.681	1.869	2.702	.250	4.406	1.344
Chest	29.200	24.500	26.500	22.333	27.674	23.850
circum. (cm)	5.733	2.000	15.458	2.333	12.650	2.947

Intersexual differences (p .05) for all values except tail length--
T-test

Intrasexual differences only for neck and chest (males) and body
weight (females)—T-test

The coat colors of trapped individuals were also recorded. Commonly, four coat color phenotypes were noted and a fifth, an incomplete dominant, appeared in a few individuals:

1. Striped tabby is the dominant or wild-type phenotype, with a typical appearance of yellow/black to buff/grey vertical striping on the flanks resulting from a mixture of agouti and non-agouti hairs. Agouti hairs are banded in various proportions with black (eumelanin) and yellow (phaeomelanin) pigments, while non-agouti hairs are a monochromatic black.
2. The non-agouti phenotype is expressed as uniformly black with only non-agouti hair types. Non-agouti individuals also exhibit a black nose and lip margins.
3. Blotched tabby results from a rearrangement of the vertical striping of striped tabby into large, irregular patches of agouti and non-agouti hairs.
4. Orange is due to a sex-linked recessive allele which is expressed as orange/cream striped individuals, with eumelanin bands on individual hairs. Because other alleles are autosomal, this phenotype may appear simultaneously with striped tabby resulting in the "tortoiseshell" or "calico" phenotype.
5. Piebald spotting appears to be an incomplete dominant allele, although its inheritance and expression are

not well understood. It is expressed as a variable amount of white on the body, beginning with the feet and moving dorsally. A 10% piebald individual commonly has only white feet, while a 90% piebald may have only a small pigmented patch on its head, tail, or perhaps back.

At Tagus Cove all individuals collected were striped tabby, and one of them was also approximately 20% piebald. On the other hand Cerro Colorado cats were divided into five phenotypic classes: 1 blotched tabby, 5 striped tabby (one with piebald), 4 non-agouti, 1 calico, and 6 orange. One of the orange cats was a female which requires that her mother was, at least, a carrier and the father was orange.

Discussion

The combined trapping efficiency of 2.4% (70 captures in 2900 trap nights) was lower than those reported in other feral cat studies where reported efficiencies were 3.9 to 9.2% (Jones 1977, Hall and Pelton 1979, Liberg 1980). Of the 70 captures there were 42 individuals and 28 recaptures, which involved only six of the individuals. Small carnivores are generally regarded to be relatively difficult to recapture. In addition to general wariness, the baiting schedule might have affected the results, although the other studies with low trapping efficiencies did not report baiting schedules. Sixty-eight percent of

all captures were made within 14 hours after fresh baits had been placed. At each study site there was an initial period of trapping success followed by a rapid decline and lengthy periods without any success.

Trap avoidance by learned associations could explain the decreased subsequent trapping success and the low rate of recaptures. It is possible that recapturing any individual is a completely stochastic event; i.e. there is no learning and a coincidental set of circumstances led to the recapture. I doubt this explanation because, if there were no learned avoidance, cats may be expected to be lured by the bait. Hall and Pelton (1979) recaptured animals only 85 times in 6632 trap nights (1.2%), while Liberg (1980) reported that 79 individuals were trapped 88 times (9 recaptures in 960 trap nights-- 0.9%). However, it is possible that any learned trap avoidance may be overcome by food stress. Female #4 at Cerro Colorado, a subadult, was trapped on eight days consecutively; she weighed only 0.75 kg at death on the eighth capture. After the third capture she became very docile, waiting quietly to be released. She did not bolt from the trap but trotted away. I believe the bait overcame any learned negative associations. These negative associations may be site-specific, that is cats only associate a trap with a particular location. This suggestion is consistent with my data and those of Hall and Pelton (1979). They achieved a 5.8% trapping success by using traps for only three nights in any one location. In my study, 15 cats (36%) were captured the first day a new trapline was established.

Although learning undoubtedly affects the number of recaptures, the density of cats and traps at each site might affect the capture rate. The rate at which cats encounter traps will change if the density of either one is increased. In Tennessee, Hall and Pelton (1979) used 48 traps and sequentially trapped small areas totaling 3400 km², roughly equivalent to 40% of the land area in the Galapagos. Jones (1977) trapped for only 356 trap nights in a 14-month study on Macquarie Island (120 km²) in the Australian subantarctic. The effective trapping areas at Cerro Colorado and Tagus Cove were 5.8 km² and 8.0 km² respectively but were covered by only 12 traps at each site. The area of attraction for each trapping area was calculated from the mean home range size of cats monitored in each area. This method emphasizes the apparent movements of cats and discounts trap placements. The other method used the outline of the home ranges of radio-collared individuals. However, it only utilizes a portion of the total adults trapped and is, perhaps, an overly conservative density estimate. The third estimate from Tagus Cove utilizes the total area of the cove and because of it may also be slightly conservative, which might indicate that the adjusted range length estimate may more closely approximate actual densities. Stickel (1954) indicated that this method overestimates densities by about 3%. I believe, with the amount of available data and estimates used, that a density estimate of two individuals per square kilometer is probably reasonable.

This density estimate falls within the range of densities reported for feral cats, both on islands and on the mainland (1.1 to 13.85 cats

per km²). Two studies from the French subantarctic islands of the Kerguelen archipelago (Derrene and Mougin 1976, Pascal 1980) indicated densities of 1.1 to 2.7 cats per km², while Jones (1977) estimated 4-7 cats per km² on Macquarie Island, Australia. Recently, van Aarde (1983) has reported coastal densities of 13.85 cats per km² and interior densities of 4.98 cats per km² on the South African subantarctic Marion Island. Coastal densities were higher because of the greater quantities of breeding seabirds. All of these estimates were based, at least in part, on rough indices of abundance determined from encounter rates while walking in predominantly open tussock grass habitats. Two mainland studies (Hall and Pelton 1979, Liberg 1980) were conducted in the mixed meadow and forest farmlands of Tennessee and Sweden. The density of Tennessee feral cats was estimated to be 5.96 cats per km², while the calculated density in Sweden varied from 2.5 to 3.3 cats per km². Hall and Pelton (1979) used trapping data solely for their Tennessee estimate, but Liberg (1980) employed both visual observations and trapping to obtain his estimates. The subantarctic island habitats differed in the number of den sites and densities of prey items, while the mainland studies were conducted around temperate farmlands. Though not always fed, the cats could expect some food supplement or shelter from the farms. I believe that my densities, when compared to these other studies, are reasonable because neither den sites nor prey are always abundant in the Galapagos. It is also possible that unmeasured physiological stresses, such as overheating, might have contributed to the observed low densities.

The population structure in the Galapagos appears to be heavily weighted in favor of the adult age class (69%). Pascal (1980), Liberg (1980), and van Aarde (1983) also found that the adult age class constituted the largest proportion of the population. This is not surprising considering that all cats that are one year old or older are in this group, while only cats less than one year old are considered to be juvenile or subadult. In addition, however, the distributions of age classes and mortality reveal that subadults and adult females suffer the highest rates of mortality. These are probably nutritionally related causes (cannibalism, starvation, disease) as indicated by Jones and Coman (1982a) for their cats in an arid region of Australia. They found that, at the summer peak, the number of adults was approximately equal to the number of subadults and juveniles combined, but during the winter minima the population comprised mainly adults. Two different studies from the subantarctic revealed that first-year mortality is extremely high, especially for females (Pascal 1980, van Aarde 1983). Van Aarde reported that first-year mortality was 79%, while the next highest age class mortality occurred from age 6 to 7 years (4.4%). Among the females he found that the greatest mortality was before 12 months of age and after 48 months of age. The life table calculated by Pascal (1980) showed that mortality for the first three years was extremely high in females (21%, 23%, 23% respectively). Conversely, the first year mortality among males was only 7.4%, and the greatest age class mortality occurred between four and five years (39%).

The age structure of Galapagos cats was also distinctive. The cementum analysis of seven individuals revealed a large difference in the mean ages of males (6-8 yrs) and females (2-5 yrs). Household domestic cats commonly live for up to 20 years. Among feral cats eight or nine years appears to be the maximum (Pascal 1980, Liberg 1980, van Aarde 1983). There are differences between the sexes in mean ages for mainland and insular studies. In my study and those of Pascal (1980) and van Aarde (1983) the mean male ages were substantially greater than those of females. On the other hand, in mainland studies (Liberg 1980, Legay and Pontier 1983) the mean age of females was at least one year greater than for males. The differences in mean ages between continental and island populations are probably due to different sources of mortality. Legay and Pontier (1983) believed that the greater mortality of males is due to their "vagabonding" behavior, which exposes them to a greater risk of death from automobiles, farm machines, and hunting by humans. On the islands these sources of mortality are relatively insignificant and mortality must be due to some biological factor.

The apparent differential mortality of females is further emphasized by the male-dominant sex ratio. The sex ratios of cats trapped indicated a slight male bias among juveniles and subadults, but the sample sizes were relatively small. It is surprising that the adult sex ratio is skewed so sharply toward males (2.62:1). Trapping bias has been offered as an explanation for observed male-dominant sex ratios in the field. It has been suggested for carnivores that males

are trapped more often because generally they have larger territories, are more curious, are more aggressive, have much greater energy requirements, and because females are less active during pregnancy and lactation (King 1975, Derenne and Mougin 1976). Significantly male-biased sex ratios were found in 9 of 10 island feral cat studies, encompassing 976 individuals. Alternatively, three mainland feral cat studies did not reveal any statistical differences from the expected unity; in two of these studies females were slightly more numerous. Although differences may exist between males and females, I do not believe that trapping bias accounts for the strongly male-dominant sex ratios.

If real, the male-biased sex ratios may result from differential mortality of females caused by a combination of age of first reproduction and energetics. Female domestic cats mature sexually between 7 and 10 months of age, while males mature between 10 and 14 months of age (Jones and Coman 1981). During their first year of sexual maturity, reproducing females typically produce one litter, while in other years they are polyestrous (Kleiman and Eisenberg 1973, Pascal 1980). During that first year they are still growing and must use any extra incoming energy for growth and maintenance. In evolutionary terms, selection should favor early reproduction in females because they cannot broadcast their genes as widely as males, and therefore need to reproduce as often as possible. In males, on the other hand, which compete for access to females, delayed maturation may be selected for if the time spent in further growth confers greater survival and fecundity at a later age (Wiley 1974).

Energetic costs for females increase 25% during pregnancy and 300% during lactation above the non-pregnant levels (Scott 1976). These added requirements may create physiological stresses on the female. The lack of available fresh water, restricting the amount of protein which may be processed, can add to the stress of malnutrition. In one instance an emaciated, lactating, two-year-old female with two kittens of approximately 10 weeks of age was trapped in the Galapagos. She had a body weight of 1.25 kg, well under the mean adult female weight of 2.0 kg. The physiological stress of malnutrition may be even more intense for the still-growing primiparous females. It is well known for a variety of mammals that physiological stress can delay the onset of estrus. Even if a female did delay estrus until some minimal body size had been attained, she still might not be physiologically or behaviorally capable of handling the energetic demands of further growth plus a litter of kittens. These exaggerated costs may be so difficult to meet that a female may die of nutritionally related causes during her first year, or become so energetically depleted that she has a reduced life expectancy. Furthermore, if there is a general food shortage, females may be treated as subadult males and attacked aggressively by adult males (Lockie 1966).

The great intersexual discrepancy in first-year mortality is difficult to account for in terms of foraging ability. Both subadult males and females should face approximately the same difficulty in learning to forage independently. Females mature slightly faster than males and are frequently allowed to remain on a portion of their

subadult range, while males are aggressively expelled. On continents females may not face problems as severe as those faced on islands. If resources on continents fail, females may be able to emigrate to a new habitat or patch where resources are more abundant. Islands, however, are generally restricted in size and tend to be more homogeneous, limiting the ability of cats to find a better patch. In addition, the optimal ranges may be already occupied, relegating dispersing females to suboptimal patches which may further intensify pre- and post-reproductive foraging difficulties (Seidensticker et al. 1973). Because females may be physically dominated by males, they may be forced to the poorest patches. Liberg (1980) demonstrated that the number of households (food) was the limiting factor for females during periods of natural resource shortages in Sweden.

Energetic constraints also probably affected the body sizes exhibited by cats in the Galapagos. Males and females are both significantly smaller than their counterparts from other island and mainland studies. The mean adult body weights of 2.7 kg and 2.1 kg for males and females respectively are much smaller than other islands where the ranges for males and females were 3.7-4.7 kg and 2.9-3.5 kg respectively (Jones 1977, Derenne 1976, Derenne and Mougín 1976, Longquich 1979, van Aarde 1978, van Aarde and Blumenberg 1979, Pascal 1980). Mainland weights ranged from 3.3 to 4.8 kg (males) and 2.6 to 3.5 kg (females) (Heidemann and Vauk 1971, Derenne and Mougín 1976, Hall and Pelton 1979, Liberg 1980).

Foster (1964) and Case (1978) have pointed out that species on islands should have a body size to match the theoretical energetic low

point of available resources over a given period of time. In many cases this results in smaller individuals because of the generally depauperate nature of island faunas with respect to continents and, therefore, the lack of buffer species in times of resource shortages. The evolution of "scaled down" carnivore body sizes may have occurred in response to the lack of large prey or the absence of smaller competitors (Foster 1964, Cody 1974). Access to or utilization of fresh water has been shown to influence the amount of energy assimilated (Schmidt-Neilsen 1964, Chew 1965). The Galapagos Islands, unlike other insular feral cat study sites, lack accessible fresh water for much of the year. I believe that this may be a contributing factor to the small feral cat body sizes. Because house cats have been in the archipelago for a maximum of 200 years, these smaller body sizes may be a nutritionally related phenotypic effect.

Female cats are uniformly smaller than males of the same species, and with the exception of the mane of the African lion, wild felids appear to be sexually dimorphic only in body size (Might 1964, Guggisberg 1975, Sunquist 1981). Feral house cats also show this sexual dimorphism. Females are, on average, only 76% as heavy and 93% as long as males from the same populations. One argument has been that males are larger than females to compete for reproductive access to females and reduce intersexual aggression and resource competition (Eisenberg 1981). Another argument proposes that females are smaller than males because of the energetic costs of reproduction (Erlinge 1979, Moors 1980, Powell and Leonard 1983). We may assume that males

have the optimal body size to withstand periods of low available energy in their habitat and do not face large periodic increases in energy requirements due to reproduction. On the other hand, females do face large periodic increases in energy requirements during pregnancy and lactation. If they were the same size as the males, pregnant or lactating females might be unable to satisfy their needs for maintenance as well as provide for a litter of kittens.

The final demographic pattern examined in the Galapagos cats was the distribution of coat color phenotypes. In cats coat color phenotypes directly reflect gene frequencies contained in a population. The coat color frequencies found at the two study sites were very different from each other. Cats from Tagus Cove were all striped tabby, predominantly buff and gray. Tagus Cove is isolated from the nearest village, Villamil, by distance (72 km) and the Isthmus of Perry, a 16 km wide strip of aa lava stretching from the east to west coast of Isabela. This strip of virtually impenetrable lava has so far effectively barred northward migration of terrestrial mammals (Thornton 1971). Tagus Cove is further isolated from the adjacent areas of Playa Negra (North) and Crater Beagle (South) by recent lava flows of several ages. It is likely that the sole source of introduction was the sailing ships of whalers and buccaneers that used the cove as a sheltered anchorage. Feral cats were first recorded there as a well-established population in 1865 (Salvin 1876).

On the other hand, Cerro Colorado, where there was a mixture of five phenotypes, is located only 19 km from Puerto Ayora, a village of

approximately 3000 inhabitants that was established in the mid-1920's. There are no geographical barriers to dispersal from Puerto Ayora, and it is likely that there is constant recruitment from the village.

The sex-linked orange phenotype occurred in my study in greater frequencies than every study but one, on Macquarie Island where it also occurred in equal frequencies with striped tabby (Jones 1977). On that island no other phenotypes were reported. Van Aarde (1980) reported that although orange was present on Marion Island in the originally introduced pair, it disappeared at the end of one generation. With the loss of the orange phenotype, non-agouti (black) was seen the most frequently (64%) in the cats sampled. Derenne and Mougín (1976) and Dreux (1974) reported frequencies of 99.9% and 97% of the non-agouti frequencies in Kerguelen Island. They believed that on the volcanic, subantarctic islands non-agouti and other dark colors have a selective advantage over lighter phenotypes with respect to heat absorption and crypticity. My study and Cooper's (1977) study on Dassen Island found only 23.5% and 19% of the population displayed the non-agouti phenotype.

The striped tabby (wild type) phenotype usually occurs in all populations. The few individuals observed by Derenne and Mougín (1976) and Dreux (1974) that were not non-agouti were striped tabby. At Cerro Colorado no one phenotype has an apparent selective advantage over another. The orange phenotype occurred in 35% of the population, which is nearly equal to its most frequent occurrence elsewhere in the world (Todd 1977).

The diverse patch types in the study area at Cerro Colorado provide a variety of background colors ranging from the yellow-brown of the dried grasses on the grassy plain to the black klinker lavas. But the relatively small patch types relative to the movements of cats would probably not confer a selective advantage to any one phenotype. In addition both selection and recruitment from surrounding areas may be operating to maintain the observed genetic frequencies. On the other hand, at Tagus Cove recruitment is unlikely and the habitat is extremely uniform in composition and substrate color. The homogeneous coat colors observed there are probably due to selection and the presumably small founding population.

CHAPTER III FEEDING ECOLOGY

Methods

Information on food habits was gathered by observing predation, collecting feces, and sampling transects. An effort was made while observing predatory bouts to determine the prey species and success or failure of each attempt. Scats were collected whenever found, although obviously deteriorating or very old scats estimated by a powdery, gray appearance were not taken. Often, trapped cats defecated while in the trap. In addition, marked individuals were frequently observed defecating. Scats collected from known individuals yielded data on seasonal and individual preferences. The relative ages of scats were estimated on the basis of color. Older scats of indeterminate ages were analyzed to provide information on foods eaten in different areas. Scats of recent deposition were collected individually to provide area and seasonal prey preference information.

Transect lines were established to assess the relative abundances of some of the more conspicuous potential prey species. At each study site a 300 m line transect was established. The transect was sampled twice a week at 0800, 1200, and 1600 hours by walking the line in 10 minutes. All potential prey items seen within 10 meters of either side

of the line were counted. These were measures of apparency and not censuses, because no trapping or sweep net sampling was conducted. However, I felt that these counts would approximate the apparency of these species to the cats, which are predominantly visual hunters. The counts might have been biased to some degree by differences in visibility and individual sizes of the three groups sampled. But assuming the counts were performed uniformly, they provide a rough index of availability for prey species at different times.

Feces were analyzed in a manner similar to those used by Johnson and Hansen (1977, 1978) and Johnson (1982). Dry fecal samples were weighed and placed in fine mesh nylon curtain material, soaked for 20 hours in a commercial pre-wash solution, and held under a stream of hot running water for an additional 20 hours. Commercial clothes washers and dryers were found to be too turbulent, and their use resulted in several ruptured bags. All samples were dried in a laboratory drying oven and weighed again. All samples were crumbled by hand and passed through a series of standard geology sieves (nos. 14, 25, 35, 45) to remove dust and other particles too small to identify. Fifty scats were selected to serve as a standard sample for this study. These scats were separated into smallest taxa that could be accurately discriminated, although plants were combined because they constituted such a tiny portion of the scats. The taxonomic specificity of the diet categories is highly variable because the removal of specimens for reference collections is stringently controlled by the Galapagos National Park. Once separated the weight of each taxon was divided by

50 in order to calculate the average dry weight occurrence of each taxon in the standard scat. The composition of other scats was determined by recording the presence or absence of any of the predetermined dietary categories. Johnson and Hansen (1977) showed that there are no significant differences between complete analyses of individual scats and scats analyzed relative to a predetermined standard.

The masses of prey actually eaten were calculated using the prey digestibility indices of Johnson and Hansen (1978), Golley et al. (1965), Johnson (1982), and Greaves and Scott (1960). The g-dry weight caloric values for each diet category were taken from a set of values calculated for related taxa by Cummins (1967).

Results

The availability of prey was determined from transect data and by recording plants and animals observed at each study site. Appendices I and II contain a list of observed vertebrates, larger invertebrates, and dominant plant species recorded at Cerro Colorado and Tagus Cove. Many of these species were never or rarely recorded on the transects which, of course, does not exclude them from consideration as prey. The transect data (Fig. 5) for both study sites were lumped and averaged to provide, by month, the apparent daily abundances of the more conspicuous potential prey species: birds, lizards, and grasshoppers. These large categories represented the accumulations of

BIRDS
 REPTILES
 GRASSHOPPERS

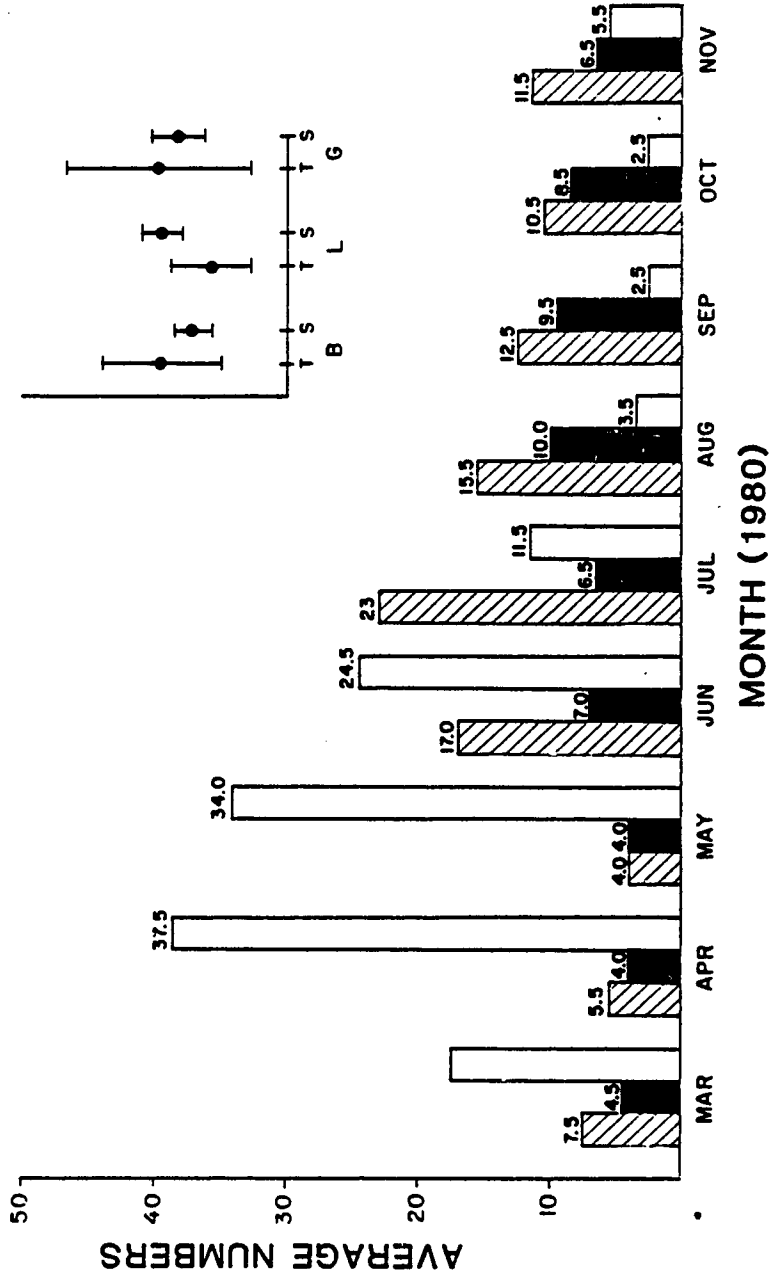


Figure 5. Average monthly transect occurrence of birds, reptiles, and grasshoppers for 1980 with a comparison of transect and scat occurrences.

several taxa. Passerine birds, which include the finches, warblers, and mockingbirds, were the group observed most consistently, although wading and shore birds (Charadriiformes and Ciconiiformes) and dark-billed cuckoos (Coccyzus melacoryphus, Cuculiformes) were observed rarely on one transect. The reptiles included only the marine iguana (Amblyrhynchus cristatus), seen twice, and lava lizard (Tropidurus albemarlensis). Grasshoppers included the genera Schistocerca and Halmenus. Because the transect was sampled only during the day, it would not include nocturnal species. In addition, there may have been species, especially birds, present on the transect which were frightened off by the census taker and not recorded. In essence, the transect line represents a measure of presumed prey items; however, the three recorded categories did constitute a large proportion of the diet.

The numbers of birds counted decreased from March to May during their reproductive period and then began to increase in the dry season months of June and July with the addition of the newly fledged young and the formation of mixed species feeding flocks. Although not included in any of the transects, there was a large concentration of brown pelicans (Pelecanus occidentalis) and boobies (Sula neboxii and Sula dactylatra) in Tagus Cove along with smaller numbers of flightless cormorants (Phalacrocorax harrisi) and Galapagos penguins (Spheniscus mendicula). From late June until late August the populations of these birds more than tripled in Tagus Cove. This is probably a response to the cove's proximity of the upwelling of the Cromwell Current, a cold, deep water current that brings dissolved oxygen and rich organic

nutrients to the surface. The resultant explosive bloom of phytoplankton attracts dense concentrations of clupeid and engraulid fish, which in turn attract large numbers of piscivorous birds.

Reptile numbers did not vary greatly throughout the year. The presence of marine iguanas on inland transects will be explained in a later section. The slightly lower counts of lava lizards in the wet season were probably due to the higher ambient temperatures of that season and the abundance of available insects, reducing the number of foraging movements, the need to forage widely, and the time exposed while foraging.

Grasshopper numbers began to increase rapidly in the wet season. The seasonal rainfall triggers new leaf growth and fruit and seed production in the xeric-adapted plants. The general appearance of the coastal areas is quickly transformed from a dull gray-brown to green. Grasshopper counts reached a peak in April and began to decline as the wet season changed to dry and leaves were lost from many shrubs and trees.

Although potential prey items were seen frequently, the cats were not always successful in capturing prey. Attempts to capture live prey were observed 104 times with 33 successes, an overall predation efficiency of 31.7%. Successful captures of grasshoppers and lava lizards were observed frequently enough to calculate meaningful predation efficiencies of 43% (19/44) and 37% (10/27) respectively. Several other attempts were seen closely enough to identify the prey: various finch species (Fringillidae), Galapagos mockingbird (Nesomimus

parvulus), sally lightfoot crab (Grapsus grapsus), and centipedes (Scolopendra galapagoensis). On several occasions cats were seen to closely approach adult marine iguanas but made no attempt to touch them.

Hunting-related behavioral observations constituted the greatest proportion of the 206.5 hours of visual observation. Hunting techniques and prey handling behavior were similar to those described for cats by Kleiman and Eisenberg (1973) and Leyhausen (1979). At both sites cats were frequently observed alternately scavenging carcasses and hunting live prey. An adult male from Tagus Cove was watched continuously for five and a half hours as he foraged along the shore on 7 September 1980. During this time he was seen to eat plant material, scavenge the carcasses of booby chicks and pelicans, and made six attempts to capture lava lizards, capturing and eating only one. At Punta Vincente Roca, Isabela Island cats apparently drove boobies (Sula spp.) from their nests and ate the abandoned eggs (Alan Moore, trip report for Charles Darwin Research Station). On two occasions at Cerro Colorado I saw cats feeding on discarded crackers and noodles left out for birds.

At Tagus Cove, on four occasions, I observed two possibly related males hunting together. They were walking in parallel approximately 5 m apart along the shore of the cove. Unfortunately no attempt to capture prey by either one or both of the males was seen. I termed these observations "synchronous hunting." Although I believe that these males were cooperating, perhaps even facultatively, I did not have direct evidence of cooperation.

Prey handling was relatively uniform among all cats seen. Birds were at least partially plucked before eating and then entirely eaten with the exception of large sea birds, which could only be partially consumed. Lava lizards were totally consumed; intact feet with skin were occasionally found in the scats. Most arthropod prey were entirely eaten, although there was some variability in eating grasshoppers. Some cats ate the entire grasshopper, while others ate only the abdomen.

Visual observations provide insight into prey eaten by individuals, especially when the food is likely not identifiable in the feces. On the other hand, fecal collections provide abundant data of the seasonal food habits of several populations. Fecal collections were made at four locations: Punta Pitt, San Cristobal Island; Punta Cormorante, Floreana Island; and the two principal study sites. These data were examined for general food habits of feral cats in the Galapagos. Only the 640 scats from the two principal sites, for which I had acceptable dates of deposition, were used in the dietary comparisons. Ten diet categories were defined based on the degree of taxonomic discrimination possible and the relative frequencies and weights of occurrence in the sample scats. In addition, the sand and bits of lava frequently found were deleted from all analyses because they probably do not contribute to ingested energy. The diet categories were Rodents, Birds I, Lizards, Grasshoppers, Arachnids, Beetles, Plants, Birds II, Crabs, and Fish.

The rodents included only the black rat (Rattus rattus). Although the house mouse was seen, it was not found in the feces. Both of the extant endemic species of Oryzomys now occur only on islands where feral cats are not found. Birds I contained the smaller species, predominantly passerines. The birds almost invariably included only Darwin's finches, the Galapagos mockingbird, the broad-billed flycatcher (Myiarchus magnirostris), and the yellow warbler (Dendroica pitechia). Of these species, Darwin's finches appeared in the scats more often than all other bird species combined. Although few, if any, other small birds were represented, the endemic dove (Zenaida galapagoensis) appeared infrequently. Birds II included larger birds and sea birds. This category was distinguished from Birds I by feather composition and bone sizes. Typical species found in this group would include the boobies (Sula spp.), swallow-tailed gulls (Creagrus furcatus), red-billed tropic birds (Phaethon aethreus), flightless cormorants, frigate birds (Fregata spp.), herons (Ardeidae), and Galapagos penguins.

Only three genera of iguanid lizards occur in the archipelago, Tropidurus (7-11 spp.), Amblyrhynchus (1 spp.), and Conolophus (2 spp.). In addition, there are eight species of geckos in two genera, Gonotodes and Phyllodactylus. By far the greatest consumption was of Tropidurus because of their higher numbers, small size, visibility, and wide distribution. Marine iguana skin appeared regularly in the scats. These were almost certainly hatchling iguana, because the bones were only slightly larger than lava lizard bones. Two pieces of marine

iguana skin, found in a scat on 2 December 1980, contained the plastic marking beads used by Howard Snell, Colorado State University, to identify hatchlings. That particular scat contained the beads for two individuals marked in May 1980. Within a few months marine iguanas grow to a size that would likely make them relatively invulnerable to cats. Land iguanas no longer occur at Cerro Colorado, and only three individuals have been found at Tagus Cove in recent years. The geckos are nocturnal and so small (s-v length 4.0 cm) that they are probably rarely seen by cats at night. Also, their bones are very small and could have easily been missed in the fecal analyses.

The grasshoppers were limited to the orthopteran acridids, Schistocerca melanocera and Halmenus spp. Identification was simplified by the poor digestion of the distinctly colored exoskeletal body parts. Arachnids comprised not only the few scorpions (Centruridae) identified but also the centipede (Scolopendea galapagoensis, Chilopoda). It was not usually possible to identify the beetles below the family Tennebrisridae, although it appeared that the genus Stomion was well represented. Few skeletal elements other than mandibles and elytra were intact enough to allow even a partial identification. All vegetation was classified together because it constituted such a small proportion of the feces, although the leaves of Graminae and the berries of the simabourid genus Castela were identifiable. Only one species of littoral zone crab, Grapsus grapsus, was found. Fish vertebrae could be readily discriminated from other vertebrae, but little other material was available to identify even

families. I am virtually certain that cats were scavenging dead fish, because the depth of the inshore waters increases rapidly, and there were no tidal pools in the study area.

After the scats had been carefully analyzed, it was possible to compare the transect occurrences of birds, reptiles, and grasshoppers with their occurrence in the scats (Fig. 6). Although the apparent populations of each of the three fluctuate, sometimes more than four-fold, the levels of consumption remain relatively uniform. It is interesting to note the trends indicated by the shape of the consumption curves, especially for reptiles and grasshoppers. During the wet season, when reptile apparency is lowest, the consumption is much higher. As reptiles become more apparent the consumption is marginally reduced until late in the dry season, when the two curves are approximately equal. The differences are more striking for grasshoppers. When the numbers of grasshoppers are highest, the consumption is low until the beginning of the dry season, when the two curves cross. Throughout the dry season the numbers of grasshoppers eaten are higher than their apparent numbers.

Temporal differences in fecal composition were assessed in several ways. Table 4 displays the monthly and seasonal occurrences of each diet category in the feces. Although the transition between seasons is variable and indistinct, the wet season was considered to be December through May, while the dry season was June through November. No collected scats could be confidently assigned to May. Monthly comparisons were made with both a Pearson "r" Correlation Coefficient

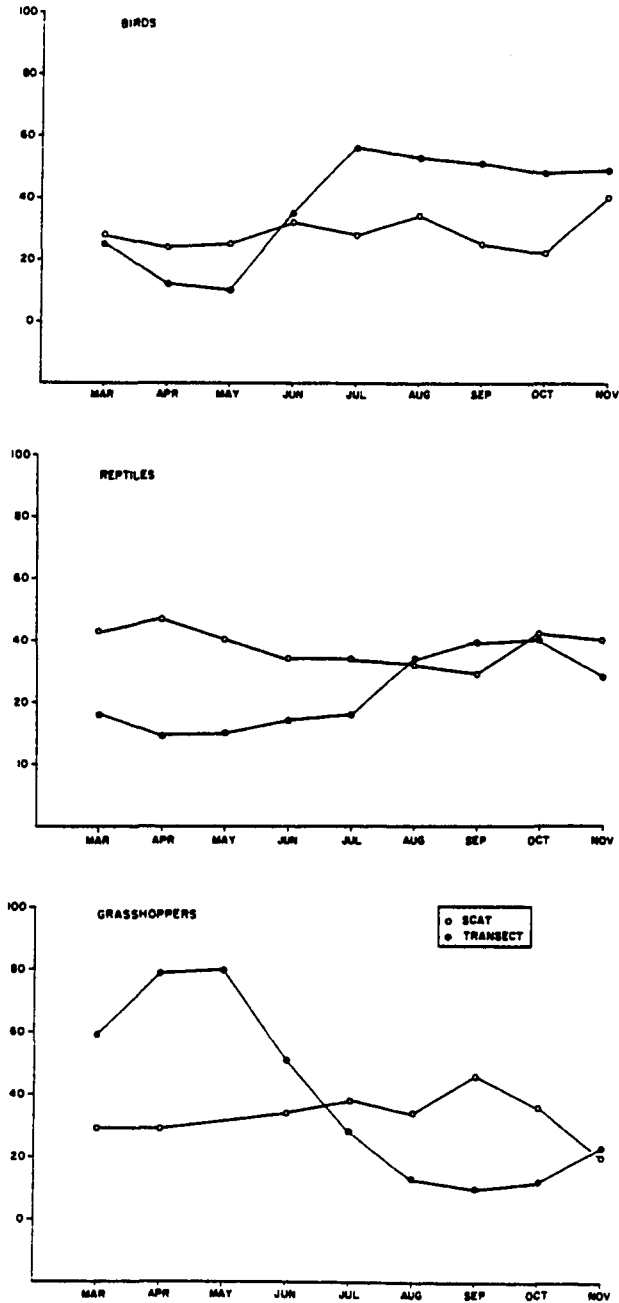


Figure 6. Relative occurrence of birds, reptiles, and grasshoppers on the transect versus their occurrence in the scats for 1980.

Table 4. Monthly and seasonal occurrences of diet categories in scats, including contingency table comparisons.

Taxon	Wet Season							Dry Season					
	Dec	Jan	Feb	Mar	Apr	Sum	Jun	Jul	Aug	Sep	Oct	Nov	Sum
Rat	5	14	56	35	9	129	88	65	61	82	28	49	373
Bird	5	14	64	23	9	115	98	61	68	49	21	43	340
Lizard	4	14	37	35	18	108	103	73	64	56	41	43	380
Grasshopper	7	19	64	24	11	125	103	81	69	90	35	22	400
Arachnids	5	19	46	34	3	107	65	46	40	73	19	20	253
Beetle	1	11	10	2	5	29	81	67	77	61	20	12	318
Plant	1	14	32	1	1	49	88	32	42	41	27	2	232
Seabird	0	0	11	0	0	11	12	3	25	18	5	23	86
Crab	0	0	0	0	0	0	12	26	25	42	1	1	107
Fish	0	0	0	0	0	0	12	0	9	42	0	0	63
# samples	8	21	64	36	21	150	103	87	89	96	59	56	490

Wet season vs. dry season vs. taxon; G-value, 28 df, p .001

for untransformed monthly category totals and the Spearman Rank Correlation Coefficient for ranked monthly totals. No significant differences ($p > 0.05$) were found between adjacent months in either test. The monthly data were combined into seasonal data and compared with a contingency table (10 x 2 x 2). In essence, a contingency table is a multi-way Chi-square that allows the examination of the association between two or more variables. Contingency tables were used to compare the presence or absence in the feces of a diet category by season. The calculated G-value for this comparison was highly significant ($p \ll 0.001$, $df = 28$). This indicates that the proportional presence of a category does not vary independently by season.

A second part of the contingency analysis is the three-factor analysis which determines if there is a significant interaction of one or more categories rather than the diet en toto. The three-factor interaction for seasons was also significant ($p < 0.001$). This test validates performing further analyses on individual diet categories. Each diet category was tested with a 2 x 2 Chi-square. Rodents appeared significantly more frequently in the wet season, while arachnids, beetles, birds II, crabs, and fish were found more frequently in the dry season (Table 5). There were no statistical differences in the occurrence of birds I, lizards, and grasshoppers.

It was also possible to separate scats by location and subject them to a similar contingency table analysis, substituting site for season (Table 6). The G-value and three-factor analysis were both

Table 5. Chi-square occurrences of diet categories with respect to seasons and sites.

Category	Seasons Probability df = 1, p ()	Sites Probability df = 1, p ()
Rat	7.124 (.01)	16.310 (.001)
Bird	3.052 (NS)	1.024 (NS)
Lizard	1.904 (NS)	7.368 (.01)
Grasshopper	.230 (NS)	8.068 (.005)
Arachnids	18.702 (.001)	.794 (NS)
Beetle	100.246 (.001)	105.762 (.001)
Plants	10.256 (.005)	31.794 (.001)
Seabird	343.82 (.001)	2.546 (NS)
Crab	63.452 (.001)	50.040 (.001)
Fish	35.706 (.001)	18.664 (.001)

Table 6. Site occurrences of diet categories in scats, including site contingency analyses.

	Tagus Cove # scats per Total (318)	Cerro Colorado # scats per Total (172)
Rodent	233	152
Bird	253	130
Lizard	263	124
Grasshopper	272	129
Centipede	153	90
Beetle	231	43
Plant	178	51
Sea bird	45	34
Crab	68	2
Fish	21	0

G-value = 2005.94 ($p \ll 0.001$)

significant ($p < 0.001$, $df = 28$), and the individual category Chi-squares were performed (Table 5). Rodents were found in the scats more frequently at Cerro Colorado than Tagus Cove, while lizards, grasshoppers, beetles, plants, crabs, and fish were found more frequently at Tagus Cove. There were no site differences for arachnids or birds I and II.

These analyses suggested that there may be some diet differences by season and site caused by changes in either climate or availability. Diet diversities were calculated using Levin's formula (1968)

$$B = 1/\sum p_i$$

where B is the diversity or breadth and p_i is the proportion of the sample contained in any specific unit. Diversities were calculated for individual months and plotted as a histogram (Fig. 7). The diversities from December to January increase from 5.52 to 6.71 items, but in subsequent months the diversity decreases sequentially to a low value of 4.71 items for April. The dry season value for June is substantially higher than that for April (no values were available for May), 7.58 to 4.71 items respectively. The high value calculated for the dry season occurred in September (8.89 items).

Accumulated fecal analyses were used to calculate diversities for each site. At Cerro Colorado the diet included more than one less item than at Tagus Cove (6.67 to 7.83 items). In order to compare seasonal diet breadths the monthly diversities were summed to calculate a mean monthly diversity. The wet season mean was 5.67 ± 0.86 items ($n=5$,

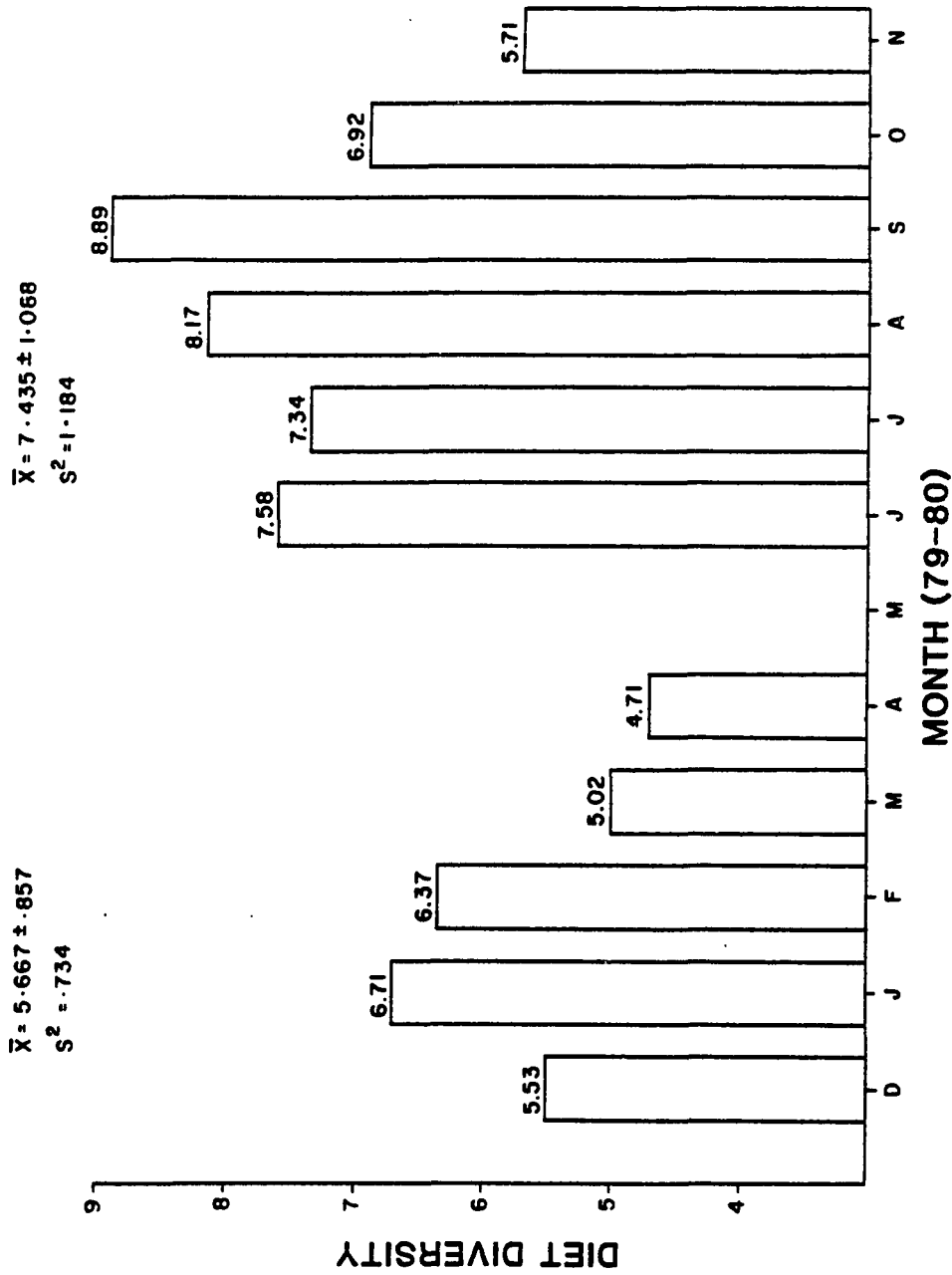


Figure 7. Monthly diet diversities in items in the diet for 1980 with seasonal means and variances.

$s^2 = 0.73$), while the dry season mean was 7.44 ± 1.09 items ($n=6$, $s^2 = 1.18$). The seasonal means were compared with a Student's t-test and found to be different ($p < 0.02$, $t_{\text{calc}} = 2.94$, $df = 9$).

When compared to the monthly rainfall histogram (Fig. 4), the plotted diversities suggest that diet diversity may be inversely related to rainfall, although the almost total lack of precipitation in the dry season prevented any meaningful statistical comparison. The lowest diversities occurred in the rainiest months. This suggests that the availability of freshwater allowed the cats to specialize on fewer prey species, perhaps due to greater digestive efficiency associated with water.

The amount of dietary overlap was also compared between seasons and sites. The amount of overlap was calculated by the proportion of similarity (PS) index of Feinsinger et al. (1981):

$$PS = 1 - 0.5 \sum |p_i - q_i|$$

where p_i is the proportion of population "p" in the "ith" state and q_i is the proportion of population "q" in the "ith" state. Not surprisingly, the dietary overlap between seasons and sites was very large, 81.6% and 83.0% respectively.

The fecal analyses, site and seasonal diversities, and dietary overlap indicate that the same items appear at both sites and in both seasons. Although differences may reflect changes in abundance, items seen regularly probably also indicate preferences. Not all of the recorded items occurred in every scat. Seventy-five individual scats were examined encompassing both seasons and sites, although it was not

possible to adequately investigate both seasons at both sites, because there were insufficient wet season samples from Tagus Cove. Wet season scats from Cerro Colorado averaged 2.77 diet categories per scat, while the dry season mean was 2.33 categories. The dry season scats at Tagus Cove averaged 2.62 categories. Site and seasonal comparisons, where possible, were made with a t-test. There were no seasonal or site differences, indicating that at all times of the year cats typically eat relatively few different dietary items in a 24-hour period.

Because cats do eat few items per day, it may be possible to predict some prey preferences by examining single scats for prey occurrences. The occurrences of diet categories were recorded for scats containing 1, 2, 3, or 4 or more categories (Table 7). Only rodents, lizards, and birds I and II were found as single items in scats. Rodents (n=7) were found alone more than twice as frequently as any other category and more often than the others combined. In the two-item sample rodents, birds I, lizards, and grasshoppers were each found more than twice as frequently as any other category and constituted 73% of this sample. In the three-item sample arachnids join the above categories. In scats containing four or more items lizards and grasshoppers are found the most frequently, but seven of the eight items present occur in relatively equal frequencies. These data demonstrate an expanding pyramid of items included in the diet. Those items occurring the most frequently in all scats are likely to constitute the preferred prey with respect to nutrition, availability, and satiety. Secondary prey are added when the preferred prey are either unavailable or found in insufficient quantities.

Table 7. Composition of single scats in terms of the number of dietary categories per scat.

Category	Items per scat			
	1	2	3	4
Rodent	7	9	11	6
Bird I	3	14	11	8
Lizard	1	10	15	10
Grasshopper	-	8	18	10
Arachnids	-	4	10	3
Beetle	-	2	-	5
Plant	-	3	6	7
Bird II	2	3	3	1
Crab	-	3	-	-
Fish	-	-	-	-
Total	13	56	74	50

The cats' daily energy intakes were estimated a posteriori from the fecal data, based on the mean weight of each scat and the composition of the calculated standard scat. The mean weight of 640 scats was 7.42 ± 2.86 g. The weight of the standard scat calculated from the diet category components was 8.39 g, well within one standard deviation of the mean weight. The weight of the standard scat will be used for all further energetic calculations. Mean weights were calculated for seasonal and site specific scats, but no differences ($p < 0.05$) were found in any comparison using a t-test.

The percentage digestibility of each item was extrapolated from studies of coyotes, bobcats, and domestic cats (Table 8) (Greaves and Scott 1960, Golley et al. 1965, Johnson and Hansen 1978, Johnson 1982). Although the digestibilities were higher for other felines, those studies did not include high diet variability or high bulk (i.e. hair, feathers, or bones) and were conducted with ad libitum water. High bulk and water directly influence food intake and digestive assimilation efficiency (Chew 1965, Schmidt-Nielson 1974). The weight of each diet category in a scat represents the indigestible fraction or $1 - (\% \text{ digestibility per category})$. Using the digestibility and dry weight of occurrence, the amount of matter digested can be calculated. The calculated average caloric value can be derived by multiplying, for each category, the calculated dry weight digested times the gram dry weight caloric value and summing the products. The calculated average caloric value per scat was 169.97 kcal. Vertebrate components make up 71.9% of each scat by weight but contain 93.4% of the caloric

Table 8. Standard scat composition, digestibility, and caloric value of diet categories.

Category	Occurrence g dry wt. (freq.)	Digestibility %	Kcal/ g-dry wt*	Kcal/ scat
Rodent	2.10 (.250)	85	5.163	61.440
Bird I	1.25 (.143)	80	6.552	32.760
Lizard	1.25 (.143)	80	6.567	32.835
Grasshopper	1.37 (.163)	50	5.386	7.378
Arachnids	0.37 (.044)	50	5.504	2.036
Beetle	0.10 (.012)	50	5.504	0.550
Plant	0.62 (.074)	0	4.492	-
Bird II	1.25 (.143)	80	6.552	32.760
Crab	0.04 (.005)	50	3.115	0.124
Fish	0.04 (.005)	50	4.256	0.085
	<u>8.39 (1.00)</u>			<u>169.968</u>

* Cummins 1967

value. Rodents contribute 36.1% of the total calories, while birds I and II contribute 38.2% and lizards 19.1%.

Scott and Scott (1967) and Scott (1976) reported the daily caloric requirements for various age classes of cats per kilogram body weight: kittens (5 wks) 250 kcal, subadult-adult (30 wks) 100 kcal, adult male and non-pregnant female 80 kcal, pregnant female 100 kcal, and lactating female 250 kcal. Using these values along with the mean body weights of Galapagos males and females (2.69 and 2.08 kg), the average daily requirements for males and non-pregnant females would be 215.8 and 166 kcal respectively. According to Scott's figures, a pregnant Galapagos female would require 208 kcal per day, while a lactating female would need 520 kcal per day, well above the estimated intake (169.97 kcal).

Discussion

The Galapagos Islands are geologically relatively young, with some age estimates as low as four million years since the formation of the first island, Espanola (Bailey 1976). If one considers the potential rates of natural introduction for an oceanic archipelago 1000 km off the coast of Ecuador and the amount of time required before the volcanic islands might have become habitable, it is not surprising that they are still relatively depauperate today. The flora of the archipelago is disharmonic; though several families from the nearest mainland area are totally absent, others are richly represented

(Thornton 1971, Wiggins and Porter 1971). The insect fauna is very poor for a tropical archipelago (129 families, 395 genera, 618 species), while the Hawaiian Islands have several hundred species of a single genus, Drosophila (Linsley and Usinger 1966). Among the reptiles there are 10 species of iguanid lizards, 7 species of geckos, 3 species of snakes, and 1 species of giant tortoise with 15 subspecies (Thornton 1971). Harris (1978) has listed only 56 resident and 31 regular migrant species of birds; 26 species are endemic. Of the native mammals only two species of the original six species of Oryzomys still exist along with two native bats of the genus Lasiurus, and two pinnipeds. There are also seven species of introduced mammals. Of this relatively small faunal community, many species can probably be eliminated as potential prey solely on size considerations.

The rainy season stimulates bird reproduction, especially among the finches. The wet season triggers male courtship displays, conspicuous songs and flights, and nest building, making the birds briefly more conspicuous to the human observer and presumably to the cats as well. Once pair bonding and egg laying are completed, the observed numbers of birds decline, probably because of (1) reduced visibility due to seasonally thick foliage, (2) increased nest attendance by both sexes during brooding, and (3) reduced travel because of enriched and localized food sources. With the coming of the dry season the observations of birds increase as both the insectivorous and granivorous birds must search more widely for food. In July and August the granivorous ground finches (Geospiza spp.) coalesce into

mixed species feeding flocks in their search for food. In addition, the newly fledged young have been added to the population, swelling their numbers even more.

Few lava lizards were seen during the wet season. During this time they do not have to search as widely for food with the large available populations of insects. Midday surface temperatures (44° to 51° C, H. Snell, unpublished data) also reduce the amount of tolerable exposure. Marine iguanas nest during January and February on the flat area immediately inland from Cerro Colorado, where a transect was established. Although the females were probably too big to be handled easily by cats, the hatchlings emerge at the end of May over a period of about a week and are immediately vulnerable to Galapagos hawks, Galapagos snakes, common egrets, and feral cats (Thornton 1971).

Periodic fluctuations in prey numbers might have greater consequences than on the mainland where some predators can move as the prey resource changes. Islands, in addition to the general reduction in numbers of species relative to continental faunas, also restrict the movements of predators in response to periodic shortages. Marshall (1961) reported that on the 30.5 km² Little Barrier Island, New Zealand, migratory sea birds are present only during the austral summer. The dietary preferences of feral cats shift from birds while they are present to rats when the birds are absent. Without the opportunity to emigrate during shortages of preferred foods, cats must be opportunistic and feed on whatever foods are most available (McMurry and Sperry 1941, Heidemann and Vauk 1971, Iverson 1978, Jones and Coman

1981). Even on large islands, such as the two main islands of New Zealand (268,000 km²), feral cats are opportunistic (Fitzgerald and Karl 1979). In the Galapagos Islands rodents, birds, lizards, grasshoppers, centipedes, and beetles each appeared in more than half the total number of scats collected.

Even if forced to be somewhat opportunistic, feral cats may continue to feed on a preferred species disproportionately to its decreasing abundance. The levels of birds, lizards, and grasshoppers appearing in the scats and on the transects were compared. The consumption of each is relatively uniform over the span of time tested, but the observed transect abundances vary widely. Clearly, cats are not tracking the apparent populations in their consumption of prey items.

Hart (1980) stated that cats have an innate preference for rodents as prey. This appears to be borne out in a number of studies (McMurry and Sperry 1941, Sladek 1970, Heidemann 1973, Iverson 1978, Dilks 1978, Fitzgerald and Karl 1979). But two other studies (Jones 1977, Jones and Coman 1981) indicated that rabbits, not rats were the preferred prey species. Finally, studies of subantarctic populations revealed that cats would totally ignore rabbits and partially ignore mice in favor of burrowing procellariform birds (Derenne 1976, Derenne and Mougin 1976, van Aarde 1980). Therefore, it is likely that prey preference is determined by abundance, accessibility, and ease of handling.

Many of the potential vertebrate prey species in the Galapagos Islands are readily accessible, because they have reduced or lost their wariness. For these species, abundance and ease of handling will principally determine preferences. Preferences may be thought of energetically as the maximum number of calories available (abundance) minus the handling costs (ease of handling). Leyhausen (1979) stated that domestic cats can kill anything not larger than themselves. In the Galapagos, cats repeatedly have been observed attacking frigate birds and pelicans (J. Gordillo, pers. comm.). These birds are certainly larger, though frigate birds weigh less, than the cats and would contain a large number of calories, but their potential for defense, ability to flee, seasonal availability, and relatively low numbers would reduce their importance in the diet. Derenne (1976), Derenne and Mougín (1976), and van Aarde (1980) all indicated that feral cats on Atlantic subantarctic islands do not frequently attack the grey petrel (Adamastor cinereus), because it is very aggressive, even though not substantially larger than other sympatric burrowing procellariiform birds. Marine iguanas are relatively abundant throughout the year and very accessible, but their large size (± 5 kg) and tough skin makes them relatively impervious to attack by cats.

Black rats are very abundant throughout the year (618 km^{-2} , D. Clark 1980) and larger than all prey species except large birds and iguanas. However, black rats are introduced mammals and apparently have not lost as much defensive ability as have the endemic Oryzomys. In fact, black rats are very aggressive and have, on occasion, been

known to attack their attacker even though they had an available avenue of escape. Leyhausen (1979) described the jump-attack of rats and the relative ease with which they were able to repulse even experienced cats. He said that even when an approach was made, generally only one in three attempts resulted in a successful kill.

Lizards and birds I are also very abundant and very accessible but are much smaller than rats. The largest of these may weigh 30 g or about one-fourth the weight of an average-sized rat. All the arthropod prey species, even though more abundant than rats, are much smaller, and the high percentage of chitin reduces the realizable energy. Furthermore, centipedes are nocturnal and have a strong mechanical and slightly venomous bite. Fish are only encountered accidentally. Therefore, the a posteriori attempt to rank prey by their occurrence in scats containing few items is probably valid. Rats are ranked first because the balance of abundance, accessibility, and ease of handling yields the greatest number of net calories. Birds I and lizards should be ranked below rats but ahead of grasshoppers, arachnids, crabs, and beetles respectively. Birds II are relatively rarely taken because of their potential for defense and patchy and irregular occurrences; however, when they are taken they provide a large caloric reward. Because plants are relatively indigestible and fish are encountered fortuitously, they are probably not actively sought. However, plants may be taken for moisture, to aid digestion, or to serve as an emetic.

Prey preferences and the caloric value of the diet calculated from the fecal analyses should provide some insight into daily activity and

energy intake. The mean calculated caloric value of 169 kcal per scat was determined making four assumptions: (1) the calculated mass (8.39 g) for a standard scat was generally applicable, (2) the caloric values taken from Cummins (1966) are roughly equivalent to the taxa represented in the scats, (3) the approximated prey digestibilities are roughly equal to those of Galapagos feral cats, and (4) cats usually defecate once and only once in 24 hours, as indicated in studies by the National Pest Control Association (1964) and Might (1964). Using these assumptions, this calculation should produce a conservative but realistic estimate. Although unlikely, a 5% increase in digestibility could increase the daily energy derived per scat by 46.4% (248.8 kcal per day). Such an increase is unlikely because hair, feathers, and bones will act to reduce assimilation efficiencies (Ackerman 1982). For the sake of this discussion the effect of both energetic intake values (169 kcal and 248.8 kcal) will be considered.

The predictions from the smaller value would indicate that only non-pregnant females do not face daily energetic deficits. Based on mean body weights, adult males, pregnant females, and lactating females all would face daily deficits of 46.8 kcal, 39 kcal, and 351 kcal respectively. The higher estimate would be sufficient to fulfill the daily energetic requirements of adult males, non-pregnant females, and pregnant females. This estimate is still insufficient to account for the energy intake required of a lactating female but it reduces her daily deficit from 351 kcal to 251.8 kcal.

These data are merely estimates that reveal the large intersexual differences in energy requirements. Jones and Coman (1982a) also found that females and subadults suffered the greatest nutritional stresses of all cats in the arid region of Australia where they worked. Females probably suffered from reproductive-related deficits, while it is likely that subadults suffered energetic stress while learning to hunt independently. These differential stresses give credence to the idea of differential mortality of females and subadults, which would help explain the sex ratio and population structure discussed in Chapter II.

Because sufficient daily energy is so difficult to attain, cats should adopt a strategy of energy maximization. They should take every prey item encountered that yields a net energy increase. If two different prey items are encountered simultaneously, then the cat should rank them by total net realizable energy and choose accordingly. If cats were to bypass "lower" ranked items encountered alone in the expectation of encountering a "higher" ranked item, they might well fail to meet their daily energy quota. Even though rats are moderately difficult to handle and encounter rates are uncertain, if a rat is captured and eaten, the cat has fulfilled one day's energy requirement. It then has the option not to forage further, but to devote time to other activities, such as territorial defense. Further foraging is pointless, because felids in general have low amounts of subcutaneous fat and cannot stockpile much energy against future failure (Jones and Coman 1982a). This assumes that cats can estimate the net caloric reward contained in any prey item and can debit every item eaten from the daily energy requirement.

Because sufficient daily energy appears difficult to achieve, males and females might be forced to incorporate territorial defense and mate acquisition into periods of foraging. Males forage continuously while active, pausing intermittently to spray-mark a bush or defecate and form a scrape. Females are probably detected by visual or olfactory means. Vocalizations, which might alert prey, occurred rarely. In 502 field days, adult vocalizations were recorded only once.

There is no evidence of consort pair formation during estrus. Only courtship and copulation would require some substantial period of time. Otherwise males can forage continuously with infrequent stops (10 sec) to spray-mark boundary perimeters. This may help explain the relatively large overlap observed in male home ranges (Chap. IV). Males may spray-mark portions of their home ranges to advertise their presence and relative dominance but may not have a sufficient energy surplus to make active defense economically feasible.

Female strategies must include their different energy requirements and the need to attend to litters. Regardless of which energy estimate is accepted, breeding females face chronic malnutrition and should therefore attempt to complete foraging in as brief a time as possible to minimize energy expended foraging. In addition, a female with kittens must remain close to the den site for defense and feeding. Therefore, females might have smaller home ranges, but of higher quality, where the density of food resources is maximal, while males have larger ranges predominantly to gain access to females.

CHAPTER IV MOVEMENT ECOLOGY

Methods

Feral cat movements were determined from radio telemetry and visual observations. Visual observations, totalling over 200 hours, were used primarily to determine activity periods and rates of activity. Radio telemetry data were gathered hourly in 6-hour segments, eventually spanning a 24-hour cycle. The uneven terrain and high iron content of the soil affected signal clarity. In order to maximize signal reception, areas of raised ground were chosen at both sites. At Cerro Colorado two fixed receiving stations were established on small peaks (\approx 50 m high) approximately 200 m apart. At Tagus Cove two pairs of fixed points were established to gain better coverage of the high relief in the area. Bearings were taken on all collar signals at one receiving station using a hand-held compass matched with the two-element Yagi antenna; then the process was repeated within five minutes at the second location. Movements were also observed by "homing in" on an individual's radio collar and following the animal visually.

Movement data were plotted with the aid of the AIDA (Apple Interactive Data Analysis) program purchased from Action Research

Northwest of Seattle on an Apple II-plus mini-computer. Compass heading pairs were entered and mathematically transformed to yield a pair of distances which define a unique location. Each location was calculated as a distance (m) to the north or south and east or west relative to one of the fixed receiving stations (origin). At Tagus Cove the positions from one pair of receiving stations had to be further transformed and plotted so that all positions for an individual were plotted relative to the same point. The straight line distance between the reference point (receiving station #1) and the cat's position was calculated as

$$L = (\sin \theta_2 \pm \theta_3) / \sin (\theta_2 - \theta_1) d$$

where L = distance (m) from Station 1 to cat

d = distance (m) from Station 1 to Station 2

θ_1 = compass heading (radian degrees) from Station 1

θ_2 = compass heading (radian degrees) from Station 2

θ_3 = angle (radian degrees) of the line connecting Stations 1 and 2 and the line through Station 1 from magnetic north.

Theta three is added to theta two if the line connecting Stations 1 and 2 lies west of north and subtracted if the line lies east of North.

Relative to the reference point, the cat's position is calculated as a pair of rectangular coordinates in meters from the origin:

$$\text{North or South} = L \cos \theta,$$

$$\text{East or West} = L \sin \theta.$$

Positions North and East will have a positive sign: South and West a

negative sign. Plots of radio location were performed on the Apple Computer. Because the screen formatting of graphics is rectangular and in order to have equal linear spacing on both axes, the relationship of compass directions had to be reversed. This created the following orientation

North
East West
South

and the perspective of viewing the distribution of points from below rather than above. However, the relationship of compass points to the distribution of radio locations is irrelevant. The relationship of a cat to topographic features and the locations of other cats is more important.

It was also possible to select specific sequences of locations in order to plot monthly and daily activities. The area of total and monthly home ranges was calculated by the minimum perimeter method of connecting the outermost points of the distribution and measuring the area enclosed. Areas were measured on the Apple computer with the area option of the Apple Graphics Tablet. Areas of home range overlap were also calculated with the graphics tablet.

Rates and percentages of activity were calculated from radio telemetry and visual observations. Rates of activity were calculated from the hourly radio locations. Planar linear distances were measured as the distance between two sequential radio locations. Because radio locations were taken once an hour the distance equals the hourly rate

of activity. All distances for a particular time period were averaged and plotted by study locations. Percent of time active was calculated from visual observations made during the daylight hours from 0600 to 1000 hours. During visual observations the length of time spent in each activity was recorded. The time spent grooming, sitting, or lying were considered resting and all others as active. The percentage of time spent in resting versus activity was calculated in 2-hour segments.

An a posteriori set of calculations was made to estimate the energy expended in activity. Rates of activity were obtained from the radio telemetry data. These rates were calculated as the linear distance travelled in one hour. However, cats were not active for the entire hour at any time. The percentage of each hour spent in movement was used to modify the average rate into a calculated "actual" rate of travel. For example, if cats were active for only 15 minutes in one hour and travelled one kilometer in that time, then their actual rate of travel would have been four kilometers per hour for 15 minutes. Once the actual rates had been calculated, the data were converted into velocities measured in meters per second and used in the energetic equation of Taylor et al. (1970):

$$VO_2/M_b = Y\text{-intercept} + \text{slope} \cdot v$$

where VO_2/M_b is the mass specific (kg) volume of oxygen consumed, the y-intercept is defined as the energetic cost of standing which, depending on the author, varies between 1.6 and 1.7 times the predicted basal metabolic cost for that species (Kleiber 1961), the slope is a

power or scaling function for metabolic rates, and v is the velocity measured in ms^{-1} . The value obtained has the units $\text{ml O}_2\text{kg}^{-1}\text{s}^{-1}$ which can be mathematically converted to $\text{kcal kg}^{-1}\text{min}^{-1}$. The actual energetic cost at a given rate for a given period of time can be calculated by multiplying the number of minutes in activity by the cost per minute. This accounts for the energetic cost of locomotion. When cats are not active, they still have the cost of basal metabolism. This value was assessed directly from Scott's (1976) value of 80 kcal per kilogram per day and the proportion of the day that cats were not active.

Results

Fourteen individuals were monitored for varying periods of time at the two principal study sites. Due to variable trapping success and the deaths of some individuals, it was not possible to have all collars in place simultaneously for the entire study period at a particular site. Table 9 depicts the sexes, ages, and the length of observation time for each individual from its initial trapping date to termination of observations. The length of time an individual was monitored ranged from two weeks to six months. However, the number of radio locations for individuals ranged from 20 to 600, totalling almost 2400 separate locations. Of the 14 cats monitored, only three had less than 70 locations, while seven cats had more than 150 locations.

Table 9. Sex, age, and number of days observed for radio collared cats from both study sites.

TAGUS COVE				CERRO COLORADO			
#	sex	age	days obs.	#	sex	age	days obs.
1	M	SA	130	1	M	SA	53
2	M	A	120	1A	M	A	120
4	M	A	132	2	M	A	181
5M	M	A	110	3	F	A	56
5F	F	A	91	3A	M	A	54
6	F	A	110	4	F	SA	14
				5	M	A	14
				6	M	A	179

Total home ranges were calculated for each radio-collared cat at each study site (Table 10). The mean home range size for males ($3.04 \pm 2.64 \text{ km}^2$) from both sites was substantially larger than for females from both sites (0.82 ± 0.86). The small sample size and large standard deviations about the means resulted in no significant differences in a t-test comparison. Within each study site males also had much larger mean home ranges than females. At Tagus Cove male home ranges were $1.49 \pm 1.46 \text{ km}^2$, while female home ranges were only $0.35 \pm 0.20 \text{ km}^2$. At Cerro Colorado male home ranges averaged $4.97 \pm 2.84 \text{ km}^2$, while those for females were only $1.30 \pm 1.14 \text{ km}^2$. The average home range size of all individuals at Cerro Colorado was $3.38 \pm 2.75 \text{ km}^2$, substantially larger than the average home size of $1.11 \pm 1.28 \text{ km}^2$ at Tagus Cove. Intersexual, intrasexual, and site comparisons were made with a t-test; none was found to be statistically significant, although I believe the trend is clear. Home range sizes for individuals were plotted against body weights and fitted to a linear regression equation. The coefficient of correlation was less than 0.5.

For each study site, the home range outlines of all monitored cats were plotted together (Fig. 8). The coastlines of the two study sites were drawn in to provide a frame of reference. At Cerro Colorado the home range outlines of all cats overlapped extensively with other cats. The home ranges of three individuals were completely enclosed by the home ranges of two other cats. At Tagus Cove the home range outline of each cat was overlapped to some degree by all other

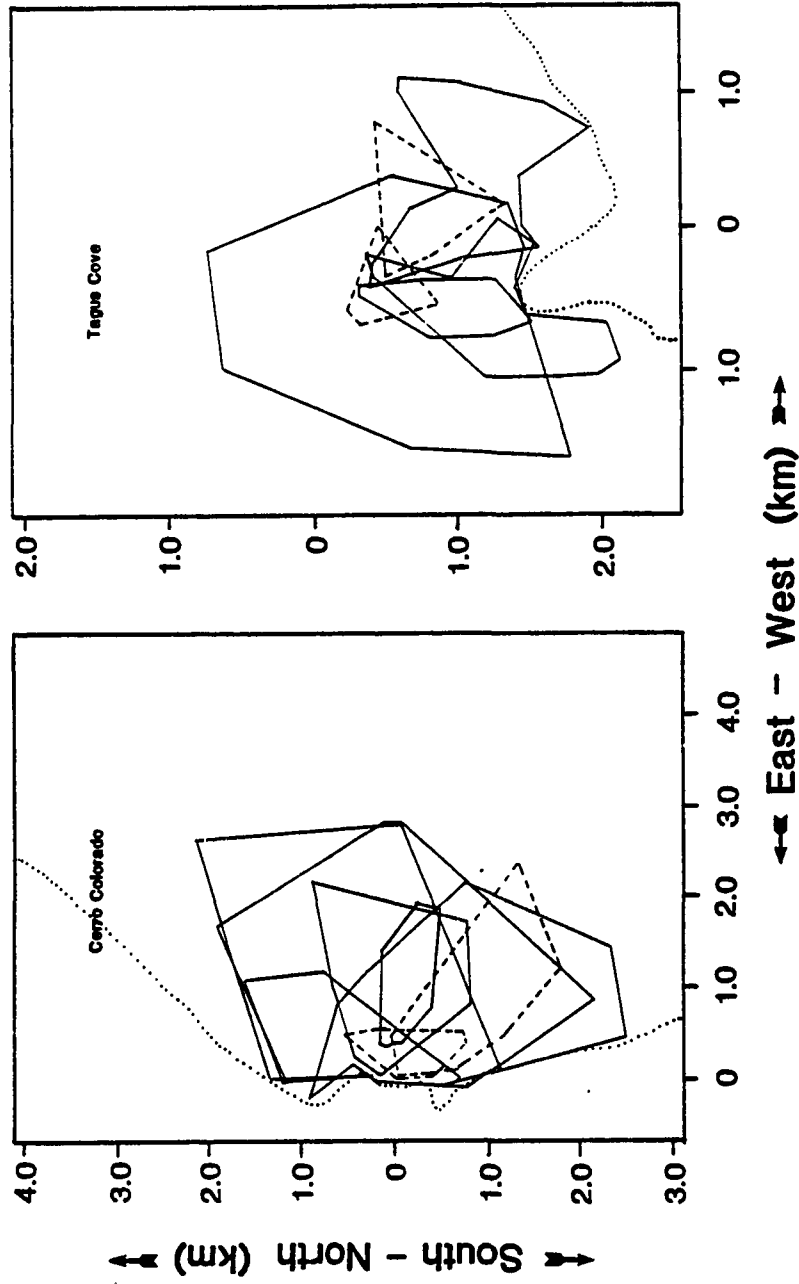


Figure 8. Home range outlines for all cats at Cerro Colorado and Tagus Cove.

monitored cats, but the amount of overlap was less than that at Cerro Colorado. To provide a less confusing explanation of spatial relationships, several typical examples were chosen.

Cerro Colorado males #2 and #6 were both mature adults weighing 3.0 and 3.75 kg respectively. In several observed encounters #6 was always dominant to #2, while #2 was dominant to all other cats it interacted with. The home ranges of both cats had areas of concentrated activity directly inland from Cerro Colorado (coordinates 0,0), and #2 shared approximately 50% of its home range with #6 (Fig. 9). With the exception of one long excursion point to the south, #2 had a range which was distributed to the north and west of Cerro Colorado. On the other hand, #6 had a home range oriented more southerly. The home ranges of other adult males at Cerro Colorado followed this general pattern, an area of concentrated activity near the coast and an inland distribution of locations slightly different than other males. The other males, which were subordinate to both #2 and #6, had their areas of concentrated activity slightly farther inland, although they did not follow a distinct enough pattern to indicate any hierarchical arrangement of concentrated activity areas.

Adult males from Tagus Cove had a different pattern of home ranges from those at Cerro Colorado. Adult males #2 and #4 were both mature individuals with respective body weights of 3.25 and 3.75 kg. There were insufficient visual observations to discern any dominance relationships between individuals at Tagus Cove. The distribution of locations was relatively uniform over a majority of the home ranges,

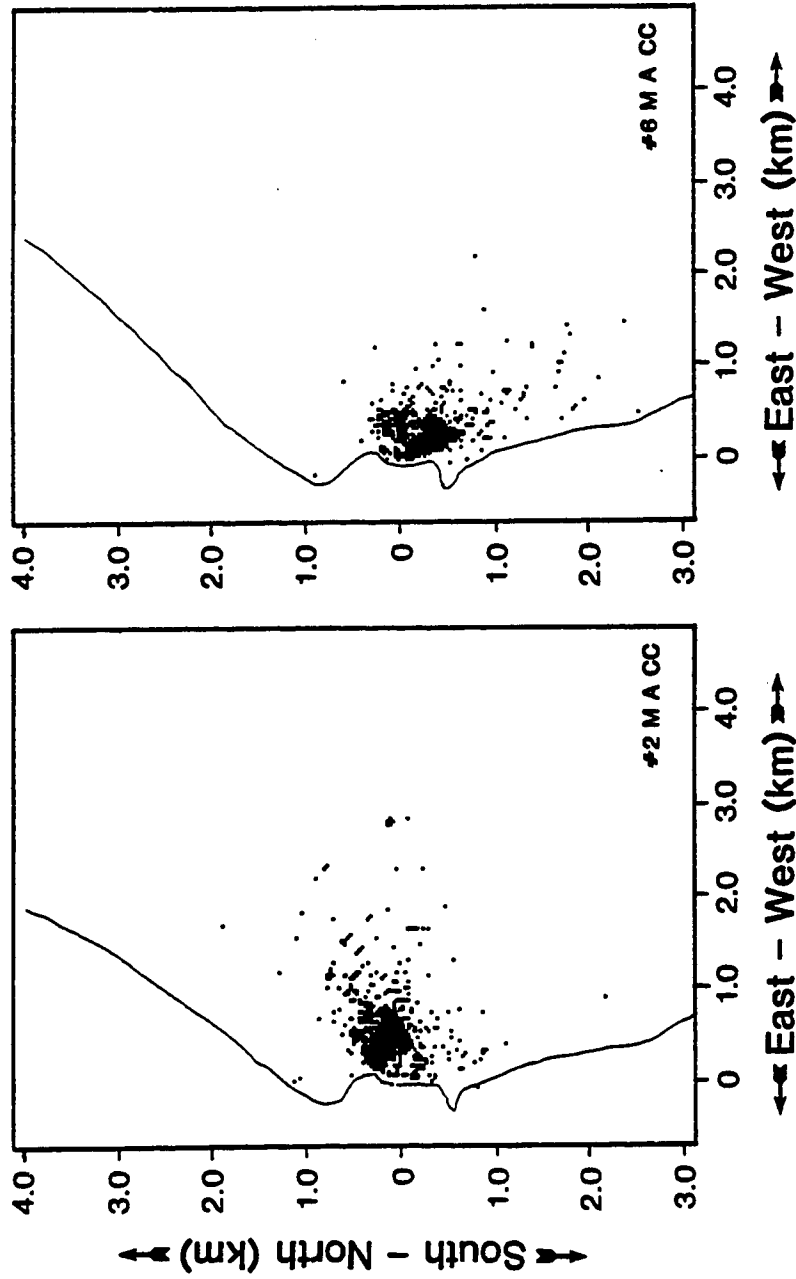


Figure 9. Distribution of radio locations for two adult (A) males (M) at Cerro Colorado (CC).

with no areas of concentrated activity (Fig. 10). The amount of overlap between males of Tagus Cove was also much less than at Cerro Colorado; the home ranges of #2 and #4 overlapped less than 10%.

Subadult males might be expected to exhibit a slightly different pattern than adult males. Subadult males disperse more frequently than other age and sex classes in order to find a range where there may be reduced competition for food and reproductive access to females. One subadult male from each site was radio collared to examine subadult home range patterns (Fig. 11). The subadult from Cerro Colorado had a relatively restricted home range (2.41 km²), which was less than half the average home range for males and was displaced farther inland than other males. The spatial distribution of locations was very concentrated; if overlaid with other male home ranges from Cerro Colorado, it appears that this subadult was using an area relatively unused by other monitored males, even though its home range was completely enclosed by the ranges of two of those males. In contrast, the subadult male from Tagus Cove had a home range that was almost 2.5 times the mean male home range size at that site and half again as large as that of the Cerro Colorado subadult male. The distribution of locations was very different with no areas of concentrated activity. Less than 40% of the Tagus Cove male's range was overlapped by those of the other radio collared cats.

Females at each site had home range patterns similar to their male counterparts, although their ranges were smaller and the amount of intrasexual overlap was less (Figs. 12 and 13). At both sites female

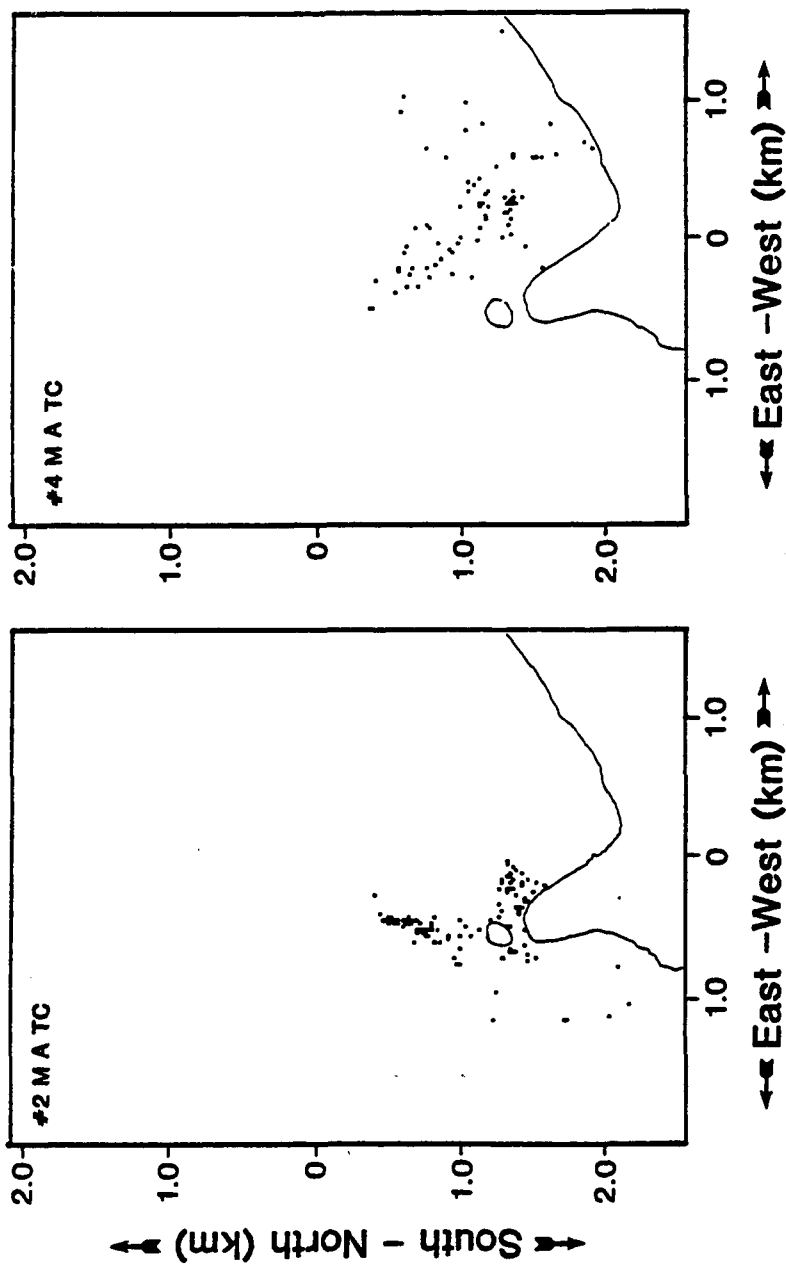


Figure 10. Distribution of radio locations for two adult (A) males (M) at Tagus Cove (TC).

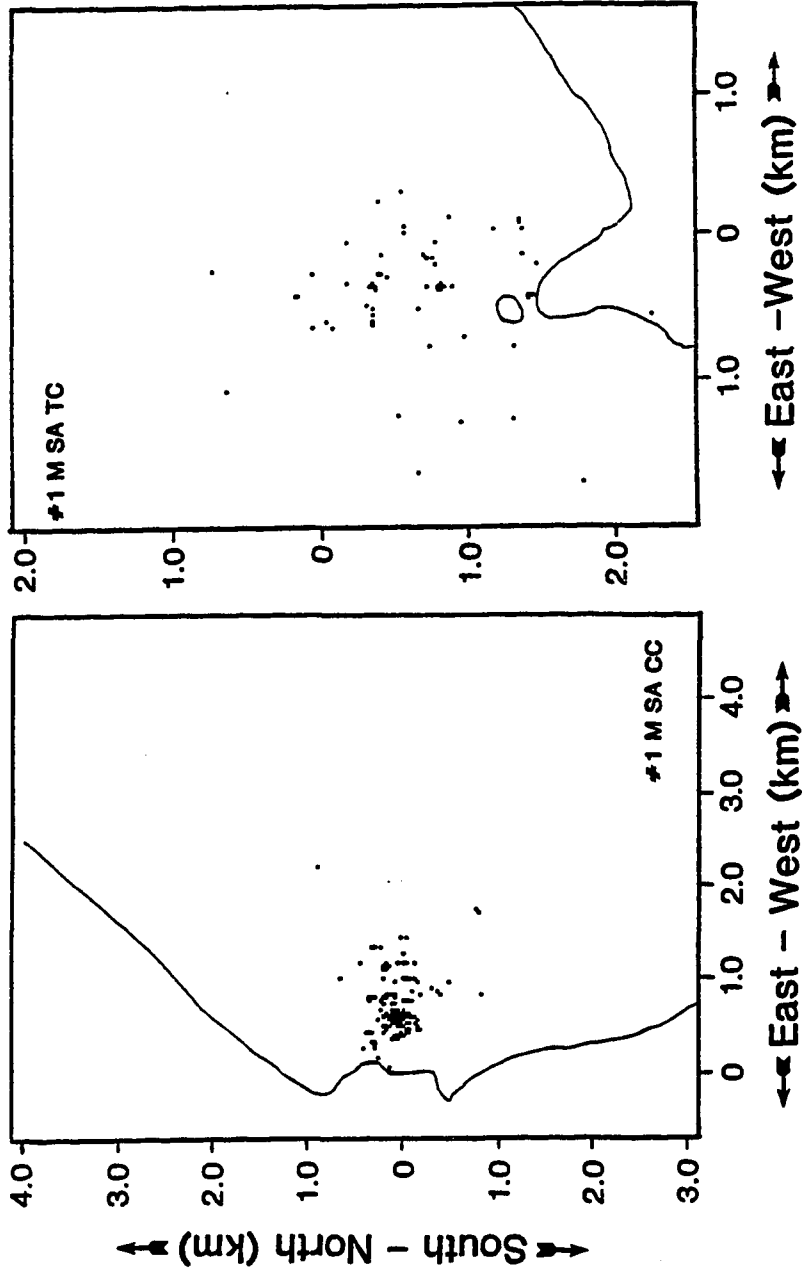


Figure 11. Distribution of radio locations for two subadult (SA) males (M) at Cerro Colorado (CC) and Tagus Cove (TC).

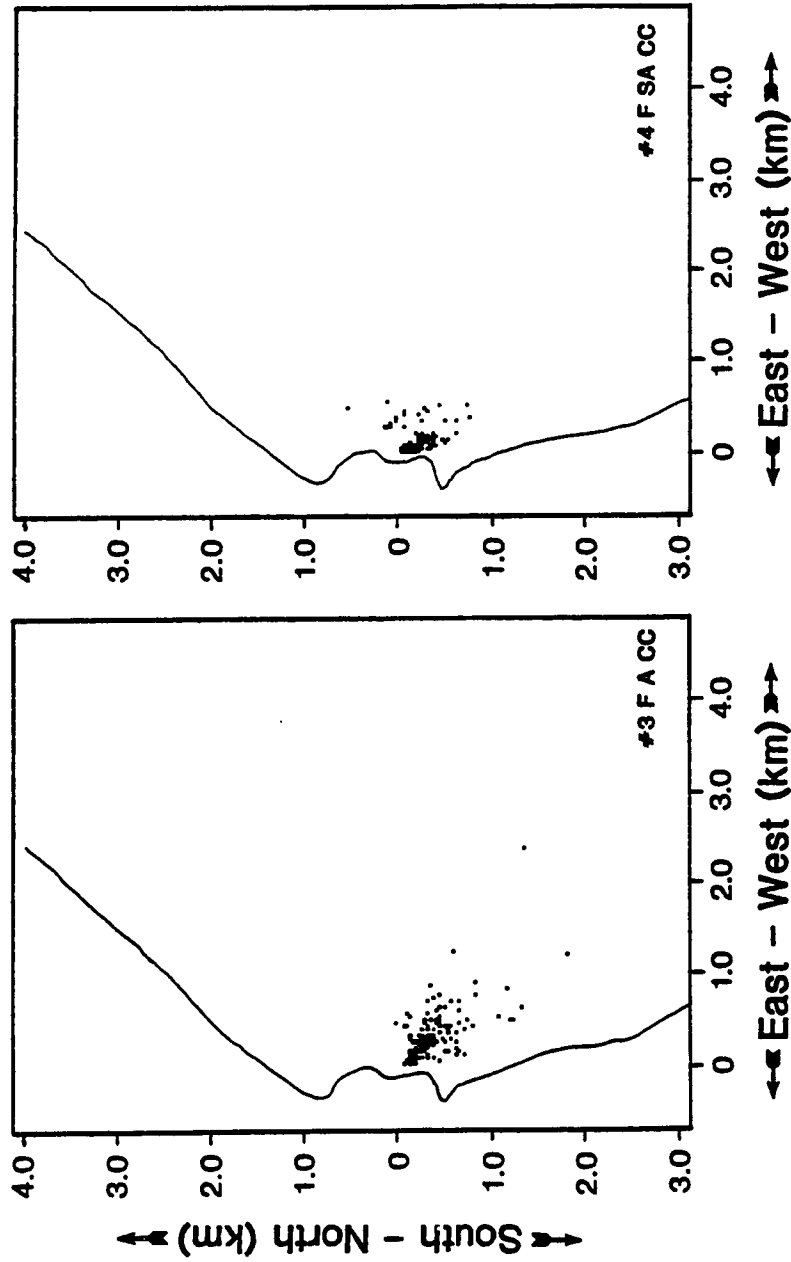


Figure 12. Distribution of radio locations for adult (A) and subadult (SA) females (F) at Cerro Colorado (CC).

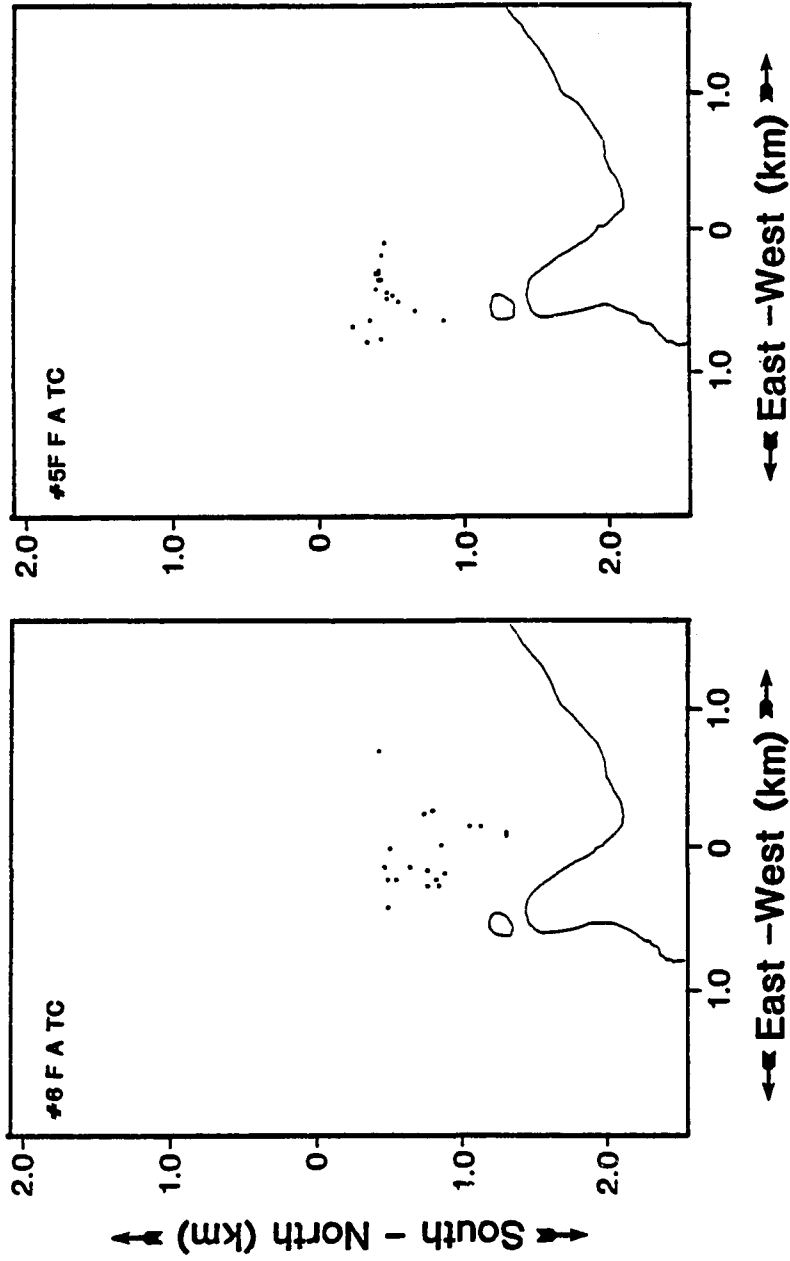


Figure 13. Distribution of locations for adult (A) and subadult (SA) females (F) at Tagus Cove (TC).

home ranges were approximately 25% of the average male home range at the same site. At Cerro Colorado females #3 and #4 had concentrated patterns of home range use. Female #3 shared only about 14% of her home range with female #4. At Tagus Cove the home ranges of two females were smaller than those at Cerro Colorado. Females #5F and #6 displayed no areas of concentrated activity, and female #6 shared only 5% of her home range with #5F.

All the radio collared individuals overlapped with each other at both study sites (Table 11). At Cerro Colorado the percent of total range shared with other cats averaged 94.8%, while at Tagus Cove cats overlapped for only 70.7% of their total range. Differences in the amount of an individual's home range which was shared were tested for with a t-test and found to be significantly different at the two sites ($p < 0.05$). Paired comparisons were then made between individuals to look for any patterns in proportion of range shared (Table 11). Because of variations in home range sizes, no pattern in shared usage could be determined.

The pattern of habitat use was addressed by calculating the number of times an individual was found in a particular patch type (Table 12). These calculations apply only to Cerro Colorado, where there were four distinctly separable patches (Fig. 2). At Tagus Cove the habitat is essentially uniform and there are no distinct patches. Five of the eight cats monitored were found more frequently in the lava/shrub patch than in any other. The average usage of that patch was 49% (range 22-88%). The next most heavily visited patch was the sandy plain,

Table 11. Percent of an individual's range shared with other radio collared cats and the percentage of the total range shared. The individuals are listed in the column and shared range read horizontally.

Tagus Cove									
	% Range Shared With						# cats	%	
	1	2	4	5M	5F	6	overlap	shared	
1	-	19.5	11.1	9.6	6.0	9.9	5	36.0	
2	80.1	-	9.2	31.8	8.0	1.2	5	80.1	
4	37.1	7.2	-	8.6	4.4	23.3	5	39.6	
5M	95.0	72.6	25.0	-	13.6	7.3	5	95.0	
5F	100.0	31.3	22.0	23.3	-	10.6	5	100.0	
6	72.4	2.1	51.4	5.5	4.7	-	5	73.3	

Cerro Colorado										
									# cats	%
	1	1A	2	3	3A	4	5	6	overlap	shared
1	-	94.3	100.0	21.2	19.0	9.3	28.3	64.7	7	100.0
1A	33.2	-	85.0	12.8	25.2	6.8	10.3	34.4	7	85.0
2	31.5	76.0	-	22.8	22.6	6.1	9.2	51.2	7	96.8
3	24.8	42.6	85.0	-	7.6	13.6	5.3	95.3	7	95.3
3A	26.5	100.0	100.0	9.0	-	19.9	3.5	49.1	7	100.0
4	48.2	100.0	100.0	60.1	73.7	-	10.9	19.7	7	100.0
5	96.7	100.0	100.0	15.3	8.5	7.2	-	13.0	7	100.0
6	30.2	45.7	75.8	37.9	16.4	9.0	1.8	-	7	80.9

Table 12. Patch type usage (%) by radio-collared individuals at Cerro Colorado and averages for all individuals.

	Patch Type			
	A	B	C	D
1	13	65	23	-
1A	22	27	45	5
2	33	46	17	5
3	28	64	9	-
3A	67	22	4	7
4	71	29	-	-
5	-	88	12	-
6	29	57	14	-
	—	—	—	—
Average	38	49	18	6

directly inland from Cerro Colorado (38%). The palo santo woodland, the most extensive patch, was used only 18% of the time, while the grassy areas were the least frequently used area (6%). Differences in patch type use were tested for with a multi-way contingency table. The test results indicated that the lava/shrub was used significantly more often than other patches ($p < 0.01$).

It is possible that the total home range of an individual may represent a combination of temporally or seasonally smaller home ranges. Monthly home range outlines were drawn for each individual. Monthly home ranges averaged only 38% of the area of the total home range sizes. As a typical example, the monthly home ranges of adult male #2 from Cerro Colorado, for which I had the most radio locations, were plotted together (Fig. 14). The monthly home range areas averaged only 31% (range 10-58%) of the total home range (6.81 km²). The home ranges for April and May are substantially smaller than the others. The general orientation and shape of monthly home ranges are relatively the same with the exception of January, which was altered by a single excursion point.

With overlapping home ranges and areas of concentrated activity it is likely that two cats might have been in the same area simultaneously. The daily movements of three cats were plotted for the same day over the same time period (Fig. 15). Adult males #1A, #2, and #3A from Cerro Colorado were selected. It can be seen that the daily paths intersected at least one other daily path, and #2 intersected both of the other cats. However, an examination of actual location

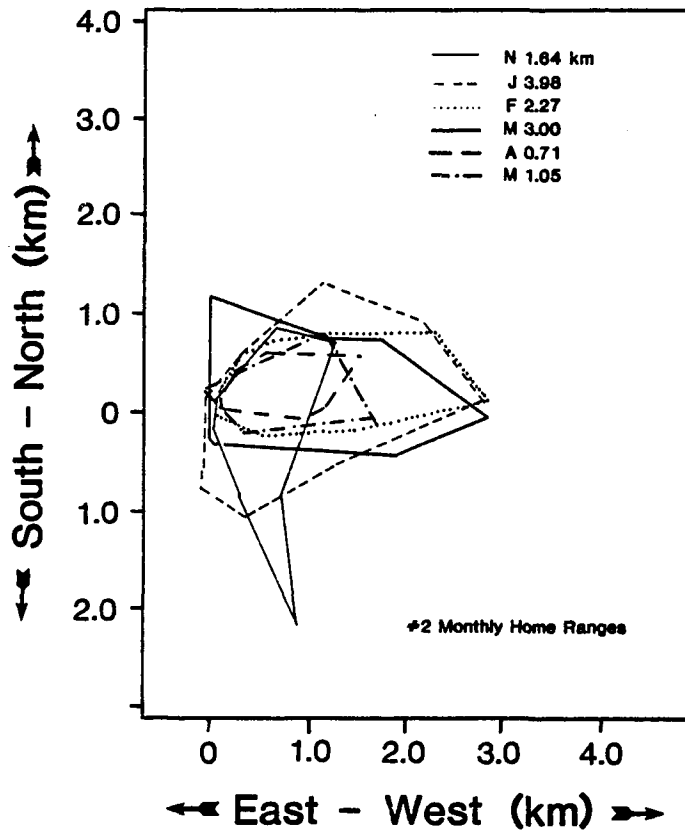


Figure 14. Monthly home range outlines and areas for one adult male at Cerro Colorado for six months in 1979 and 1980.

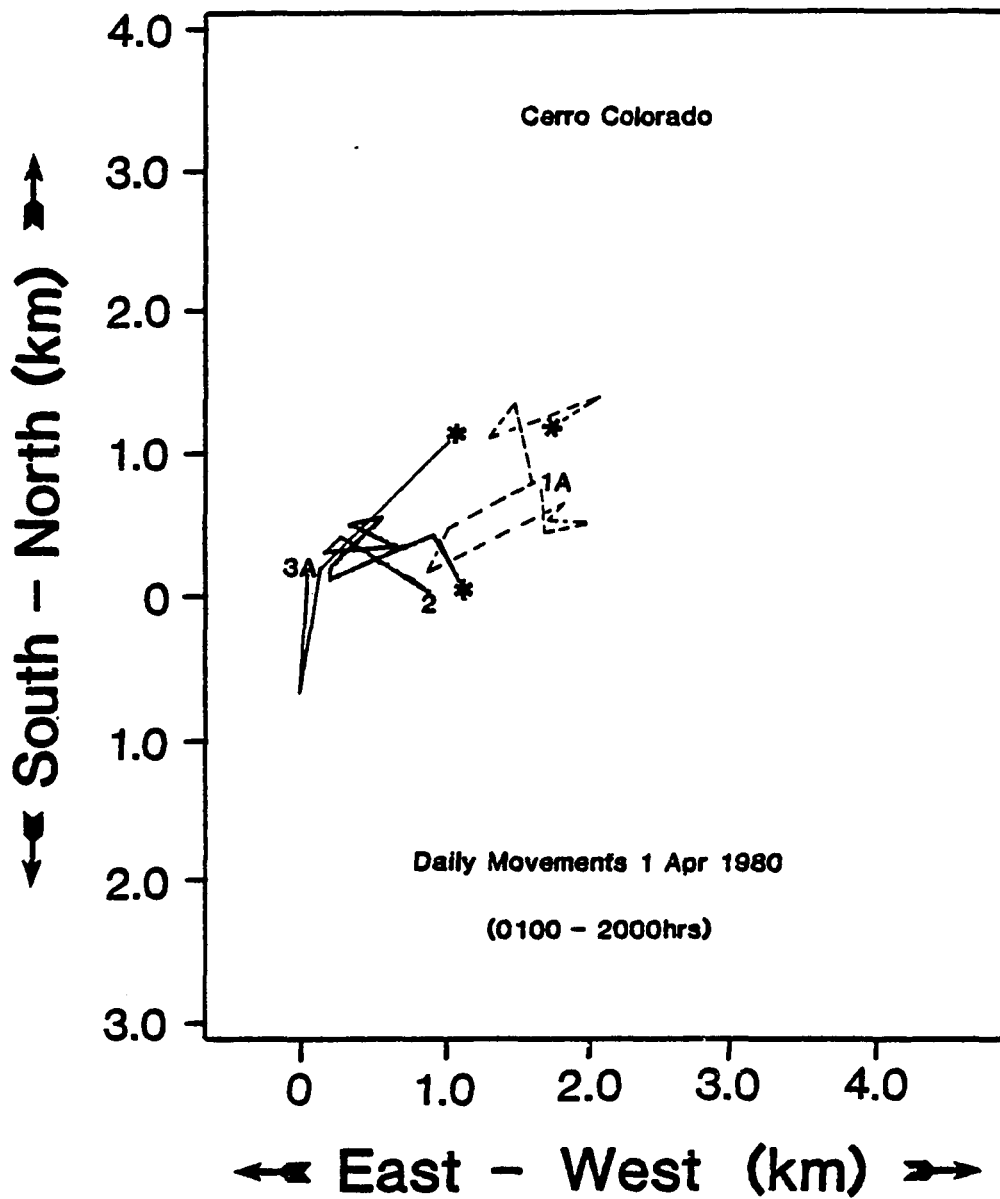


Figure 15. Daily movements of three individuals on the same day at Cerro Colorado. (Numbers indicate starting points, and asterisks indicate end points.)

coordinates revealed that no two cats were closer than 100 m at any time during the observation period. The shape of the daily paths for these three individuals was fairly typical of cats at Cerro Colorado (Figs. 15 and 16). The path crossed itself several times during a day and finished relatively close to the point of origin. At Tagus Cove typical daily paths were somewhat different (Fig. 17); although the paths terminate near where they began, a path generally ran straight away from the point of origin and then back along an almost parallel line.

From over 200 hours of visual observation and radio telemetric calculations, it was possible to calculate the percentage of each hour that cats were active (Fig. 18). Cats could be observed from shortly before 0600 to almost 2000 hours. It was not possible to obtain undisturbed visual observations at night. Around sunrise (0600 hrs) the cats were active for an average of 73% (43.8 min) of every hour. From 0800 to 1000 hrs the percentage of active time dropped to 55% (33 min) of each hour and dropped further to 53% (31.8 min) from 1000 to 1200 hrs. The lowest percentages of activity were observed from 1200 to 1400 hrs (32%, 19.2 min) and 1400 to 1600 hrs (25%, 15 min). In the late afternoon the percentage increased to 60% (36 min, 1600-1800 hrs) and from 1800 to 2000 hrs it equalled the early morning percentage (73%, 43.8 min).

From the radio telemetry data I calculated the relative rates of activity for cats during most hours of the day at each study site (Fig. 19). At Cerro Colorado the rate of activity for each hour of the day

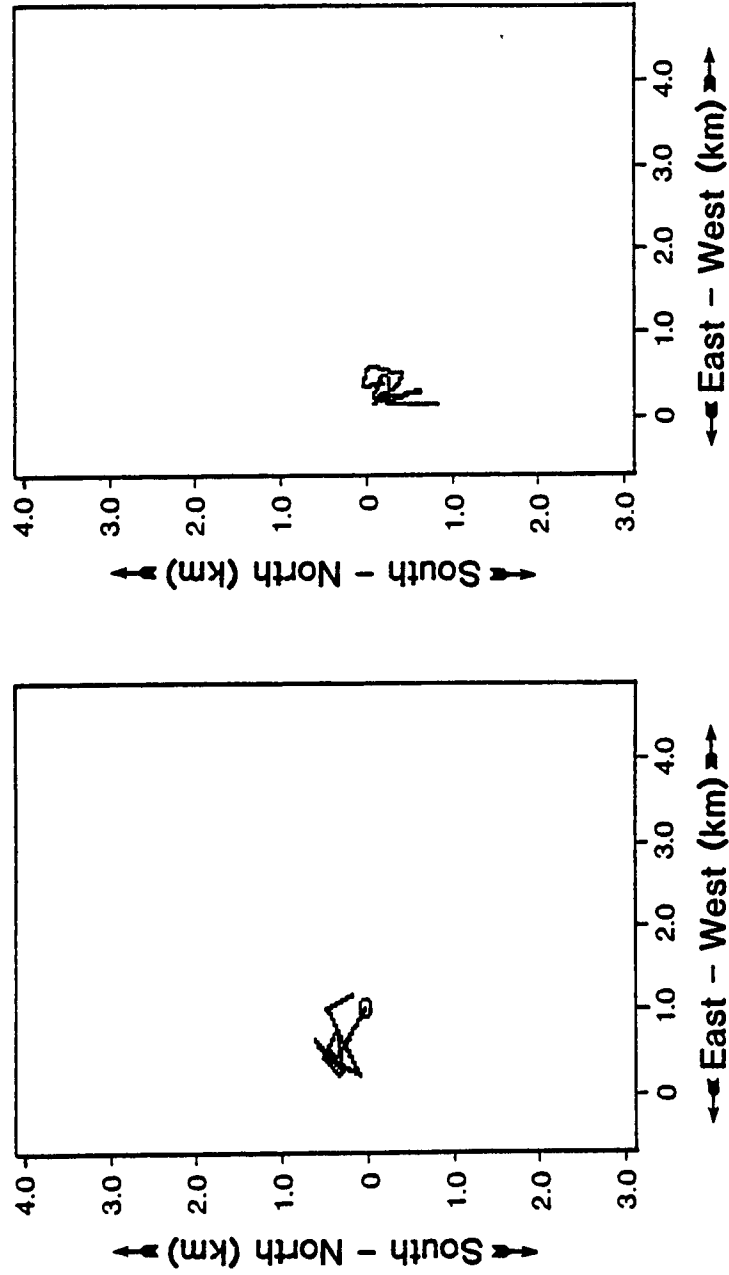


Figure 16. Typical crisscrossing daily movement patterns of individuals at Cerro Colorado.

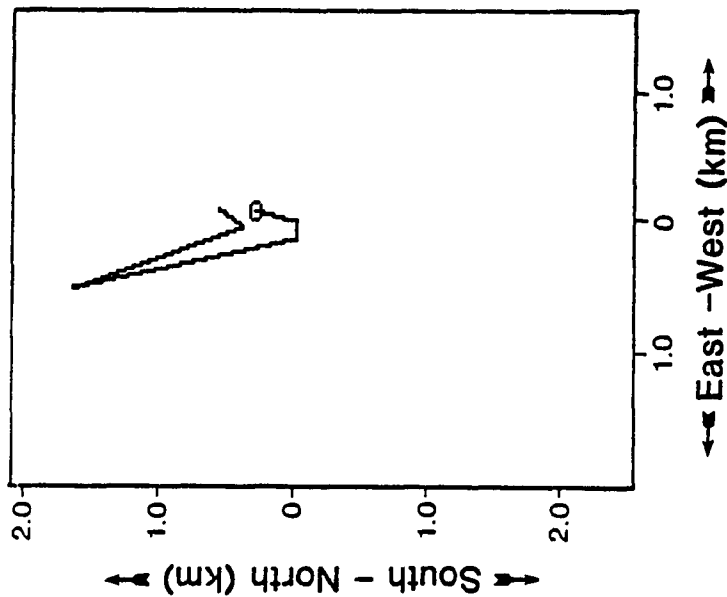
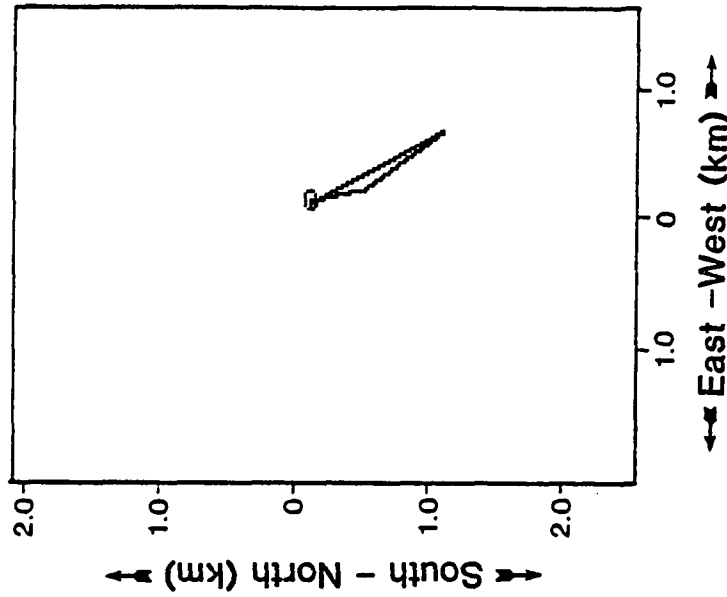


Figure 17. Typical straight-line daily movement patterns of individuals at Tagus Cove.

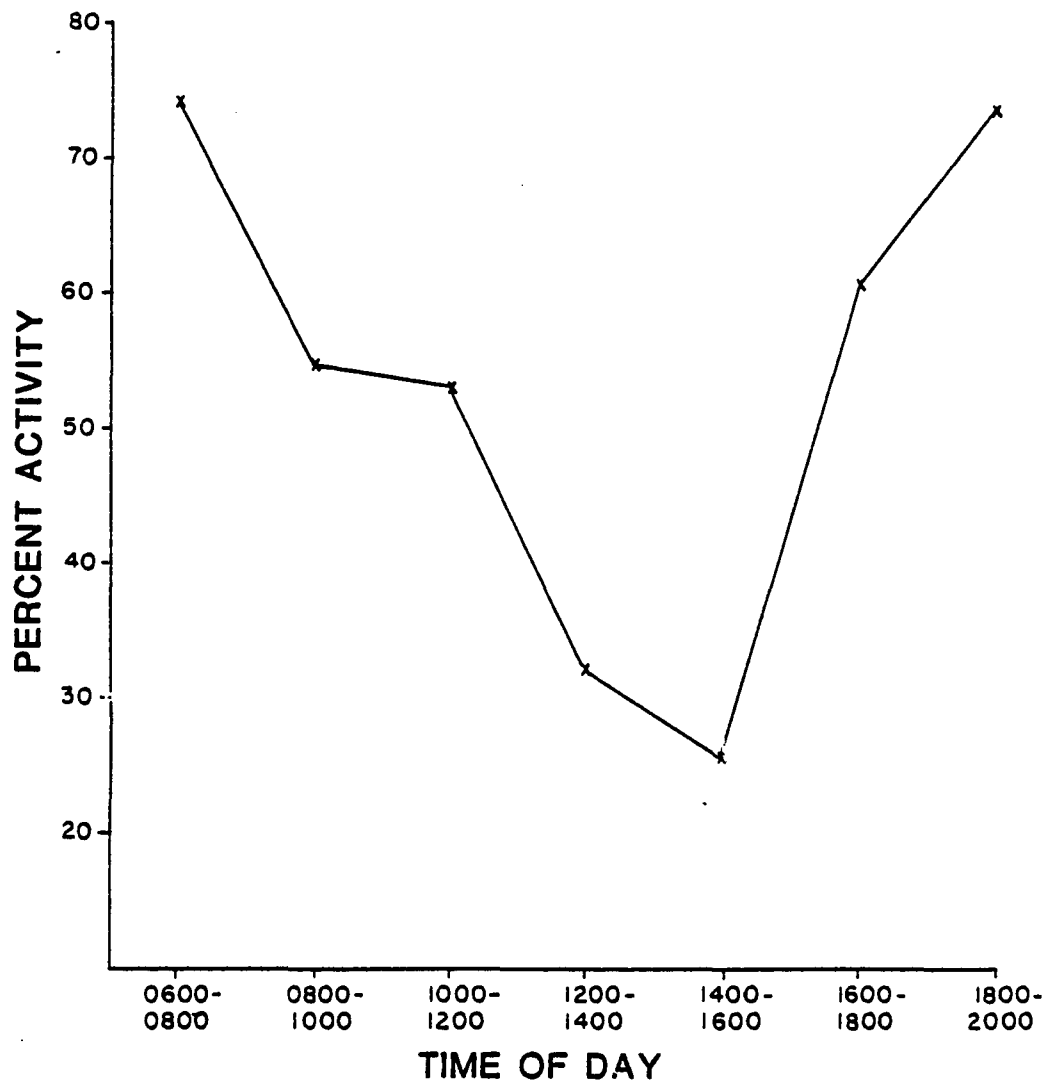


Figure 18. Average percent of each hour spent in activity during daylight hours.

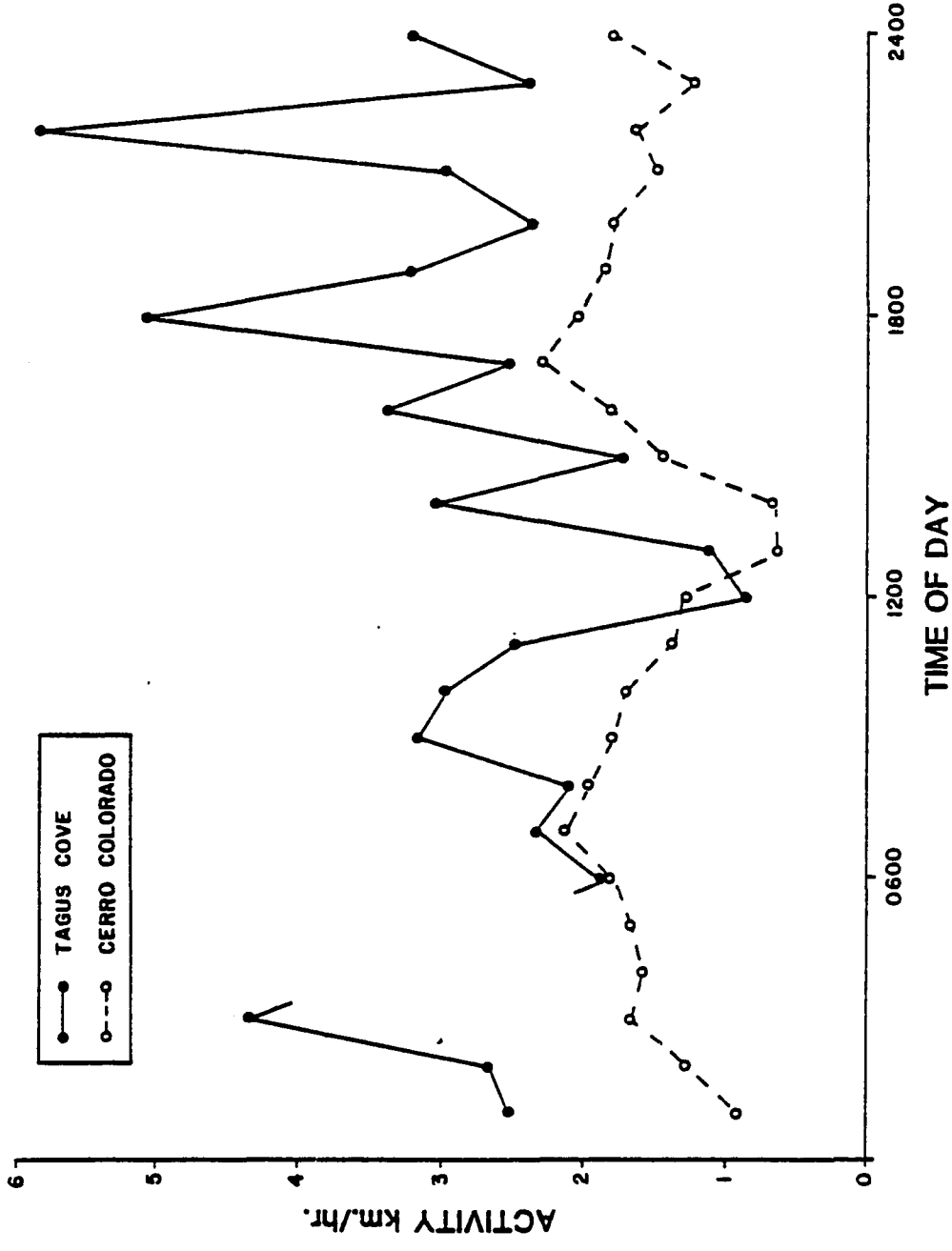


Figure 19. Average rates of activity (km hr^{-1}) during 24 hours at each study site.

was represented by a sample size of 25 to 80 data points. At Tagus Cove, with fewer total usable locations, each rate was represented by a sample size of 10 to 19 locations, and no usable data were available for 0400 and 0500 hrs. The general pattern of activity was roughly bimodal at both sites, with peaks of activity at Cerro Colorado at 0700 and 1700 hrs, just after sunrise and before sunset. The lowest rates of activity at Cerro Colorado occurred at 0100 and 1300 hrs. I believe the few obtainable data for Tagus Cove were responsible for the high variability there. The rates of activity at Tagus Cove were higher than at Cerro Colorado.

An attempt was made to assess the total daily energetic costs by adding the calculated energetic costs of locomotion and basal metabolism. I assumed that both males and females travelled at the same rate for each hour. The average daily cost of locomotion for females was estimated to be 142.2 kcal, while additional basal metabolic costs were 43.2 kcal, totalling 185.4 kcal. Average daily locomotion costs for males were found to be 183.9 kcal and basal costs 56 kcal for a total of 239.9 kcal per day. These values are remarkably close to the predicted daily costs for males and females of 215 kcal and 166 kcal respectively (Scott 1975).

Discussion

To date only one other study has extensively used radio telemetry to follow movements of free-ranging feral cats (Jones and Coman

1982b). However, the sample size in that study was only seven individuals and 499 total locations. Many studies examining the movements of carnivores used sample sizes of less than 10. In studying the movements and energetics of the fisher, Powell and Leonard (1983) gathered their data from a single female. Van Orsdol (1982) radio collared only a single female from each of his study prides of African lions. Even though lions are social, these data likely provide an incomplete or distorted picture of individual or pride movements. Zezulak and Schwab (1979) monitored seven individuals at each of their two study sites, the largest sample size of bobcat studies to date. I also had 14 individuals over a 13-month study period at two study sites. The number of radio locations for each individual varied from 20 to nearly 600, totalling nearly 2400 locations. Criticisms of radio telemetry calculations are often based on the period of observation required to estimate the asymptotic home range size, the point at which the home range will not increase substantially. Ables (1969) estimated that only 16 to 20 days were required to measure the home ranges of red fox. Although the number of locations and observation periods varied among radio collared individuals, only two cats had observation periods of less than 50 days. I believe these data are complete enough to clearly indicate the use of space by the cats.

In the Galapagos Islands male home ranges averaged about four times (3.71) larger than those calculated for females. In Australia Jones and Coman (1982b) also found that male home ranges were almost four times (3.65) larger than female ranges. Among other felids, male

tigers had ranges that averaged slightly more than three times the female average home range size (Sunquist 1981). For bobcats, Fritts and Sealander (1978) and Buie et al. (1979) found that male home ranges were between 2.0 and 2.5 times larger than females, but Zezulak and Schwab (1979), working in the arid Mojave Desert, found no intersexual differences in home range size. Larger male home ranges may be due, in part, to a need to maintain reproductive access to females, and to differences in energy requirements. Among the solitary felids, male home ranges typically overlap those of several females (Seidensticker et al. 1973, Sunquist 1981). Thus males may more easily detect estrus among overlapped females and gain access to them before rival males.

Larger male body sizes and greater average daily energetic requirements may also mean that males need larger home ranges to meet these needs, but pregnant and lactating females have energy needs equalling or surpassing those of males (Chap. III). Females may still have smaller home ranges, however, because they appear to use their home ranges more intensively, take smaller, more numerous prey than males, and return to their den frequently during lactation (Fritts and Sealander 1978, Jones and Coman 1982b). Because females have smaller ranges they then should select areas of higher productivity to be able to forage successfully and return to the den frequently.

Two important factors that must be understood before comparing conspecific home ranges from two areas are resources and population density (Calhoun 1955). Scarce resources should expand home ranges and dense populations contract them. Lockie (1966) cautioned that home

range sizes should not be compared unless food resources are known. Van Orsdol (1982), after assessing habitat productivity, found that lion prides in poor areas had home ranges 1.8 times larger than prides in more productive areas. Zezulak and Schwab (1979) found that home range sizes were increased by more available patch types in one area than in another. Although Cerro Colorado appeared to be a more productive area than Tagus Cove, they had approximately equal densities of cats. It is possible that because Cerro Colorado is not isolated from surrounding areas transient individuals might have increased the instantaneous density and not be reflected in other density estimates. One might also expect, because of its greater productivity, the home ranges would have been smaller at Cerro Colorado; yet the opposite was found, producing more overlap in the Cerro Colorado ranges. Cerro Colorado, however, has more patch types than Tagus Cove. If cats found no food in one patch, they could switch to another patch in the expectation of foraging successfully there. This would tend to increase the individual home range sizes and also explain the greater degree of overlap found at Cerro Colorado.

At Cerro Colorado there were four distinct patch types: sandy plain, lava/shrub, grassy plain, and palo santo woodland. The patches of lowest use were the grassy plain and palo santo woodland. No measures of patch productivity were made but qualitatively these two patches appeared to be relatively depauperate in numbers of animal species. The sandy plain was used more frequently and appeared to be somewhat richer in numbers of animal species present. In addition, it

was a more open habitat and adjacent to the coast, giving cats access to the beach to search for fish carcasses or sally lightfoot crabs. The sandy plain was also used as a nesting ground by marine iguanas, and even though adult iguanas were probably rarely preyed upon, uprooted eggs and hatchling iguanas would be an attractive source of energy. The lava/shrub was the smallest but most heavily used patch. The terrain was relatively open but sufficiently uneven to provide cover while stalking prey. This also was the most diverse patch in terms of plant and animal species seen. On the other hand, Tagus Cove had only one patch type, a palo santo woodland. This poor quality and relatively uniform habitat probably resulted in a wide, relatively uniform distribution of prey.

The amount of home range that is used may change temporally or seasonally with prey availability and climate. Many temperate carnivores show seasonal changes in home range due to fluctuating food conditions (Lockie 1966, Woodruff 1977, Jones and Coman 1982b). In the Galapagos there are only two seasons, and although the temperatures do not change markedly, the fluctuating amounts of rainfall seem to affect the kinds and numbers of prey species present at any one time (Chap. III). The sizes of monthly home ranges might be expected to vary with prey availability. Monthly home ranges did vary in size but not substantially in shape or orientation. The two months with the smallest home ranges for male #2 (April and May) had the highest numbers of grasshoppers seen but very low bird and lizard apparency (Fig. 5). The consumption of grasshoppers was also higher during this time.

Because of differences in habitat composition and quality, there may also be differences in search patterns between study sites. In a productive habitat by crisscrossing the patch, cats may be able to encounter sufficient prey and still remain relatively close to their den or point of origin. In an unproductive habitat where encounter rates are lower, cats may be more successful by foraging in a direct line away from their starting point. If it were to then crisscross that path, the prey encounter probabilities would be even lower. In the Galapagos different foraging patterns existed between the study sites. At Cerro Colorado cats frequently crossed their foraging paths, while at Tagus Cove straight-line foraging occurred more often. This may also help to explain the concentration of activity at Cerro Colorado versus the more diffuse pattern seen at Tagus Cove.

In many highly organized communities the carnivores may be temporally partitioned into diurnal, nocturnal, or crepuscular species. These labels apply to periods of highest activity, because many of these species are still active but less so at other times. In areas where the number of competing carnivores is smaller, the preferred foraging periods for cats are at dawn and dusk (Woodruff 1977, Buie et al. 1979, Jones and Coman 1982b). At these times cats take advantage of lower light levels to approach prey more easily, cooler temperatures to reduce heat-associated metabolic costs, and increased prey availability. In the Galapagos the only other predators are snakes, dogs, and raptors, which do not compete with the cats for much of their diet. In addition, the snakes and hawks are diurnal,

while the dogs and owls are nocturnal. More prey species are active at dawn and dusk than at midday or the middle of the night. At midday the surface temperatures may exceed 54° C, and few species are active. At night very few potential prey are active. Rats, perhaps the most important prey item calorically, are active crepuscularly and nocturnally. The night would be an excellent time to hunt ground-resting sea birds, if they were an important element of the diet. There are no seasonal shifts in activity cycles, because the equatorial day length varies only three minutes annually.

Marked differences in rates of activity occurred between sites: at Tagus Cove virtually all recorded rates were higher than at Cerro Colorado. Since the home ranges are smaller and the activity rates are higher at Tagus Cove, this may indicate that the habitat there is poorer and cats must more actively hunt to satisfy their energy needs.

Little is known about the energetics of free-living carnivores. Van Orsdol (1982) made estimates of prey biomass and assumptions of consumption by African lions but made no effort to directly measure energy intake. Powell and Leonard (1983) tried to assess the energetics of pregnant and lactating fishers by radio telemetry of a single female. Although they had some movement data, they had no concomitant behavioral observations, prey capture data, or prey caloric content based on the female's actual diet. In my study I collected movement and behavioral data, and a posteriori I was able to estimate energy intake from fecal collections. With these data I compared theoretical requirements with intake. When the costs of locomotion

were added to predicted basal metabolic costs while inactive, the results were slightly higher (12%) for each sex than predicted from mass specific basal rates alone. If these estimates are accurate, the cats did not expend much extra energy in locomotion. The bouts of activity measured in percent of time active compared well with Kavanau's (1971) data which showed that domestic cats have activity bouts lasting from 5 to 40 minutes throughout the 24-hour cycle. Both he and I found that the highest rates of activity were recorded near dawn and dusk.

CHAPTER V CONCLUSIONS: BEHAVIOR AND SOCIAL ORGANIZATION

Methods

Field observations of cats were often fortuitous and coincidental. It was not possible to predict where a cat would be found or when. Each record consisted of the time the cat was first seen and the behavior at that time. When the behavior changed, the time and new behavior were recorded. In this way it was possible to describe not only the behavior of feral cats, but also the relative proportions of time invested in each activity. Because sightings were fortuitous, it was not possible to gather extensive behavioral data about specific individuals. All behavioral data were combined to provide a composite behavioral description for cats. In addition, it was difficult to observe individuals for more than half an hour, although occasionally cats were observed for periods of up to four hours. Cats were also found by "homing in" on their radio collars and then following them visually, but this was difficult to do for extended time periods without being detected. Virtually all observations of behavior were made during daylight hours. I did not have a night vision scope, and I believe that spotlighting cats disrupted their normal behavioral patterns.

Results

During normal activities while searching for prey or moving from one area to another, different cats frequently used the same path but at different times. Depending on the context, individuals may want to encounter or avoid conspecifics. It was unclear at what distance or by what means cats detected other cats; however, they frequently stopped, sniffed, and then headed to a specific landmark (i.e. cactus, rock, etc.) that had been used as a scentpost. Both males and females approached scentposts, sniffed them closely, and frequently made a flehmen, which is thought to enhance olfactory discrimination. Males and females did not always mark scentposts. In 72 observations males marked only 56 times, while females marked 16 times in 23 observations. On 12 occasions males were seen to sniff a scentpost and immediately retreat in the direction from which they had come. In marking scentposts males stood erect and directed a spray of urine posteriorly onto the scentpost, while females squatted and urinated on the base of the scentpost. Other olfactory cues might have been left in the feces. In 70% of the observations of defecation (29/42) a scrape or small mound was made onto which the feces were deposited, but no cats observed attempted to cover their feces.

Forty interactions were seen between individuals, totalling only six hours. Of these interactions, 34 occurred between males and 6 between males and females. No interactions were seen between females. Male-male interactions were very stereotyped. When two males met they

investigated each other olfactorily beginning with the nose and sequentially the cheeks, nape of the neck, back, and anal region. At this point the dominant individual began a low-pitched growl. In 27 encounters the dominant individual returned to the head of the subordinate and stood broadside to it. The dominant held a rigid posture of stiffly extended legs, raised tail and highly arched back, while continuing to make the vocalizations. In the remaining seven instances the dominant male began the low-pitched growl and then quickly struck a single blow to the head of the subordinate, simultaneously accompanied by a single high-pitched vocalization. The subordinate fell to the ground, although probably not from the force of the blow, and lay on its side with head and neck extended. The dominant individual stood across the head of the subordinate in the same highly arched posture. This position was usually held for about 30 seconds; the dominant individual departed first, followed 10-15 seconds later by the subordinate in the opposite direction.

At Cerro Colorado male #6 was dominant to all individuals it was seen to meet, while male # 2 was dominant to all individuals but #6. Not all combinations of individual interactions were seen, so a well-defined dominance hierarchy could not be detected. Too few male-male interactions were seen at Tagus Cove to establish any rank order.

Male-female interactions were typically unaggressive. The olfactory investigation was similar to that between males, although males paid more attention to the female's urogenital area than to a

male's. After this brief investigation the two usually parted without any dominance interaction. No attempts at copulation were seen; on three occasions females sat down during the male's anal inspection. Little other evidence of courtship behavior (i.e. allo-grooming, etc.) was observed.

A total behavioral budget was constructed from all the behavior observed during the study (Fig. 20). Locomotion occupied 12.75 hours of each day, by far the largest behavioral category. Sleeping (4.75 hrs) and resting (3.25 hrs) were distinguished by posture and the amount of time spent per bout. Sleeping was defined as a reclining posture and a bout length of greater than 30 minutes. Resting was defined as any other stationary posture with short bout lengths. These were separated because resting postures may have been part of a hunting bout. Grooming (2.0 hrs) was usually seen in bouts of less than 15 minutes. Prey handling included all activities of prey capture and consumption and averaged about 1 hour per day. Before the first strike was made, the behavior was termed locomotion. Social behavior occupied only 15 minutes per day and included social interactions, scent-marking, and other forms of communication.

Discussion

With the exception of the African lion all felines appear to be essentially solitary (Kleiman and Eisenberg 1973, Fox 1975, Leyhausen 1979). In a majority of feral cat studies to date the data indicate a

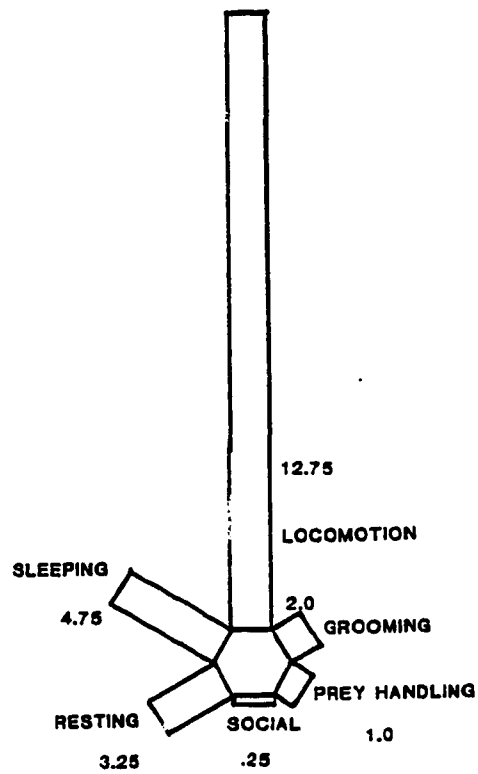


Figure 20. Daily behavioral budget of feral cat, per 24 hours invested in six behavioral categories.

well-organized social system with both relative and fixed dominance hierarchies (Leyhausen and Wolff 1959, Laundre 1977, MacDonald and Apps 1979, Leyhausen 1979, Panaman 1981). However, these studies were conducted around farmyards where cats received either food or shelter or both. Few data exist concerning the social organization of totally free-living feral cats. Jones and Coman (1982b) collected excellent food habit and reproductive data on free-living Australian feral cats, but they had little movement data and few visual observations from which to speculate about social organization. Although I had only 206.5 hours of direct observation, they represent the most abundant data available to date.

All felines studied to date use scentposts of one type or another (Lindemann 1953, Sunquist 1981). The use of scentposts by cats can provide a variety of information; several hypotheses have been proposed for their possible function (Johnson 1973). Scentposts may be used to avoid other cats and to accomplish some temporal spacing (Bailey 1974, Leyhausen 1979). The age and strength of the scent implies the time interval since last marking and the degree of caution to be exercised in further movement (Leyhausen and Wolff 1959). Although Leyhausen (1979) stated that no data exist to indicate that scentposts repel individuals, my data indicate the opposite. On several occasions animals were seen to sniff a scentpost and then observed to retreat immediately afterwards. Panaman (1981) reported that scent marking was observed most frequently during hunting bouts, as if to advertise that an area was being used. It is possible that scentposts could convey

information that would either increase or decrease the likelihood of encountering another cat. Males and females would advertise sex, reproductive condition, and time of mark (Eisenberg and Kleiman 1972, Ewer 1973, Seidensticker et al. 1973). Fecal scrapes may also contain individual information, although Wemmer and Scow (1977) stated that this is probably not long-range communication and may be as much visual as olfactory.

When two animals do encounter one another, individual identities and dominance need to be established. Leyhausen (1979) reported that male cats formed a "brotherhood." Entrance to the brotherhood was gained by combat, often severe fighting. Once admitted little or no further combat occurred and males became more tolerant of other males than females were of other females. In the Galapagos not only was there no evidence of a brotherhood of males, there was also no evidence of any fighting between males. None of the animals trapped, including older males, displayed the scarred nose or tattered ears of cats that had been involved in serious fighting. There were some highly stereotyped and ritualized interactions. Usually only one blow of little force was struck, with the males assuming dominant-subordinate positions. However, the posture of the dominant male was a combination of aggression and defensive threat, commonly seen in carnivores (Fox 1975). It would be counter-productive for males to engage in severe fights which may result in injury to either one or both and possibly decreased foraging ability. Identities and roles could be established more easily in less injurious ways.

Intersexual contacts were probably almost always sexually related (Kleiman and Eisenberg 1973). Males should attempt to establish the identity and reproductive condition of any female encountered and advertise his dominance. Males, who presumably overlap with several females, could monitor the sexual condition of each overlapped female in order to concentrate his activities in her home range when she comes into estrus. Contacts between females could have done much to elucidate their social and sexual organization, but none was observed.

The behavioral budget I obtained is substantially different from the obtained by Panaman (1981), but his data were collected around farmyards where food or food supplements were available. His cats spent nearly seven hours more per day (14.75 hrs to 8) sleeping and resting than did Galapagos cats. On the other hand, Galapagos cats spent three times as much time travelling, hunting, and handling prey. Farmyard cats spent 3 1/2 hours per day grooming, while Galapagos cats spent only 2 hours per day. On average the Galapagos cats spent only 15 minutes per day in socially related activities (i.e. scent marking, etc.); this category was not defined for farmyard cats. Without a certain and fairly rich source of energy Galapagos cats probably had to be active longer each day to acquire sufficient energy.

Based on the social data and those gathered on population characteristics, food habits, and movements, I believe that the social organization of Galapagos cats was slightly different in the two study sites. Both areas had a high adult to juvenile ratio, male dominant sex ratios, and approximately equal densities. The diet of cats in both areas is broad, with the same items appearing in the scats from

each area but in slightly different proportions, which may indicate preferences or availability. In both areas the prey were relatively mobile, not concentrated, and thereby probably undefendable. At both areas there was extensive predation and scavenging, although there were probably more scavenging opportunities at Tagus Cove due to the large sea bird colony. Estimates of energy from the diet indicate that cats face almost constant energetic stresses. This idea is further strengthened by the apparent conservative increases due to locomotion (12%). A qualitative appraisal of each site was that Cerro Colorado was probably a richer area than Tagus Cove. Tagus Cove was geologically isolated from surrounding areas, reducing dispersal. There were home range differences between the two sites as well. At Cerro Colorado the cats had larger home ranges, higher home range overlap, areas of simultaneous, concentrated use, and a daily foraging path usually crisscrossing and confined to a small area. At Tagus Cove the locations were more evenly distributed, and the foraging paths were generally straight-line.

These data suggest that the social order at Cerro Colorado was essentially a dominance hierarchy relative to feeding access with olfactory-mediated avoidance. At Tagus Cove a description of the land use system is much more difficult. Tagus Cove is relatively isolated, reducing if not preventing dispersal. The habitat was less productive than Cerro Colorado, but the home ranges were smaller and less overlapping. These data indicate that there is a higher degree of exclusive range use by cats at Tagus Cove, yet the energetic data

suggest that cats did not have sufficient extra energy for boundary patrol or defense. I believe that the land use system at Tagus Cove was more or less territorial mediated primarily by olfactory cues. Territoriality need not include defense or exclusion (Kaufmann 1983). In this unproductive habitat, as cats forage in a straight line, they spray mark an advertisement of recent passage. These spray marks serve to inform other cats of the individual who foraged in this area last and how recently. Cats encountering these spray marks do not continue farther because of the lower expectation of encountering prey rather than the chance of encountering the first cat. This is a similar situation to that reported by Kaufmann (1962) for coatis. A band of coatis foraging in the leaf litter had a more or less exclusive area because of the low expectation of a second band foraging successfully in the same area afterward.

APPENDIX 1. ANIMAL SPECIES SEEN AT CERRO COLORADO.

Arthropods

Galapagos grasshopper Schistocerca melanocera

Flightless grasshopper Halmenus spp.

Galapagos centipede Scolopendra galapagoensis

Galapagos scorpion fam. Centruridae

Sally-lightfoot crab Grapsus grapsus

Reptiles

Lava lizard Tropidurus spp.

Marine iguana Amblyrhynchus subcristatus

Gecko Gonotodes and Phyllodactylus

Galapagos snake Dromicus spp.

Sea turtle Chelonia mydas

Birds

Brown pelican Pelecanus occidentalis

Masked booby Sula dactylatra

Magnificent frigate bird Fregata magnificens

Red-billed tropic bird Phaethon aethreus

Birds continued

Brown noddy tern Anous stolidus
Swallow-tailed gull Cregrus furcatus
Galapagos gull Larus fuliginosus
Northern phalarope Lobipes lobalus
Semi-palmated plover Charadrius semipalmatus
Whimbrel Numenius phaeopus
Wandering tattler Heteroscelus incanum
Ruddy turnstone Arenaria interpres
Great blue heron Ardea herodias
Common egret Ardea alba
Lava heron Butorides sundevalli
Yellow-crowned night heron Nyctanassa violacea
Short-eared owl Asio flammeus
Dark-billed cuckoo Coccyzus melacoryphus
Galapagos dove Zenaida galapagoensis
Galapagos mockingbird Nesomimus parvulus
Yellow warbler Dendroica petechia
Broad-billed flycatcher Myiarchus magnirostris
Small ground finch Geospiza fuliginosa
Medium ground finch Geospiza fortis
Large ground finch Geospiza magnirostris
Cactus finch Geospiza scandens

Mammals

Sea lion Zalophus californicus

Galapagos fur seal Arctocephalus galapagoensis

Black rat Rattus rattus

House mouse Mus musculus

Goat Capra hircus

Burro Equus asinus

Dog Canis domestica

Cat Felis catus

APPENDIX 2. ANIMAL SPECIES SEEN AT TAGUS COVE.

Arthropods

Galapagos grasshopper Schistocerca melanocera

Galapagos centipede Scolopendra galapagoensis

Galapagos scorpion fam. Centruroidae

Sally-lightfoot crab Grapsus grapsus

Reptiles

Lava lizard Tropidurus spp.

Land iguana Conolophus cristatus

Marine iguana Amblyrhynchus subcristatus

Birds

Galapagos penguin Spheniscus mendicula

Flightless cormorant Phalacrocorax harrisi

Brown pelican Pelecanus occidentalis

Blue-footed booby Sula nebouxii

Brown noddy tern Anous stolidus

Swallow-tailed gull Creagrus furcatus

Galapagos gull Larus fuliginosus

Birds continued

Wandering tattler Heteroscelus incanum
Ruddy turnstone Arenaria interpres
Great blue heron Ardea herodias
Common egret Ardea alba
Lava heron Butorides sundevalli
Striated heron Butorides striatus
Yellow-crowned night heron Nyctanassa violacea
Galapagos hawk Buteo galapagoensis
Barn owl Tyto alba
Dark-billed cuckoo Coccyzus melacoryphus
Galapagos dove Zenaida galapagoensis
Galapagos martin Progne modesta
Galapagos mockingbird Nesomimus parvulus
Yellow warbler Dendroica petechia
Vermillion flycatcher Pyrocephalus rubinus
Broad-billed flycatcher Myiarchus magnirostris
Small ground finch Geospiza fuliginosa
Medium ground finch Geospiza fortis
Large ground finch Geospiza magnirostris
Cactus finch Geospiza scandens
Vegetarian finch Platyspiza crassirostris
Woodpecker finch Camarhynchus pallidus
Mangrove finch Camarhynchus heliobates

Mammals

Sea lion Zalophus californicus

Hoary bat Lasiurus cinereus

Black rat Rattus rattus

House cat Felis catus

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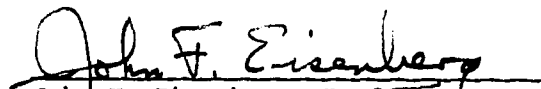
BIOGRAPHICAL SKETCH

Michael Konecny was born 11 July 1947 in Oskaloosa, Iowa. He attended high schools in Richland, Washington; Sierra Vista, Arizona; and Stuttgart, Germany. He attended the University of Arizona, where he majored in zoology and received a Bachelor of Science degree in 1969 and a Master of Science degree in 1975. In preparation for his field research he was licensed as a Naturalist Guide for the Galapagos National Park in 1977.

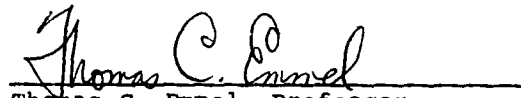
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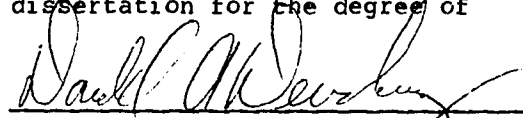
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Department of Zoology

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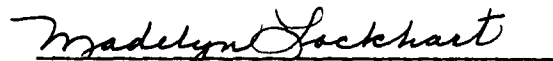

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