THE BEHAVIOURAL ECOLOGY OF THE MARA, *Dolichotis patagonum*

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This thesis presents the results of a 3 year field study on the behavioural ecology of the mara on the Valdés Peninsula in Argentina. The main goal was to investigate why the mara's social system incorporates both monogamy and communal denning, a combination unknown in other mammals. The research techniques used were behavioural observations and radio-tracking.

Radio-tracking of 9 maras revealed that pairs were continually moving into new areas, suggesting that their ranging behaviour is adapted to an irregular pattern of resource distribution. Two maras had prevailing ranges of 35 ha and moved yearly over about 200 ha. Ranges floated around a geographic centre. One constraint on the animals' movements may be the need to stay near a den site for pupping. Maras were diurnal, and spent on average 46% of the day grazing. Ranges may overlap up to 33%, but range use between neighbouring pairs were negatively correlated suggesting that animals were avoiding each other--pairs may be occupying floating territories.

Evidence that maras are monogamous in the wild is presented. The factors leading to monogamy are argued to be: (i) females are irregularly dispersed because of the distribution of food; and (ii) the brevity of the female's oestrus (1-2 hrs). A male attempting to mate polygynously would have difficulties in finding and securing a female; thus males may do best by staying with one female to ensure a successful mating. Males may enhance their reproductive success by watching for predators so that their females can spend more time feeding to meet the energetic demands of lactation and gestation.

During the pupping season, August to January, groups of 1 to 22 pairs gather at single dens. Several dens may be located near each other to form denning communities. Most pairs produce only one litter a year and there is a peak of births in September and October. Pairs visit the den once a day for a period of 5-6 weeks to nurse their young. Den sites are not limited; and the reason maras den communally appears to be the increased protection from predators accruing to pups and adults in larger groups.

Two possible routes are suggested in the evolution of the mara's social system: (i) from a monogamous starting point it has become advantageous to crêche pups; or (ii) ancestral maras were more colonial and probably polygynous, but have been forced to space out because of changes in the distribution of food, which has led to monogamy.

Finally, maras were compared with other caviomorph rodents, lagomorphs, and monogamous ruminants and were shown to be most similar to the latter in their adaptations to the environment--a remarkable example of convergent evolution.

To My Parents And Dolores

PAMPA

MADRE.
Horizonte.
Soledad.
Llanura franca al sol que sólo sabe de tu curva. Tú que nos das el orgullo de creernos un centro. Cuna, sepulcro y sustento. Creadora del gaucho afirmativo, del caballo amigo de la distancia, del puma escondido, y del chajá ascendente. Pretexto de vagabundas ansias de partir sin meta. Igualdad más invencible que la pendiente de la montaña limitada y que el abrazo sombrío de las selvas aisladoras. ¡Tú que das resignación al pequeño, empapado de infinito!

-- Ricardo Güiraldes

TABLE OF CONTENTS

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Chapter 1

INTRODUCTION

"The agouti [*sic*]....represents our hares. It differs, however, from that genus in many essential respects; for instance, it has only three toes behind. It is nearly twice the size, weighing from twenty to twenty-five pounds. The Agouti is a true friend of the desert; it is a common feature in the landscape to see two or three hopping quickly one after the other in a straight line across these wild plains."--C. Darwin, 1860.

"These little animals live in burrows, but are generally out feeding or sleeping in the grass during the day. They are excessively swift for perhaps a mile, but...soon get tired. The chase of these small deer [*sic*] afforded an agreeable relief to the monotony of the journey....they always were found in numbers where the pasture was good....It required considerable skill to bring them down with the bolas, as, if it only caught around the legs or body they disentangle themselves quickly..."--G. C. Musters, 1897.

Thus two of the early explorers of Patagonia, Charles Darwin and George C. Musters, described the mara, or Patagonian cavy. Maras (*Dolichotis patagonum*, Zimmermann, 1758) are large cursorial rodents of the desert plains and thorny bush of southern and central Argentina (see distribution map in Figure 1.1). The mara is a difficult species to describe: Darwin suggests that it is like a hare, and Musters describes it as a small deer. It is without doubt a curious species, incorporating features of both ungulates and lagomorphs while actually being a rodent. Also, as I will be showing in this thesis, amongst mammals it has an unusual, possibly unique, social system which incorporates monogamy with communal denning. As further discussed in the final chapter of this thesis, the mara is a good example of the convergence with ungulates of other

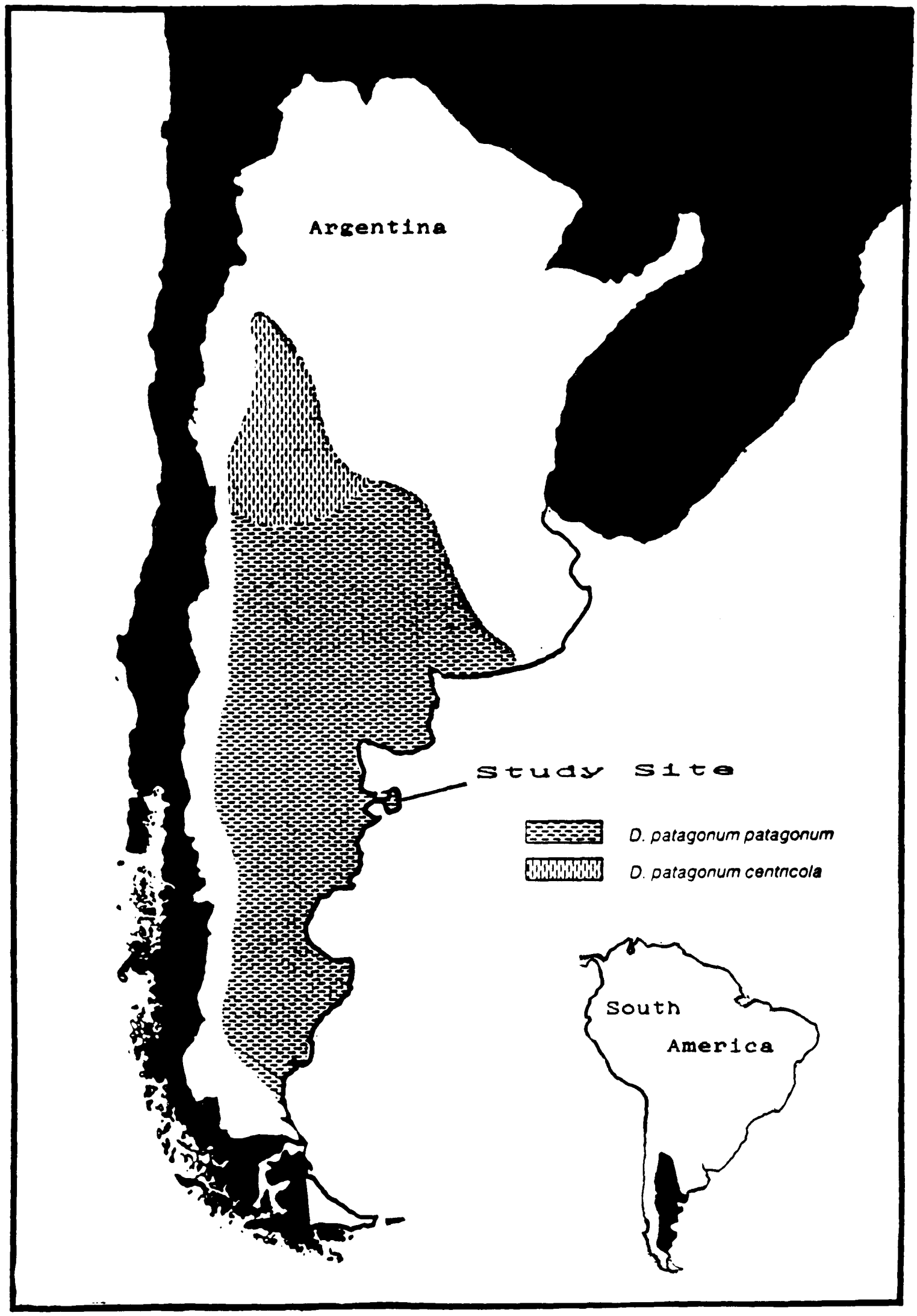


Figure 1.1.--Distribution map of the two subspecies of mara (genus: *Dolichotis*) in South America. Also shows my main study site on the Valdés Peninsula in Chubut Province, Argentina. Adapted from a figure in Yoffe (1983).

continents which some neotropic rodents have made in their evolution (see Dubost 1968, Simpson 1950, Eisenberg and McKay, 1974). Despite the relative ease with which the mara is observed in the wild, until now there has never been a major field study on this species. These features makes the mara a fascinating species to work on. In particular, it is an ideal species in which to investigate the environmental pressures leading to monogamy and group living in mammals, topics of considerable interest to behavioural ecologists today.

1.1 The Theoretical Basis for this Study

With the blending of ethology, ecology, and evolutionary biology over the past two decades, the field of behavioural ecology has become a particularly fertile area of zoological research. This has come about with the realization that the behaviour of an animal is, at least in part, genetically determined and therefore subject to the action of natural selection (as stressed by G.C. Williams, 1966). A number of theoretical ideas, which I review below, have paved the way for this flowering (also see reviews in Krebs and Davies, 1981; and Wilson, 1975).

Williams (1966) has shown that natural selection operates at the level of the individual. W.D. Hamilton (1964) and J. Maynard Smith (1964) developed the ideas of kin selection and inclusive fitness to explain altruism towards relatives (but see Grafen, 1984, on misunderstandings of these terms). Subsequently, Dawkins (1976) has further developed these ideas, convincingly arguing that selection ultimately operates at the level of the gene. Reciprocal altruism has been proposed by Trivers (1971) to explain why unrelated animals behave altruistically towards each other; he suggests that they

trade altruistic acts at different times. Game theory has been applied as a means of understanding conflicts between different animals (Maynard Smith and Price, 1973; and Axelrod and Hamilton, 1981). Maynard Smith (1976) has also developed the idea of the Evolutionary Stable Strategy, or ESS. The idea of parental investment and parent offspring conflict has increased our understanding of the relations between parents and offspring (Trivers, 1972 and 1974). Hamilton (1971) developed the 'selfish herd' theory which suggests that the risk of predation sometimes plays an important role in why animals live in groups. Optimality theory, as developed by MacArthur and Pianka (1966), has stimulated the construction of many testable hypotheses as to why animals behave the way they do. Also important has been MacArthur and Wilson's (1967) idea of r and K selection as two different strategies to enhance reproductive success. r selected populations, species, or individuals occur where the environment is unpredictable and there is a high population turnover with animals producing large numbers of offspring, few of which survive. K selection occurs in stable environments where few offspring are typically produced, but those which are have high survival. These ideas have created a rich framework for generating hypotheses in any modern field study.

Also important has been the development of the comparative approach, instigated by Crook's (1964) work on African weaver birds (Ploceinae) linking social organization with ecological factors such as food and predation. Crook showed that two types of sociality had developed in weaver birds: savannah dwelling species feed in large flocks on patchy but rich sources of grain, nest in colonies, and are polygynous; while forest dwelling species feed on dispersed insects of low abundance, nest singly on economically defendable territories, and are monogamous. Jarman (1974) has shown that body size, feeding strategies, and social organization are closely correlated in African antelopes.

INTRODUCTION

Comparisons of primates have shown a link between social organization, food, predation, range size, sexual dimorphism, and brain size (Crook and Gartlan, 1966; Clutton-Brock and Harvey, 1977, 1979, and 1980). Macdonald's (1983) work has emphasized the importance of resource dispersion on group size and patterns of space utilization in carnivores. In recent years a number of weaknesses have been pointed out in the comparative approach (see reviews in Jarman, 1982; and Clutton-Brock and Harvey, 1984).

These stepping stones in zoological thinking are not listed here merely as a recital of the high points in a modern textbook, rather they provide the theoretical framework within which behavioural ecologists approach theoretical problems today. As a result of these theoretical developments a species', or population's, social system are now viewed as the sum of the behavioural strategies of the individual as each tries to maximise its reproductive success (Gosling and Petrie, 1981). Ecological factors such as food, predators, and places to live determine the costs and benefits associated with particular strategies. Flexibility in social organization in response to environmental conditions depends on the genetic constraints fashioned by phylogenetic inertia and ecological pressures on an evolutionary time scale (Wilson, 1975). Recent studies (see review by Dunbar, 1982; also Monaghan and Metcalfe, 1985) have revealed large amounts of intraspecific variation in social systems demonstrating the importance of a flexible strategy for animals faced with a host of varying situations, not only across populations in different habitats but also within the lifetime of individuals.

One assumption behavioural ecologists often make is that animals are well adapted to their environment. For a species to be adapted to its environment means that its gene pool produces phenotypes which enhance the survival of individuals of that species relative to their survival in

different environments (Wilson, 1975). There are, however, problems with the adaptationist approach since explanations are often invented to fit the facts, and studies sometimes lack rigorous quantification of pertinent ecological factors (see Gould and Lewontin, 1979; and Clutton-Brock and Harvey, 1979). Further, with the increasing level of degradation in the natural environment as a result of human pressures, it is becoming increasingly difficult to measure, or even identify, the 'normal' selective pressures on a species. However, careful weighing of the facts, as admirably illustrated by Dawkins (1976), can help avoid many pitfalls.

One final point, numerous single species studies have been conducted in recent years which have developed and advanced the study of behavioural ecology. Examples of these are Kruuk's (1972) work on hyaenas, and Clutton-Brock et al's work on red deer (1982). It is very much in the vein of these works that this study was inspired.

1.2 What are Maras?

Maras are light bodied, long legged, and highly cursorial for rodents. The feet are compressed and rather hooflike, with three toes on the back feet and four on the front. Their powerful hind legs are longer than the front, which are geared more towards absorbing the shock of running. When fleeing from danger they can maintain a speed of 60 kmh or more for several hundred metres. In the wild, maras weigh between 7 and 9 kgs, though captive animals have reached a weight of 16 kgs, and measure between 50 and 77 cm in length (see Appendix A).

There are two subspecies of maras: *D. patagonum patagonum* and *D. p. centricola*. Based upon their distribution the subspecies investigated here was *D. p.*

patagonum (see Olrog and Lucero, 1981; and Figure 1.1). In the salt pans and scrub of the Chaco in Paraguay, Bolivia, and northern Argentina there is a closely related species called the salt desert cavy, *Dolichotis salinicola*, which is sometimes placed in the separate genus *Pediolagus*. The geographical distributions of the various species and subspecies are illustrated in Figure 1.1. In addition to the name mara, this species has also been called the Patagonian hare or Patagonian cavy. Throughout this thesis I have chosen to use 'mara' since it is in common usage in Argentina, is shorter than the others, and because it comes from the language of the Mapuche Indians--the inhabitants of the mara's range before the arrival of the Europeans.

Maras are members of the rodent family Caviidae, which also contains the guinea pigs, and are closely related to the capybara (*Hydrochoerus hyrdrochaeris*, family: Hydrochoeridae). These species are members of the suborder Caviomorpha which contains a number of families in South and Central America including the cavies (family: Caviidae), coypu (family: Myocastoridae), paca (family: Agoutidae), agouti (family: Dasyproctidae), and chinchillas (family: Chinchillidae). The caviomorph rodents are remarkable for their extensive adaptive radiations, frequently occupying niches more akin to those of ungulates than to those of most rodents (Dubost, 1968; Eisenberg and Mckay, 1974). This is conventionally considered as having arisen because South America has been an isolated island continent for long periods in its geological past (Simpson, 1950).

As stated above, no long term field project has ever been conducted on maras in the wild. There have, however, been a number of captive studies on the species. G. Dubost and H. Genest have produced an excellent ethological study on the mara's behaviour in captivity (Dubost and Genest, 1974; and Genest and Dubost 1974). They have compiled a complete ethogram of the species, suggested its morphological convergence with ungulates of Africa and Asia,

described the denning system where several pairs crêche their young together in one den site, and presented a range of data showing the strength of the mara's pair bond. Kirschofer (1960a, 1960b) has described the enurination behaviour of maras, and has made some speculations as to its social function. Mohr (1949) has described the behaviour of maras in captivity and commented on the distribution of different subspecies of maras in South America. In 1983, M.B. Kufner completed a survey of mara food habits and density in the northern part of its range (Kufner, 1983). Smythe (1970) has discussed the possible function of stotting in mara escape behaviour. Stotting is typically an ungulate behaviour associated with the approach of predators. Appendix D contains a copy of a paper on scent marking in maras based on the data I collected in 1981 (Taber and Macdonald, 1984). Relevant aspects of these papers will be discussed at appropriate places in subsequent chapters.

The most interesting observations about maras to come out of these previous studies are the monogamous nature of their social system, and communal denning. Monogamy is rare in mammals; and, in one recent paper, Kleiman (1977) reported that only 3% of the mammal species studied have this social system (see Chapter 4). Further, the combination of monogamy with communal denning has not been reported in other species of mammals. Interestingly, some of the small ruminants with which mara's converge morphologically are monogamous as well. Communal denning also sparked our interest since it raises questions about the possible role of kin selection and reciprocal altruism in cooperation between pairs sharing a den, both topics of considerable interest in behavioural studies (see above).

1.3 Objectives of the Thesis

The dearth of information on the mara's ecology and behaviour in the wild has made my research difficult since, in addition to answering specific questions about the mara's behavioural ecology, it was necessary to collect data on the species general ecology and life history within which to interpret the results of my main field work. In broad terms the project goals were to describe and interpret the behaviour of the mara within an ecological and evolutionary framework. In particular, I hoped to answer the following two questions about the mara's social organization:

1. Why are maras monogamous?
2. Why do maras den communally?

With the answers to these questions, I then hoped to compare the behavioural adaptations of maras with those of other rodents, and the morphologically similar but genotypically distinct hares and antelopes of other continents, as a means of furthering our understanding of the evolution of monogamy and group living in mammals.

Chapter Outline and Comments on the Approach Taken

The material covered in each chapter are outlined below:

Chapter 2: Study Site and Methods. The main study sites are described, as are procedures employed in animal capture, data collection, and data analysis.

Chapter 3: Spatial Organization and General Ecology. Results covering the main features of the mara's ecology are

presented. In particular, the results of intensive radio-tracking of nine radio-collared maras are used to provide a picture of the mara's spatial organization and ranging patterns relative to the movements of other maras, and habitat features. This chapter provides the ecological framework within which the results on the pair-bond and communal denning can be viewed.

Chapter 4: The Ecology of the Pair Bond. Results on the behavioural relationship between pair-bonded maras are presented. I then use these data to evaluate the validity of various hypotheses as to why maras have adopted a monogamous social system.

Chapter 5: Communal Denning. Firstly, data from this study and the literature are used to describe the mara's breeding biology covering such aspects as the length of the gestation and lactation periods, and breeding seasonality. Then, results are given on the ecology of communal denning, in particular, how many animals used each den, and what environmental features are associated with dens with different size memberships. Next, the nature of parental care of the young, the relations between adults at the den, and the relations between pups and adults are described. Presenting the results in this order provides the building blocks for understanding the communal denning system. At the chapter's end a range of hypotheses to explain why maras den communally are evaluated.

Chapter 6: Final Discussion. In this final chapter I discuss two topics. (i) I summarize the main features of the mara's ecology and behaviour reviewed in this thesis, as well as the environmental and physiological constraints on the species, as a mean of creating a synthesis of the mara's behavioural ecology. Then, (ii) the behavioural and ecological

adaptations of maras are briefly compared with those of other groups of mammals including other species of caviomorph rodents, ruminants, and lagomorphs.

As is apparent from the above, I have covered a lot of ground in this thesis. I have had to cast the net widely so as to provide a sufficient ecological background against which to interpret the behavioural results. It has always been my aim to gather data specifically relevant to my central questions. However, with hindsight some of the material covered here has turned out to be tangential to my main argument. However, at the outset, starting from scratch so far as this species was concerned, these topics might have proved vital. I include them here for the sake of completeness, and hope that some of these data prove of value in further investigations.

Chapter 2

STUDY AREA AND METHODS

2.1 Study Area

This study was conducted on the Valdés Peninsula, in the northeastern part of the Argentine Province of Chubut. Chubut forms part of Patagonia; the monotonous scrubby plain which stretches in every direction for 100's of kilometers at the southern tip of South America. It is a powerful environment, breathtaking in the way the empty plains lead the eye beyond the horizon. Charles Darwin was greatly affected by Patagonia, and wrote the following about it:

> "These plains...can be described only by negative characteristics; without habitations, without water, without trees, without mountains, they support merely a few dwarf plants....The plains of Patagonia are boundless, for they are scarcely passable and hence unknown: they bear the stamp of having lasted, as they are now, for ages, and there appears no limit to their duration through future time."--From: The Voyage of the Beagle (1860)

Patagonia was not settled by white men until the end of the last century, and the power of the great empty landscape remains much the same as in Darwin's day.

The Valdés Peninsula is located between 42° 5' and 42° 53' South, and 63° 35' and 65° 4' W. In total it covers an area of approximately 4000 km^2. It is sparsely inhabited; has about 50 sheep ranches, or Estancias as they are called, and one small town with a population of 150 people called Puerto Pirámides. The economy of the area is based on sheep ranching, and virtually every part of the Peninsula is grazed by sheep.

Besides the mara, the other large terrestrial mammals of the Peninsula are the guanaco (*Lama guanicoe*),

STUDY AREA AND METHODS

Patagonian gray fox (*Dusicyon griseus*), Geoffroys cat (*Felis geoffroyi*), and armadillos (*Chaetophractus villosus* and *Zaedyus pichiy*). Of the mara's caviomorph relatives the following are present: *Galea musteloides*, *Microcavia australis*, and *Ctenomys mendocinus*. It also has large populations of Darwin's Rhea (*Pterocnemia pennata*) and elegant crested tinamous (*Eudromia elegans*). Historically there were such large predators as puma (*Felis concolor*) and Patagonian red fox (*Dusicyon culpaeus*); but, since they prey on sheep, these species have been hunted out by the ranchers.

At a latitude of 42° S, daylength on the Peninsula varies during the year from 9:04 hrs to 15:17 hrs (see Figure 2.1). Below I describe the vegetational, geological. and climatic characteristics of the Valdés Peninsula. Most of this information comes from Rostagno (1981), Beltramone (1981), and Bertiller et al (1981).

Geology

The basic landform of the Peninsula, like much of Patagonia, is a slightly rolling plain interrupted by periodic depressions. These depressions can be quite deep: the Gran Salina, 40 m below sea level, is the lowest point in South America. They often are poorly drained so rain water stays in the dips for months at a time, forming temporary lagoons. In some of the larger depressions enormous salt pans have formed measuring 10's of km^2. Geologically the Peninsula is formed of marine sediments from the Oligocene and Miocene. On top of these sediments there is a gravel substrate, covered in most places by a sandy alluvial deposit. In some places this sandy deposit has been swept away by the wind leaving only a coating of gravel; in other areas there are dunes of substantial size.

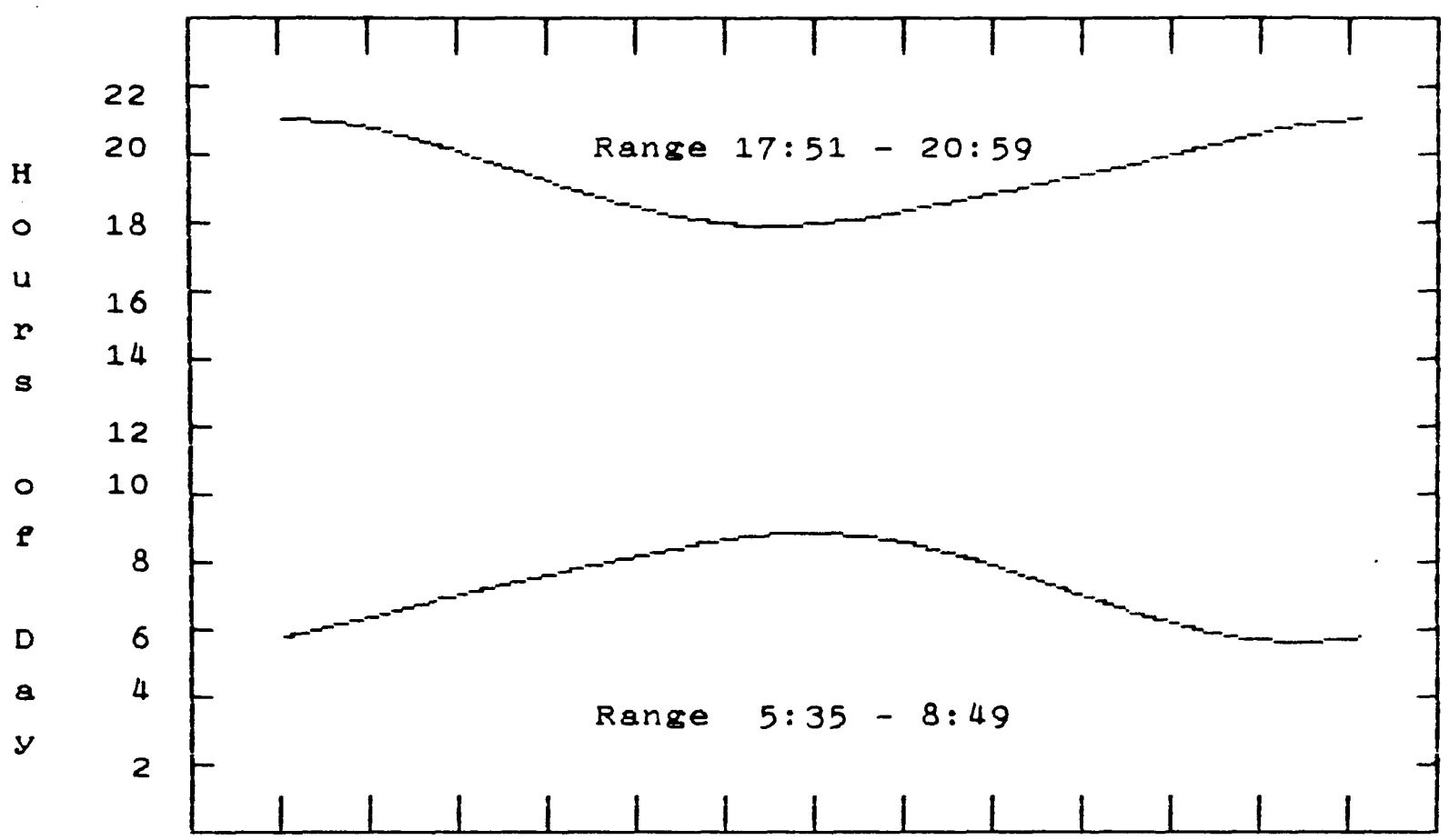


Figure 2.1.--The yearly fluctuation of sunrise and sunset times on the Valdés Peninsula. Day length varies from 9:04 hrs to 15:17 hrs during the year. The sunrise and sunset times were calculated using Program SUNRISEC (Barkstrom, 1981).

STUDY AREA AND METHODS

There are no streams or rivers on the Peninsula, and the water stored in the lagoons has a high salt content. Windmills are used to pump up ground water for the sheep, but this water is too salty for humans to drink. The main source of water for human consumption is rain water, channeled from the roofs of houses into cisterns.

Climate

The weather data on which this account is based were collected at two sites on the Peninsula: Punta Delgada and the headquarters of Estancia La Adela (Rostagno, 1981). The annual fluctuation in mean monthly temperature is shown in Figure 2.2. In February, the warmest month, the mean temperature is 17.4 degrees C°. On an average of 12.4 days a year the temperature drops below freezing.

Annual rainfall averages 246 mm, and evapotranspiration averages 680 mm; thus, following the UNESCO classification (precipitation / evapotranspiration > 0.20 and < 0.50), the Peninsula is classified as semi-arid. Annual precipitation on the coast is 175 mm, while inland it ranges from 200 to 225 mm. The Peninsula has a wetter and warmer climate than areas further inland. The water balance for the Peninsula is shown in Figure 2.3. In 11 months of the year there is a water deficit; solely in July is there a water surplus. Only a small amount of rain falls between October and March. Summer, December to February, is the driest season with 34.8 mm of precipitation, which is only 13.9% of the yearly total. Evapotranspiration is also highest in the summer where there is an average loss of 240 mm of water. There is considerable inter-annual variation in precipitation: in 1957 there were 457 mm of rain, while in 1945 there were only 94 mm. In 1983, the only study year for which I have data, the total rain fall at Estancia La

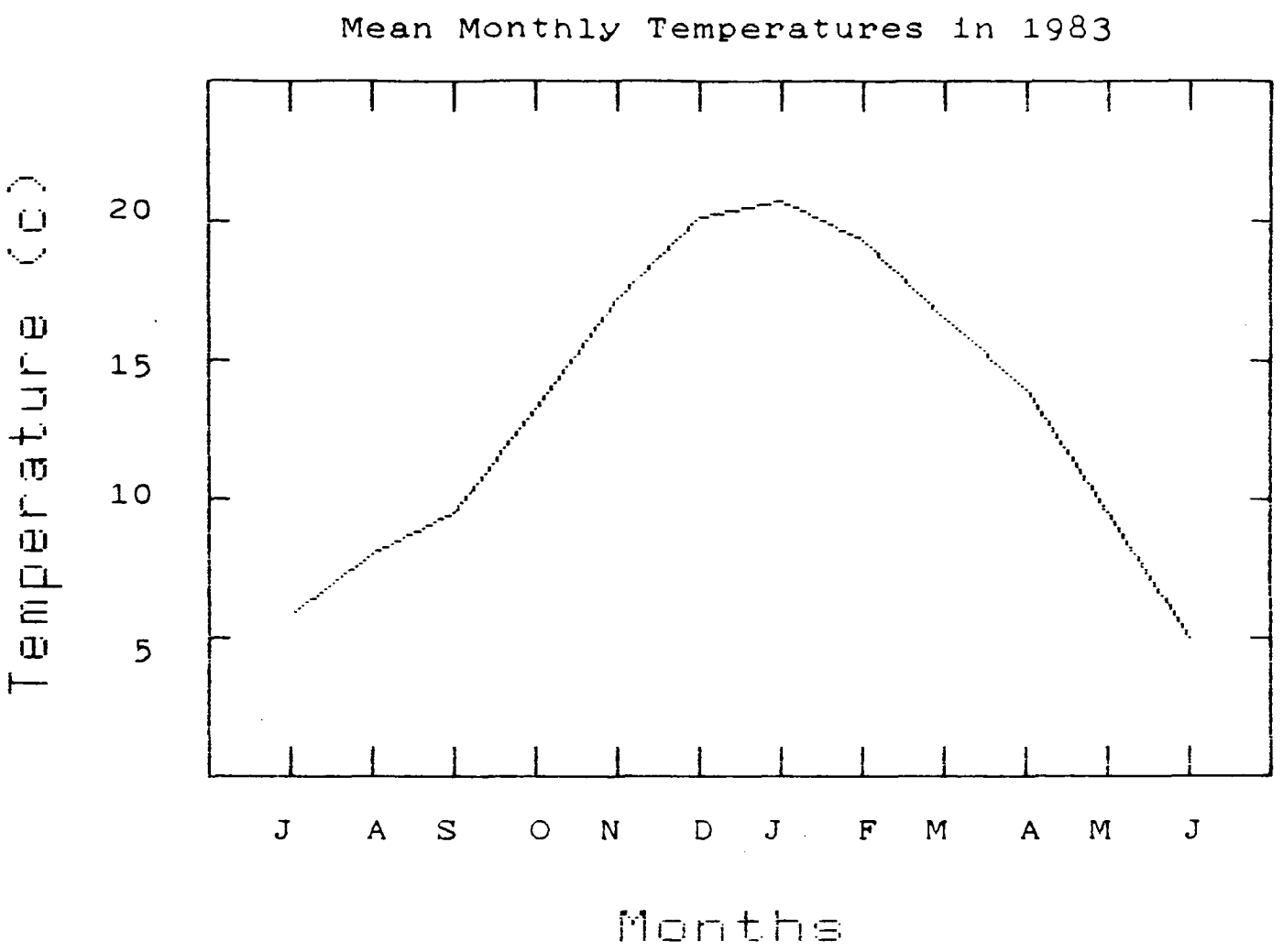
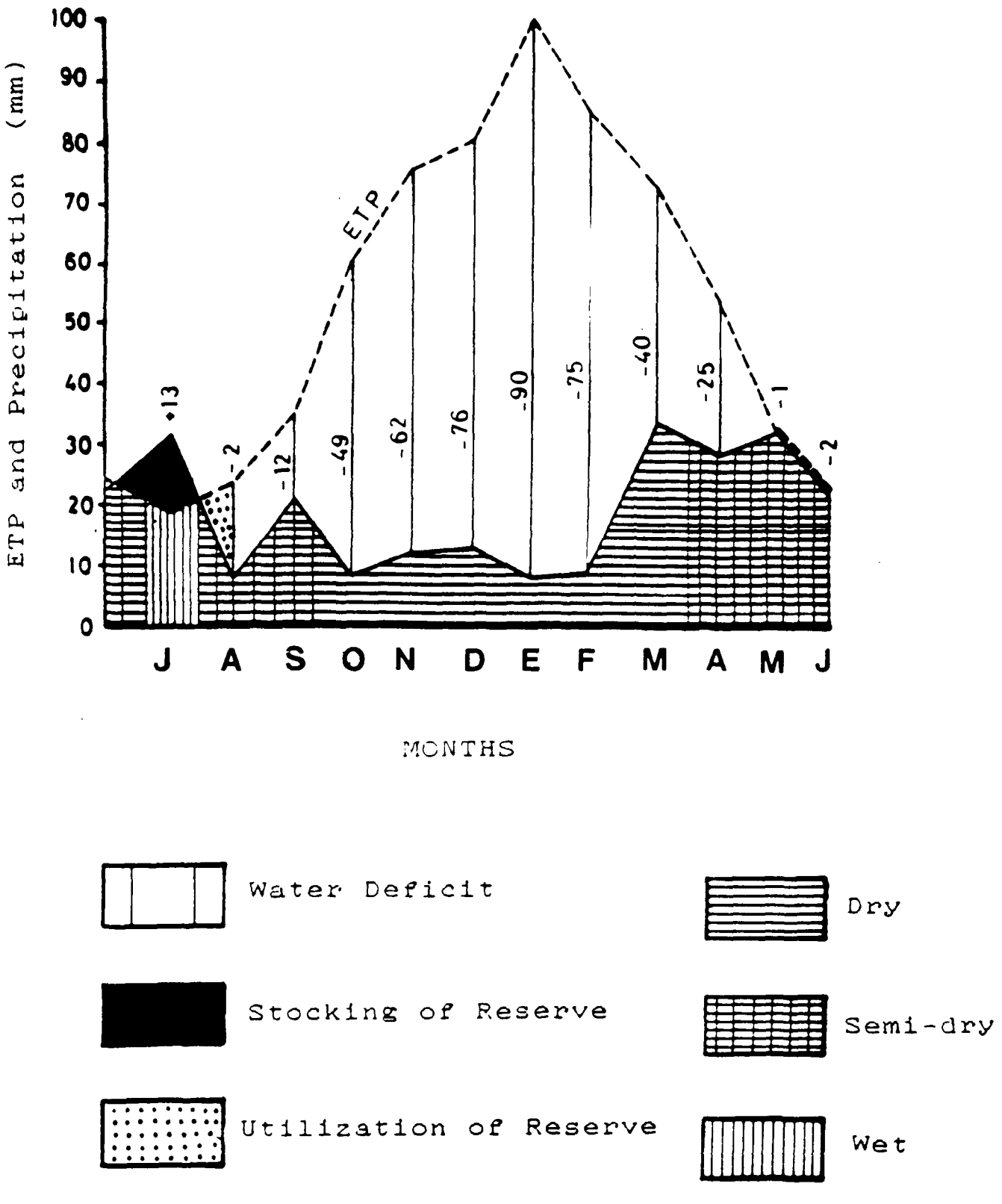


Figure 2.2.--The fluctuation of median daily temperature during 1983. Temperature data comes from Puerto Madryn; courtesy of the Centro Nacional Patagónico, Consejo Nacional de Investigaciones Cientificas y Técnicas, Secretaria de Estado de Ciencia y Tecnologia, Puerto Madryn, Argentina.

Figure 2.3.--Water balance on the Valdés Peninsula. Data comes from the Estación Punta Delgada. The map illustrates the following: (i) July is the only wet month where the water store on the Peninsula increases; (ii) June, August, September, April, and May are semi-dry; and (iii) October, November, December, January, February, and March are dry. Figure modified from one in Rostagno (1981). ETP = Evapotranspiration.



Adela was 356.5 mm. This was more than normal, but virtually all the rain fell (see Figure 2.4) in the fall and winter, making spring particularly dry (22 mm in these months compared to the normal 51 mm). Relative humidity varies only slightly during the year: the mean is 67%, with a minimum of 62% in December, and a maximum of 73% in June and July.

On the coast (my study sites were 5 to 20 km inland) the wind comes predominately from the S and SW. Monthly mean wind speeds vary from 14 to 20 kmh, with winds of up to 60 or 80 kmh not uncommon! The situation on the Peninsula fulfills well the adage that one does not need to travel in Patagonia to see it, as sooner or later most of it will blow past where one is staying. The air is almost continually filled with dust, and the constant winds can make walking uncomfortable.

On the basis of the climate data the seasons are defined as follows (see Figure 2.3):

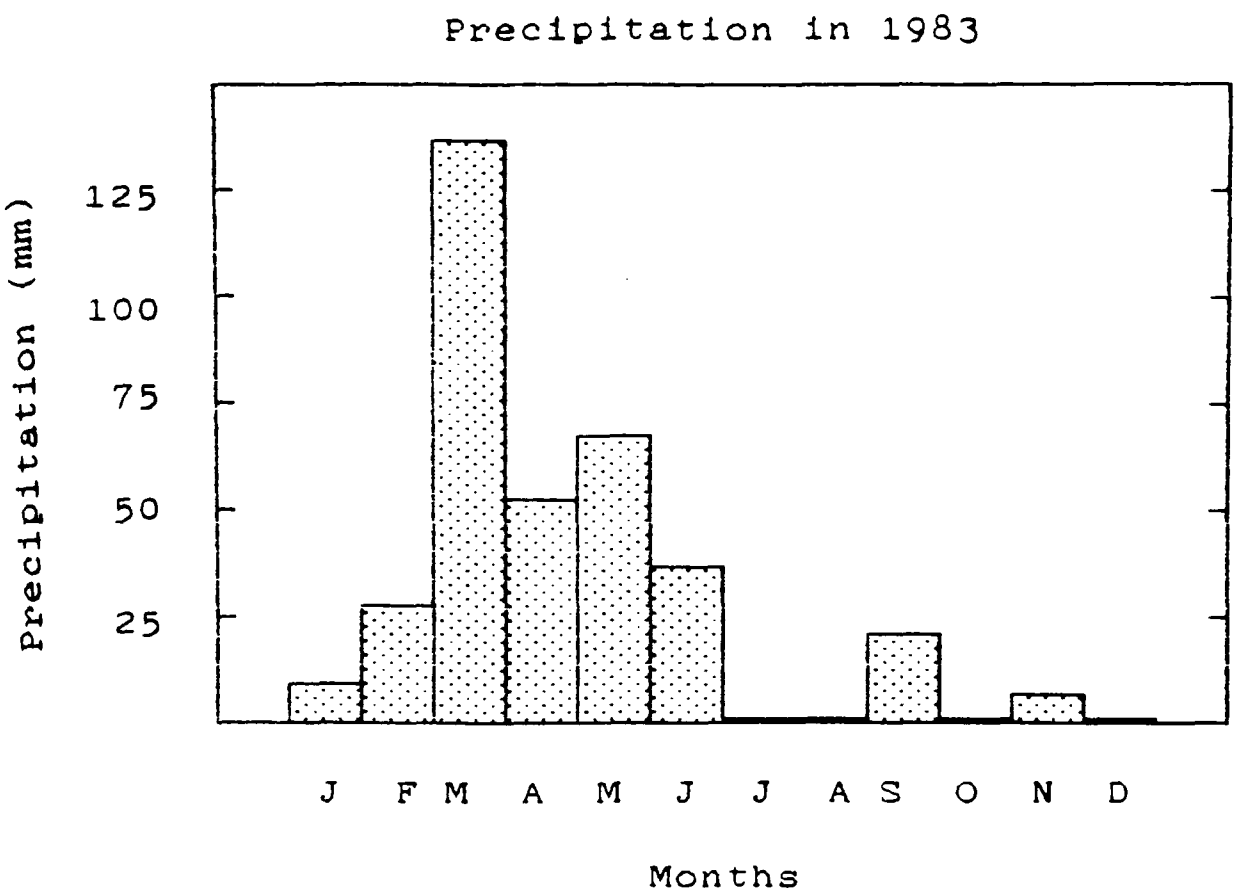
Winter	June through August--the wettest months
Spring	September through November
Summer	December through February--the driest months
Fall	March through May

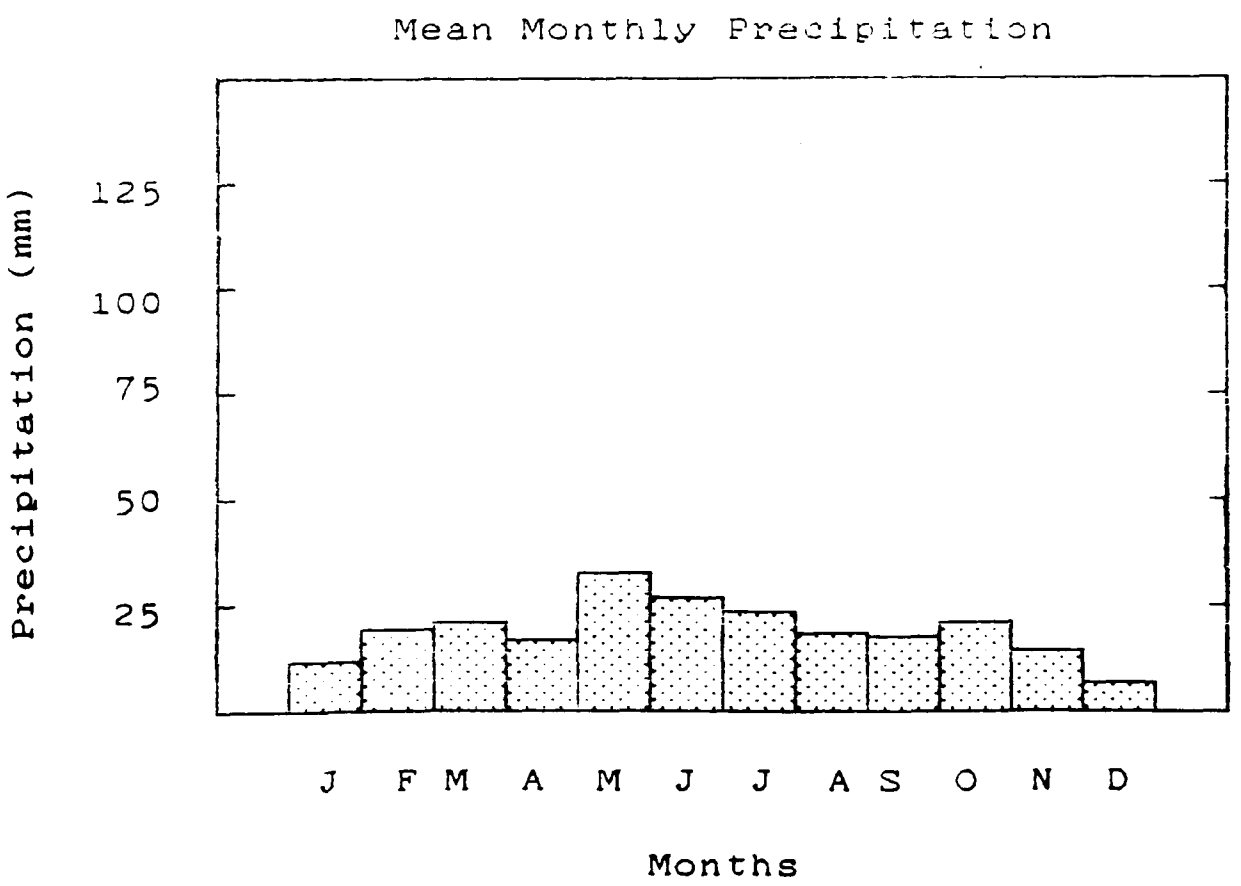
Vegetation

The vegetation of the study area has been classified as being in the Patagonian Province, subdistrict Chubutense (Bertiller et al., 1981). An area on the southern edge of the Peninsula is vegetatively classified as being in the Monte Province. The general vegetation pattern is one of a scrubby, almost uniform steppe. The scrub is waist to shoulder high with a 1 or 2 meter spacing between bushes. In this space, depending on soil conditions, grow varying amounts of grass and herbs. In areas protected from

Figure 2.4 (Overleaf).

Histograms of the amount of precipitation at Estancia La Adela in 1983 (A) and overall (B) in the different months of the year. Note that in 1983 the rain came much earlier than usual, and that there was almost no rain after June. The 1983 data is courtesy of Sr. H. Sanz (Estancia La Adela), and the overall data comes from Rostagno (1981).


Precipitation in 1983
Precipitation (mm)
125
100
75
50
25
J F M A M J J A S O N D
Months


Mean Monthly Precipitation
Precipitation (mm)
125
100
75
50
25
J F M A M J J A S O N D
Months

the wind, and with better soils, there are large open grassy patches. See Chapter 3 (Table 3.6) for a listing of the plant species encountered in the different study areas. The main vegetation types, as classified by Bertiller et al (*Op. cit.*), on the Peninsula are:

- Steppe dominated by *Chuquiraga avellanedae*
- Stepped dominated by *Chuquiraga hystrix*
- Stepped dominated by *Chuquiraga erinacea*
- Steppe dominated by *Larrea divaricata*
- Grass lands dominated by *Sporobolus rigens* and *Stipa tenuis*

2.1.1 The Individual Study Areas

I used three different study areas on the Peninsula: Estancia Larreburu, Puesto El Salitral, and Puesto La Blanca. Estancia refers to a self contained ranch under one management, where as Puesto refers to an outlying shepherds house used where an Estancia covers too much ground to be administered from one place. Table 2.1 summarizes the length of time each area was used, and Figure 2.5 shows their geographical locations. Each study area is described below:

Estancia Larreburu

This was the area I used during my first field season in 1981. The study site was contained within an Estancia owned by Sr. Larreburu (Puerto Madryn, Chubut). I worked mostly in the area on one side of a large lagoon; and had a subsidiary site 2 km away around an outlying corral and windmill in the scrub (see Figure 2.6 A). After my first field season the Estancia was sold, and I was forced to move

Table 2.1.--Summary of periods observations were made at each study site through out the research period. X's mark months where I collected data at the study site; C's mark months where C. Garcia made spot radio fixes on animals at Puesto la Blanca

Month	Estancia Larreburu	Puesto La Blanca	Puesto El Salitral
1981			
July	X		
August	X		
September	X		
October	X		
November	X		
1983			
February		X	
March		X	
April		X	
May		X	X
June		X	X
July		X	X
August		X	X
September		X	X
October	X	X	X
November	X	X	X
December		X	X
1984			
January		X	
February		C	
March		C	
April		C	
May		C	
June			
July			
August		X	X
September		X	X
October	X	X	X
November		X	X

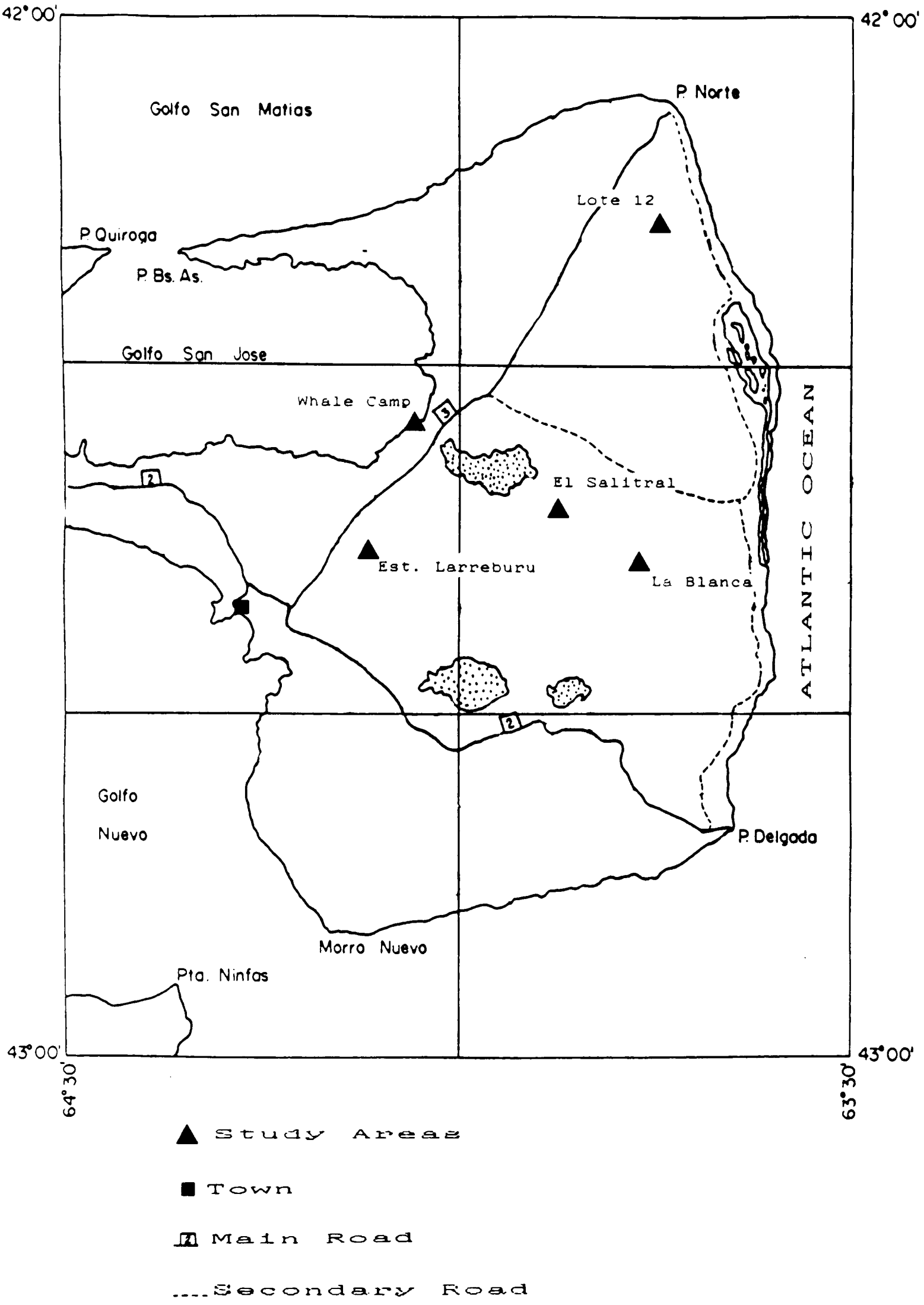


Figure 2.5.--Map of the Valdés Peninsula showing the various study sites used in 1981, 1983, and 1984.

Figure 2.6 (Overleaf).

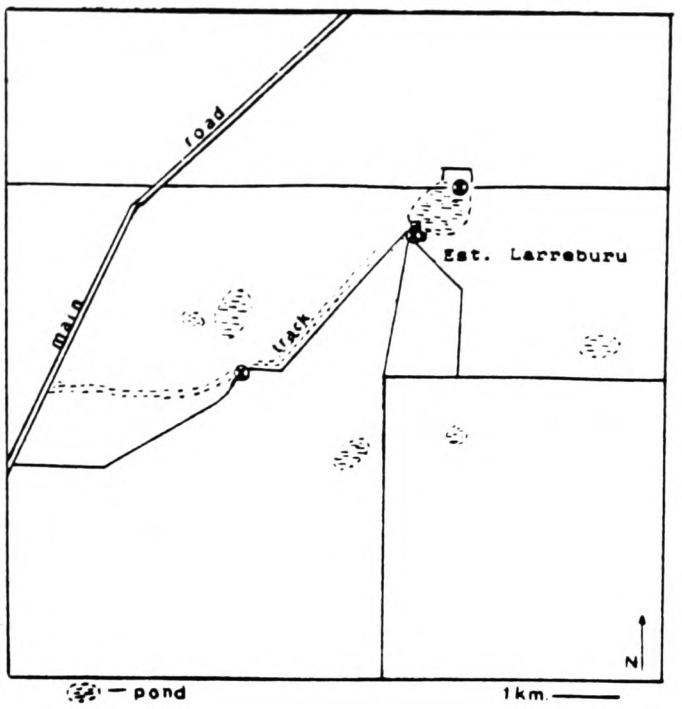
Maps of the three main study sites used on the Valdés Peninsula.

A. Estancia Larreburu

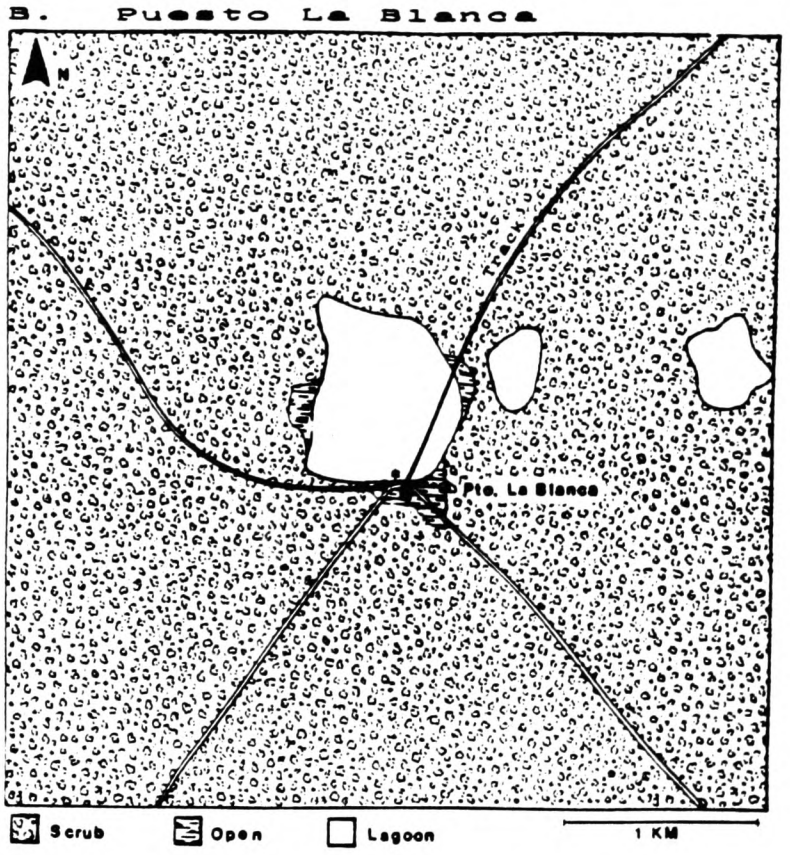
B. Puesto La Blanca

C. Puesto El Salitral

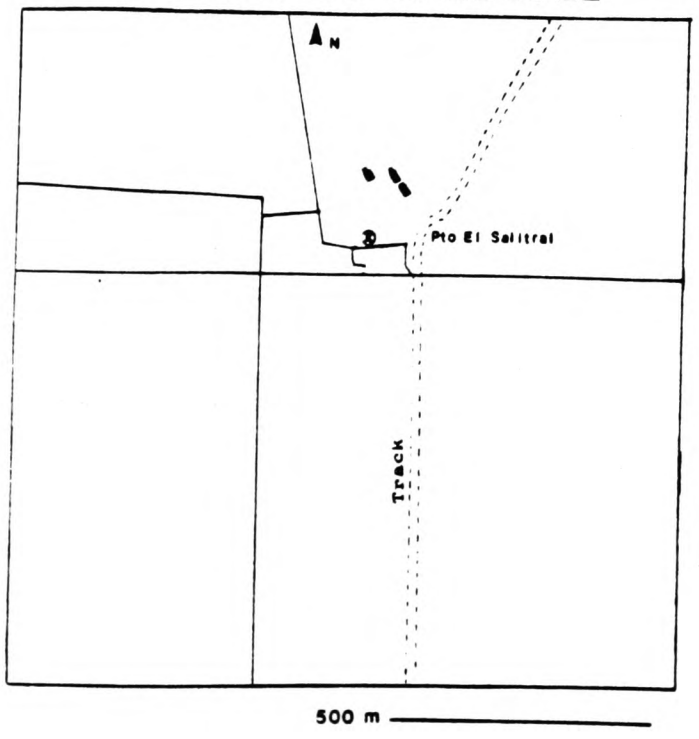
A. Estancia Larreburu



B. Puesto La Blanca



C. Puesto El Salitral



to another site in subsequent years. Estancia Larreburu is in the *Chuquiraga avellanedae* dominated habitat type.

Puesto La Blanca

This was my main study area during the 1983 and 1984 field trips. It is situated around a Puesto which forms part of the Estancia La Adela. This Estancia belongs to Sr. Ferro (Puerto Pirámides, Chubut Province) and is the largest on the Valdés Peninsula, measuring over 100,000 ha and having about 40,000 sheep on it. Like at Estancia Larreburu, my main study area here was located on the edge of a large lagoon (see Figure 2.6 B). The main habitat here is the *Chuquiraga avellanedae* dominated type.

Puesto El Salitral

This puesto, also part of Estancia La Adela, is located about 8 km from Puesto La Blanca. It was my secondary study site during my last two field trips. Unlike the other areas, this site was not centered on a lagoon, but instead was located in a small grassy valley surrounded by *Chuquiraga erinacea* dominated scrub (see Figure 2.6 C).

Other Sites

Data were collected at several other sites on the Valdés Peninsula (see Figure 2.5): (i) 4 days were spent observing maras at Lote 12, (ii) four maras were captured and 1 day was spent watching at Puesto Centenario located

about 4 km from Puesto El Salitral, (iii) three days were spent watching maras at Punta Norte, and (iv) one day was spent watching maras near the ex New York Zoological Society Research Station on Golfo San Jose. In addition, observations were recorded opportunistically whenever maras were encountered when driving around the Peninsula.

2.2 Data Collection Methods

Three separate field trips were made (see Table 2.1): (i) July 20 through November 19 of 1981, (ii) 11 February 1983 to 19 January 1984, and 24 August 1984 through 23 November 1984. A total of 21 months were spent collecting data in the field. I arranged for Sr. Carlos Garcia to radio-track maras once a month during my absence from February to August of 1983. The mara pupping season is from mid-August to early January, so by spacing trips in this way I was able to cover most of three breeding seasons. The whole year spent in 1983/1984 was necessary to collect data on the mara's annual cycle of behaviour and reproduction. Periods between field trips were spent in Oxford, where I was able to do a substantial amount of preliminary data analysis.

2.2.1 Capturing and Marking Maras

Since the study was designed to investigate a range of aspects of the mara's behavioural ecology it was necessary to follow individual maras through time. One of the problems with studying this species is that very few animals had adequate natural marks to individually identify them. In 1981 I made no attempt to capture or mark maras so that they could be observed in as untroubled a state as possible--however, the amount of data that could be

collected in this way was limited. Also, part of the project goals were to look at long term movement patterns of individual maras through radio-tracking. Thus, it was necessary to capture individual maras, both to artificially mark them, and to place radio-collars. Below I discuss the capture and marking methods used.

Animal Capture Technique

Wire neck snares were used to capture maras. In 1983 heavy gauge wire snares were used, and in 1984 bicycle clip wire snares were used (A.A. Fenn Ltd., Redditch, Worcs.). In both cases, stops were placed on the snares to prevent them from fully closing and thus choking the animals. The use of this method for capturing foxes has been described in Newdick (1983) and Doncaster(1985). The method used in this study was similar. Snares were placed on fence lines at points where maras had previously hollowed out small dips under the fence to allow passage. The snares were attached to the fence wire so that they were held open over the mouth of the passage. Care had to be taken to make the snare hole big enough so that an animals head could easily pass through it, and small enough so that it would not get a foreleg through as well. This was not an ideal technique since a number of animals were hurt in the process: 6 had badly cut hind or front legs, of which 2 may have died as a result of the injuries sustained. It was felt that the bicycle wire snares were safer, and that some injuries could have been avoided if they had been used sooner.

While open, snares were checked every 4 to 5 hours (night and day) to reduce the amount of time a mara was constrained. On four occasions, while checking the traps, I was able to maneuver animals into entering the snares. Upon

capture, animals were held between the knees, pushed to the ground so they could not move, and a piece of cloth was placed over their eyes to calm them. In most cases, the animals were anesthetized with a 0.7 ml dose of Ketamine Hydrochloride. Animals were then weighed and measured (see Appendix A for summary), ear tagged, and either plastic-collared or radio-collared. Each of the captured animals were then assigned a three letter name, with the last letter of the name showing the animal's sex: 'M' for males and 'F' for females. All animals were released within 1 hr of capture.

Eartags of five different colours (Rototags, Dalton Supplies Ltd., Nettlebed, Oxon) were used to mark the maras. Using different coloured tags in various combinations of left ear, right ear, inside tag, and outside tag a unique pattern could be placed on each individual. The expanding plastic-collars were of the same pattern as designed by Fiona Guiness (Clutton-Brock et al., 1982; see Figure 2.7). Each collar had a unique pattern painted on it with ink (Wiederhold SG Screen Ink, RI-INK Supplies Ltd., Berkshire). These collars have the advantage that they can be placed on juvenile animals since they expand as the animal grows.

Radio-collars were riveted in place, and fitted so that 2 fingers could fit between the collar and the animal's neck. Radio-collars were manufactured both by the Department of Zoology, following a design by Macdonald and Amlaner (1980), and Biotrack Ltd. (Stoborough Croft, Wareham, Dorset). The radios broadcasted on 155 MHZ. Two different weights were used: 160 gms, which had a life of roughly a year; and 240 gms, which had a life of two years. In fact, the larger collars were probably too heavy to be effectively used on maras and I only put them on 2 individuals.

Figure 2.7 (Overleaf).

Portraits of marked maras illustrating the various marking techniques used.

Above A radio-collared mara.

Below A plastic-collared mara.

2.2.2 Data Collection Methodology

Three kinds of data were collected to investigate different aspects of mara behavioural ecology: 1) radio-tracking data to look at movement patterns in relation to habitat features and the movements of other maras; 2) instantaneous scans to look at general patterns of behaviour such as yearly and diurnal time budgets; and 3) den scans to record detailed observations of mara behaviour at the den. Maras were observed from hides located near den sites (Figure 2.8), from an automobile, or from the ground. Most observations were made at a distance of 30 to 500 m using 9 x 30 binoculars (Nikon), or a 22 x 60 spotting scope (Bushnell). At the larger distances animals were only observable through the spotting scope. In practice, animals readily acclimated to the automobile and hide, but were always difficult to approach on foot. The amount of time spent collecting each kind of data depended on the point in the mara's reproductive cycle. Table 2.2 shows how the research effort was divided doing two typical weeks, one during the breeding season, and the other outside the breeding season. Below, the three data collection methods are outlined.

General Scans

This method was used to collect data on general mara behaviour patterns. It is based on the instantaneous scan method outlined in Altman (1974). A data record was recorded exactly on the minute at a set interval on every visible mara. The factor limiting the inter-scan interval was the number of animals in view: when more than 20 animals were in sight it was only possible to record data at 30 minute intervals, while when 20 or fewer animals were in view scans were made at 15 minute intervals. This is because with 20

Figure 2.8 (Overleaf).

Photograph illustrating one of the hides used for observing maras at a den site.

Table 2.2.--Sample weekly work plans during and outside the breeding season.

Day of Week	During Breeding Season	Outside Breeding Season
Monday	Den Scans at La Blanca	Radio Track Mara ELF
Tuesday	Den Scans at La Blanca	Radio Track Mara SYF
Wednesday	Radio Track Mara PAM	Observe Maras on Lagoon
Thursday	Radio Track Mara TIF	Radio Track Mara ENF
Friday	Den Scans at El Salitral	Radio Track Mara PAM
Saturday	Den Scans at El Salitral	Vegetation Sampling
Sunday	Type Data into Computer, Rest	Type Data into Computer, Rest

or more animals it could take as long as 10 minutes to record all the animals, leaving too little time to prepare for the next scan. At each scan a range of data were collected on each animal including behaviour (see codes in Table 2.3), distance to nearest neighbour, animal's name and weather conditions (see Table 2.4 and Figure 2.9).

Den Scans

This method was designed to record observations around den sites during the pupping season. Data were entered directly into an HX20 Lap held computer using program EVREC (see Appendix B). This allowed a large amount of data to be recorded easily under difficult conditions since a lot of mara activity was constantly occurring around den sites. A range of data types were collected (see protocols in Table 2.5):

1. General scans, as above, were made every 30 minutes on every visible animal.
2. Pup scans, to record the behaviour of all visible pups at 10 minute intervals.
3. Den scans, to record the total number of adults and pups at the den, and general activity patterns, every 10 minutes.
4. Arrival and Departure times for all adults visiting the den.
5. Continuous focal pair sampling. One pair was intensively observed during their entire visit to the den. A data record was entered into the computer every time the animals in the focal pair changed what they were doing, or pups or other adults were reacting to them. This allowed a detailed time budget of activities

Table 2.3.--Behavioural categories used during this study. The categories are divided into two types, states and events, following Altman (1974). Descriptions are not given for self-explanatory behaviours. Many categories are similar to those given in Dubost and Genest (1974).

Category	Description
	STATES
AC	Active--animal not in sight, but changes in radio signal strength show animal is moving.
IN	Inactive--Animal not in sight, but steady signal strength suggest animal is inactive.
OO	Animal not in view.
LI	Lying on ground (sphynx posture).
RN	Running.
WK	Walking.
TR	Trotting.
SD	Standing.
ST	Sitting.
OT	Stotting--stiff legged gait used under a variety of circumstances. In maras may have two functions (neither properly tested): (i) distraction display to draw predator away from den, and (ii) advertisement of fitness.

Table 2.3--Continued

Category	Description
	EVENTS
GZ	Grazing.
BR	Browsing--animal feeding on scrub vegetation.
RT	Rooting--pawing at ground while eating.
DR	Drinking.
ZZ	Zig Zag Display--male moves body in a figure of eight pattern in front of a female. A display used when pairs are in close (<30 m) proximity to each other.
AA	Aggressive Approach--One male runs towards another at beginning of aggressive interaction between two males.
MS	Mince Step--kind of aggressive approach; male trotts, almost on tip toes, towards another male.
BT	Bite--adult bites another; usually on the rump, side of the face, or neck.
CH	Chase--one mara chases another at a run.
LS	Low-Neck-Stretch--two males arch backs and face each other. One almost immediately gives way and is chased by the other.
CF	Chin-Rump-Follow--male walking with nose almost touching rump of a female. Precedes copulation.
CL	Chin-Rump-Lead--female walking ahead of chin-rump-following male. Female walks slowly with rump slightly raised.
PG	Present Genitals--standing female raises rump and presents genitals to sniffing male. In pups: pup raises rump, offering it to a sniffing adults nose.
SG	Sniff Genitals--male sniffs a female's genitals.

Table 2.3--Continued

Category	Description
CO	Copulate--intromission visible judged by males arched back.
MN	Mount--male mounts a female, but intromission not obtained.
GB	Grumbling--animal emitting a low pitched sound which can only be heard within about 10 m. Possibly a contact call between mates.
PT	Paturition--female giving birth.
WH	Whistle--usually used by females to attract pups.
BC	Bite Pup--adult bites pup.
CC	Chase Pup--adult chases pup.
GC	Grooming pup.
SN	Sniff--adult sniffing pup or other mara.
NS	Nurse--female nursing one or more pups.
RC	Repell Pup--adult noses away pup who is trying to obtain access to a teat.
WC	Adult with pups, but temporarily out of sight behind a bush or in the den mouth. Recorded to show that there may be a break in the timing of a nursing sequence since out of sight animal could be nursing pups.
FH	Frisky Hop (Rood, 1972)--characteristic 'play' behaviour. Pup suddenly leaps in the air, runs in a circle at full speed, or even somersaults backwards. It is contagious, and surrounding pups will often respond by frisky hopping as well.
RA	Pup retreats from adult.
TA	Pup runs towards adult.
TC	Pup runs into den (Cueva from the Spanish).

Table 2.3--Continued

Category	Description
SQ	Squabble--pups fighting amongst themselves.
SS	Suckle and Squabble--suckling pup pushes other away from teat.
SU	Pup suckling.
TS	Try to Suckle--pup trying to gain access to a teat.
AD	Anal-Drag--Animal drags rump along the ground leaving a short mark in the soil, and usually a few faeces.
BE	Bipedal Enurination--bipedal stance taken by males while urine-spraying their mate or another female.
EB	Enurinate Back--female stands with rump raised, and sprays urine back towards an approaching male.
ND	Nose down and sniffing the ground.
AL	Alert--Sitting with head upright and actively looking around.
SL	Sleep--animal lying on ground in a relaxed state--eyes closed and head relaxed forward and nearly touching the ground.
CP	Coprophage--mara re-ingesting faeces.
DF	Defecating.
UR	Urinating.
GM	Grooming.
RL	Rolling on ground.
SR	Stretching.
DG	Digging at den mouth.
EC	Enters den.

Table 2.4.--Data collection protocols used for collecting radio tracking and observation scan data.

Record Type Code (Column 1). In all record types but 1, 2, and 5 the data is written across the data sheet free-form.

0	Start Observation Session
1	Individual Radio Tracking Record--see below for other protocols
2	General Scan Record--see below
5	Special Observation Record--see below
6	Special Comments--written free-form across page
7	Weather record--Every time the weather changes during a session the following data were recorded: time, temperature, wind speed (Beaufort Scale), % cloud cover, and weather condition code (light rain, medium rain, heavy rain, clear, etc...)
9	End of session

Table 2.4--Continued

For record types 1, 2, and 5 the following protocols were used:

1. Time of day. Recorded to second.

2. Identification Code. Two letter mara identification code. 'UM' signifies unidentified mara; double letters (e.g. 'AA', 'BB', 'ZZ') signify unmarked animals which were consecutively followed over several scans. Two different letters (e.g. 'LR', 'TE', 'SL') signify individually identifiable animals known from natural or artificial marks (plastic collars, eartags, and radio-collars).

3. Sex-Age-Code. Recorded according to the following format:

0--Adult mara, sex ?
1--Adult male
2--Adult female
3--Pup (< 1/2 adult)
4--Male pup
5--Female pup
7--Juvenile (> 1/2 adult)
8--Male juvenile
9--Female juvenile.

4. Behaviour-Code. As in Table 2.3. States are given first, followed by event (e.g. STGZ for sitting and grazing).

5. Nearest-Neighbour Distance. Distance to the closest mara, usually a mate.

0) Touching
1) 0 - 2 m
2) 2 - 5 m
3) 5 - 10 m
4) 10 - 20 m
5) 20 - 40 m
6) 40 - 75 m
7) 75 - 100 m
8) > 100 m
9) Unknown

6. Location Code. Location relative to a central point in each study site. The Y (North-South) coordinate is given first, followed by the X (East-West) coordinate. e.g. N005E005 is at a position 50 meters north and 50 meters east of the study area's grid reference point.

7. Habitat Code. A total of 14 habitat codes were used. They are shown in Table 3.3 (see Chapter 3).

8. Comment Code. Double digit comment codes were used to record a range of details about an animals activities including: (i) orientation relative to mate, (ii) location relative to den sites, (iii) reacting to predator, (iv) radio fix confidence.

Figure 2.9.--Sample data sheet used for recording general scan and radio-tracking data in the field.

OBSERVATION DATA SHEET-1983 Start Time-_____ Date-_____ Location-_____

Temp-____ Wind-____ Ovc-____ RH-_____Comment- _____ Page ____/_____

typ	Time	ID	Behv	Tel	Location	Hab	Com

typ	Time	ID	Behv	Tel	Location	Hab	Com

Table 2.5.---Den Scan/Event Recorder data collection protocols. This data was collected using the EVREC program (see Appendix B) on an EPSON HX20 portable computer. It was used exclusively while recording data at breeding den sites. All but DATE lines start with the time. Capital letters are entered as they are; £ represents variables which must be filled in.

Begin and End Session--To mark start and finish of an observation session.

yymmdd DATE	First line of observation session; yymmdd = year month day.
loc	Den location code.
STR	Starting observations now.
END	End observation session.

Scan Formats begin(level) Den Scans--Made at 10 min intervals.

SCNT££W££S££	Start Den Scan, T££ is temperature, W££ is wind speed, S££ is % cloud cover
A££	Number of adults present
E££	Number of adults feeding
L££	Number of adults resting
N££	Number of adults nursing
C££	Number of pups present
S££	Number of pups suckling
G££	Number of pups grazing
CV£	Distance of main body of non-suckling pups from den
E££	End den scan

Pup Scans--Made at 10 min intervals.

SCS	Start pup scan
£££	For each pup present record: (i) pup size, (ii) activity (0--inactive, 1--grazing, 2--suckling), (iii) distance to nearest other pup
ECS	End pup scan

Table 2.5--Continued

General Scans--Made at 30 minute intervals. These data are reformatted and then fed into the observation record data base.

SGST££W££S££	Start general scan, weather data as in pup scans
L£££££££	Location to nearest 100 m (ege N01E01), and habitat code for the maras following in scan. Maras in more than one location can be entered by repeating location record.
£££££££	Mara name, sex, behaviour code, nearest-neighbour distance, distance to next pair, comment code (all coded as in behaviour scans).
EGS	End general scan.

Special Event Scans--To record behavioural interactions or any unusual behaviours seen.

SPC	Start special event scan
£££££££	Individual mara record as in General scans above
ESP	End special event scan

Mara Pair Arrival and Departure--One record is recorded each time a pair arrives at, or leaves, the den area.

A££M££	Group size, number of females, and mara pair identification code for each pair or lone adult mara that arrives at the den.
L££M££	Departure record, same coding as above.

Table 2.5--Continued

Continuous Focal Pair Records--Used to maintain continuous data record on focal pairs. A data record is entered every time the focal pair changes what they are doing.

FOCM££	Declare focal pair, ££ is focal pair name
FOB	Focal animals obscured by brush
FVW	Focal animals back in view
FQ£	Focal pair in queue for den at £ mara lengths from den
FV£	Focal animal £ mara lengths from den
FD£	Focal pair £ mara lengths from pups
FW£	Focal with £ pups
FN£	Focal nurses £ pups
FC£	Focal animal chases pup size £
FL£	Focal female lunges at pup size £
FSH	Focal female stops nursing because of pup harassment
FSA	Female stops nursing because of adult interruption
FMA	Female moves away
FSS	Female stops suckling
FS£	Female sniffs size £ pup
CT£	Size £ pup trying to suckle focal female
CF£	Size £ pup following focal female
CH£	Focal female chase size £ pup
CSS	Pup stops suckling focal female
CSQ	Pups suckling and squabbling
CSR	Pup being sniffed raises rump
CSH	Pup being sniffed hides/lowers rump

to be recorded for the focal pair since the exact length of time they spent engaging in each behaviour could be obtained.

Radio-Tracking

Standard radio-tracking procedures were used as described in Macdonald and Amlaner (1980), and Doncaster (1985). A 3 element Yagi aerial (following design by Amlaner, 1980) was used with a radio receiver (AVM Instruments Co., Champaign Illinois, U.S.A.) to track the animals. Most tracking was done from a vehicle using the receiver and aerial to home in on a radio-collared animal. If possible, the tracked animal was approached until it could be seen so that its position could be verified and its behaviour recorded. However, it was often not possible to sight the animal at every fix because of the risk of scaring it off, or otherwise affecting its movements. When an animal could not be approached to within sighting distance its position was ascertained by triangulating from two known points using the yagi aerial and a sighting compass (Silva). These data were entered onto general scan data forms (see Table 2.4 for data protocols). Radio-tracking data were only intensively collected at Puesto La Blanca

Relying on triangulation alone for fixing an animal's position can be problematic since radio signals may be affected by topographic features such as hills and valleys. I was fortunate, however, that the La Blanca study area was fairly flat so that this problem was minimized. To avoid this problem, an effort was made to sight the radio-tracked animal every hour to verify its position and minimize errors in the location records.

Another problem with radio-tracking the same animal continuously is that of data independence: fixes taken in

quick succession cannot be regarded as independent of each other, and therefore are not suitable for statistical treatments requiring independent locations. To minimize this problem radio fixes were made at 15 minute intervals; and where necessary in subsequent analyses data were selected at larger intervals to limit auto-correlation.

2.2.3 Data Summary

A total of 31 animals were captured during the course of the field study; 11 of which were radio-collared, and 20 plastic collared (see Table 2.6). Two of the radio-collared animals' (one of which was the only animal radio-collared at Puesto El Salitral) radios failed shortly after capture, so only 9 animals were effectively tracked. Only 12 of the other collared animals (including the two maras with failed radios) were re-sighted post-capture. A further 7 animals had adequate natural marks to be repeatedly recognized. So a total of 28 animals were followed for varying lengths of time during the field study. Table 2.7 summarizes results showing how much data were collected on these animals. The total number of hours spent collecting each data type at each study site are shown in Table 2.9. In total, maras were observed or tracked over 2099.2 hours.

2.3 Analysis Methods

2.3.1 Data Preparation

In the field, scan and radio-tracking data were typed into the HX20 computer and stored on microcassette. These, and the continuous den-scan data (stored directly on

Table 2.6.--Summary of individually recognizable maras at the three study areas.

Study Area	Naturally Marked	Plastic Collared	Radio Collared
Estancia Larreburu	2	-	-
Puesto La Blanca	3	6	10
Puesto El Salitral	2	4	1
Total	7	10	11
	Total Marked Animals =		28

Table 2.7.--Summary of data collected on each of the individually recognizable maras at Puesto La Blanca and Puesto El Salitral. Data given for each animal are: date first seen or trapped, total number of observation records, and the total number of hours within which observations were made.

Mara Name	Date First Seen	Total Number of Records	Total Number of Hours
----------Puesto La Blanca----------			
ENF[R]	5.3.83	652	171
ELF[R]	20.3.83	847	333
SQM[F]	24.3.83	1	1
PJF[F]	24.3.83	53	12
PAM[R]	11.4.83	802	288
GCM[R]	14.4.83	182	103
CAM[F]	22.6.83	20	14
BFF[N]	14.9.83	13	4
HLM[N]	19.9.83	3	2
LEM[R]	30.9.83	125	58
SYF[R]	1.10.83	539	225
TIF[R]	1.10.83	403	177
TIM[R1]	1.10.83	32	20
SLF[R]	1.10.83	114	50
WOF[R]	1.10.83	137	68
TEF[F]	1.10.83	15	9
PUF[F]	2.10.83	55	32
BAF[N]	6.10.83	12	4
TUM[R]	27.9.84	136	63
----------El Salitral----------			
WAM[R1]	31.5.83	174	44
JAF[F]	20.6.83	189	41
NAF[F]	16.6.83	56	18
GIF[C]	27.7.83	1	1
SAF[C]	29.7.83	140	56
LFF[N]	21.9.83	11	2
NLF[N]	16.9.83	17	5

Notes: [R] Radio-collared. [R1] Radio-collared, but radio functioned only briefly. [N] Naturally marked. [C] Animal originally captured at Puesto Centenario. [F] Plastic collared

Table 2.8.--Number of hours spent radio-tracking and collecting general scans in each month of the year. Data from all study sites are combined. It does not include time spent collecting spot radio fixes.

Month	-Year- 1981	1983	1984
1	-	-	90.4
2	-	31.03	12.33
3	-	100.99	5.7
4	-	98.25	1.87
5	-	59.25	7.17
6	-	78.17	-
7	13.76	13.0	-
8	28.65	102.57	14.83
9	134.59	115.9	106.98
10	137.71	347.15	201.42
11	47.45	198.91	38.35
12	-	112.74	-
Total	362.16	1257.96	479.08

Table 2.9.--Number of hours spend collecting the different data types at each study area by year. A total of 2099.2 hours were spent watching and radio tracking maras during 21 months of field work.

Study Site	1981	1983	1984	Total
Est. Larreburu	362.16	7.07	1.75	370.98
Puesto La Blanca	-	999.37	471.91	1471.28
Puesto El Salitral	-	228.08	5.41	233.49
Other Areas	-	23.45	-	23.45
			Total Number Hours =	2099.20

microcassette), were then transferred to a VAX mini computer. On the VAX a series of data checking programs were then run on the data to search for such errors as: impossible dates and times, non-existent behaviour codes, impossible distances, and impossible behaviour combinations such as male nursing-pup. The mistakes were checked against original data records and corrected. Radio-tracking and general scan data were then transferred to an ICL 2988 mainframe computer, and inserted into a CAFS (Contents Addressable Filestore) data base system accessed through QUERYMASTER. This data base was large, it contained 44140 data records, but the used of CAFS allowed rapid sorting and extraction of results from the data set for subsequent analyses. It also allowed some cross-tabulations to be done interactively.

Data Analysis

The PSTAT and MINITAB statistical packages were used to do most statistical analyses. Some X^2 and other tests were done on a WREN EXECUTIVE CP/M 80 micro computer using The PERFECT CALC spreadsheet program, OXSTAT statistical package, and a number of Basic programs. A total of 22 computer programs (in Basic or Fortran) were written to run on a VAX mini computer and ICL 2988 main frame computer to sort, error check, and analyze these data.

2.3.2 Statistics

Because the data used in many of the analyses did not meet the assumptions of parametric tests (Sokal and Rohlf, 1969) several non-parametric statistical methods were used. To test for normality the normal scores test (MINITAB) was used. Means are given with ± the standard deviation, unless other wise stated. Below I list the main statistical tests used in this thesis:

Non-parametric X^2 test, Kruskal-Wallis test, Spearman's correlation of rank coefficient, and the Mann-Whitney test.

Parametric Student's t-test, one and two way analysis of variance, and Pearson's product-moment coefficient of correlation.

Chapter 3

MARA ECOLOGY AND SPATIAL ORGANIZATION

3.1 Introduction

The purpose of this chapter is to establish the ecological framework within which the following detailed analyses on monogamy (Chapter 4) and communal denning (Chapter 5) can be viewed. The principal questions to be tackled are: (i) what is the size of the mara's home range; (ii) how frequently do animals cover their range; (iii) can ranging and behaviour patterns be explained in terms of specific climactic, seasonal, and habitat features; and (iv) what is the nature of the spatial relationship between pairs of maras living in close proximity. Finally, at the end of the chapter, the mara's ecological adaptations to the environment will be summarized, and compared with those of some selected species of mammals.

3.2 Methods and Study Site

3.2.1 Study Site

Maras were only radio-tracked extensively at the La Blanca study site so, unless stated otherwise, results presented here are based on data collected at this site only. Puesto La Blanca is an outlying sheep station normally occupied by one shepherd, with the nearest neighbour 8 km away. The shepherd's house was located on

the edge of an ephemeral lagoon measuring about 20 ha. Observations were made on maras within a 4 km radius of the house. See Chapter 2 for more details of this and other study sites, and a summary of climactic data for the surrounding area.

Since there were few natural landmarks against which to locate an animal's position, the La Blanca area was divided by a 500 X 500 m grid marked with 2 m high flagged poles. Each pole was located by using a 100 m line to measure the distance travelled, and following a compass bearing from a previously 'fixed' location. These locations were checked by using compass bearings to triangulate against previously fixed markers. All positions were located relative to the La Blanca windmill, about 60 m from the house, on the magnetic (declination in 1963 was 6° 45' E) rather than north-south axes.

For many analyses the data were grouped in seasonal blocks. Seasons were delineated as follows: Fall, 1 March to 30 May; Winter, 1 June to 31 August; Spring, 1 September to 30 November; and Summer, 1 December to 28 February. See Chapter 2 for details of the climatic data in the study area, and for the rationale for delineating the seasons.

3.2.2 Animal Tracking

The main technique used to locate animals for investigation of movement, home range size, and habitat use patterns was radio-telemetry. This technique, and the methods used to capture and mark animals, is described in Chapter 2. The resulting data are summarized below.

A total of 11 maras were radio-collared. However, only 9 animals, 4 males and 5 females, were followed for a sufficient length of time (more than 1 month) to be used. Radio-tracking was conducted between 5 March 1983 and 22 November 1984. I left the field from 19 January to 24 August 1984, but arranged for Sr. Carlos Garcia, a resident of

Puerto Madryn, to visit the study site once a month to locate the radio-collared maras. The animals tracked were: ENF, ELF, PAM, GCM, LEM, SYF, WOF, TIF, and TUM (Tables 3.1 and 3.2 summarize the data collected on each animal). As described in Chapter 2, the last letter of a mara's three letter name shows the animal's sex: "F" for females and "M" for males. The longest period over which an individual mara was tracked was 409 days for PAM (11 April 1983 to 22 November 1984). Over 400 radio locations, or fixes, were obtained on each of ENF, ELF, PAM, SYF, and WOF. A grand total of 3794 radio fixes were recorded over the 19 month period during which I had radio-collars on maras.

Two to five days a week, depending on other data collection commitments, were devoted to intensive radio-tracking. On radio-tracking days one animal would be followed for 6 to 12 hours, with consecutive fixes recorded at 15 min intervals. While intensively tracking one animal an attempt would be made to locate the other radio-collared maras twice a day. On other days, whenever spare time could be found, I would try to locate as many of the radio-collared animals as possible. A full day of radio-tracking was made on each mara 3 to 4 times a month. Figure 3.1 show the intensity of tracking effort for each of the nine maras during the study period.

All the animals tracked spent most of their time with an accompanying animal of the opposite sex (see Chapter 4); so when I refer to one of the radio-collared animals I am usually referring to the pair of which that animal was a member. The only pair in which I was able to radio-collar both members was LEM and TIF. They were found together for the first 70 days they were tracked (83.10.07 to 83.12.15). After 15 December 1983 they were not seen together again; probably because by then LEM, who had been injured when caught, was rapidly losing condition. LEM was found dead by a shepherd several days after being last tracked on 22 February 1984.

Table 3.1.--The date captured and the duration of time radio-tracked (in days) for each of the nine intensively followed maras.

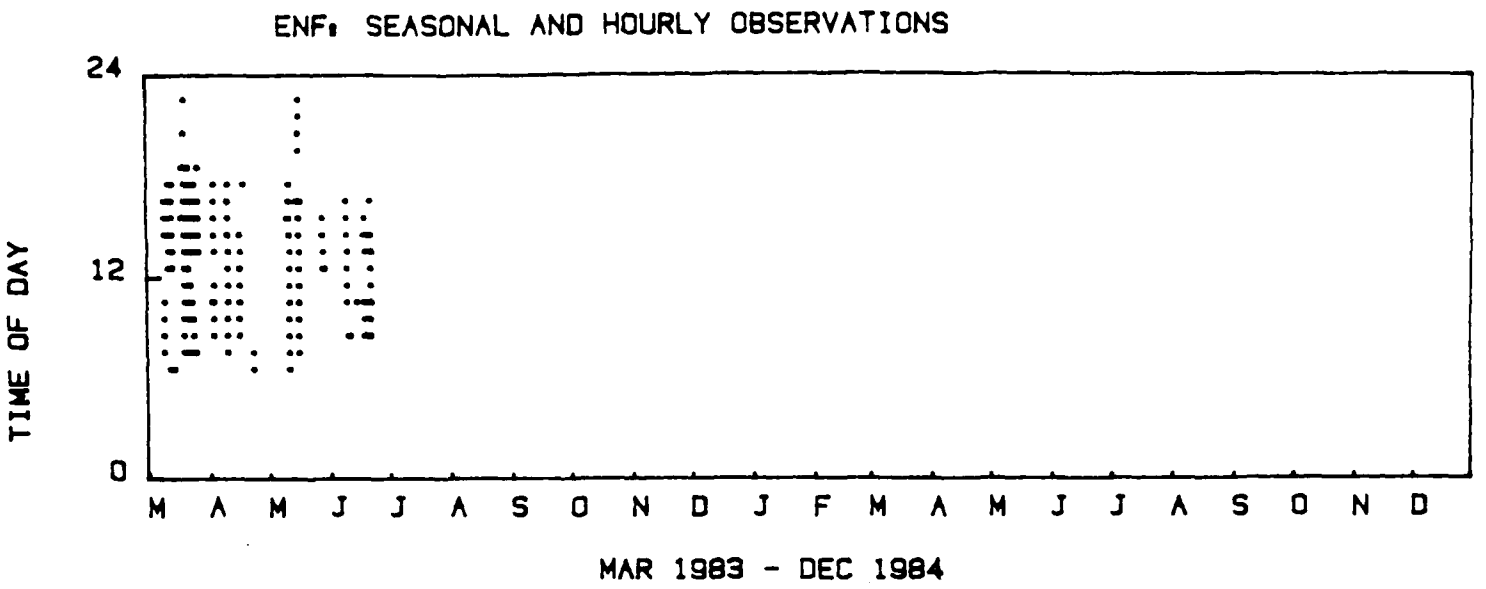
Mara Name	Date Captured	First Tracked	Last Tracked	Duration Tracked	Total No. Fixes
ENF	5.3.83	9.3.83	24.6.83	108	649
ELF	20.3.83	21.3.83	2.5.84	409	841
PAM	11.4.83	13.4.83	22.11.84	590	797
GCM	14.4.83	18.4.83	18.1.84	276	181
LEM	30.9.83	7.10.83	22.2.84	139	122
SYF	1.10.83	5.10.83	23.11.84	416	531
WOF	1.10.83	7.10.83	8.4.84	185	136
TIF	1.10.83	7.10.83	23.11.84	414	401
TUM	25.9.84	28.9.84	23.11.84	56	136

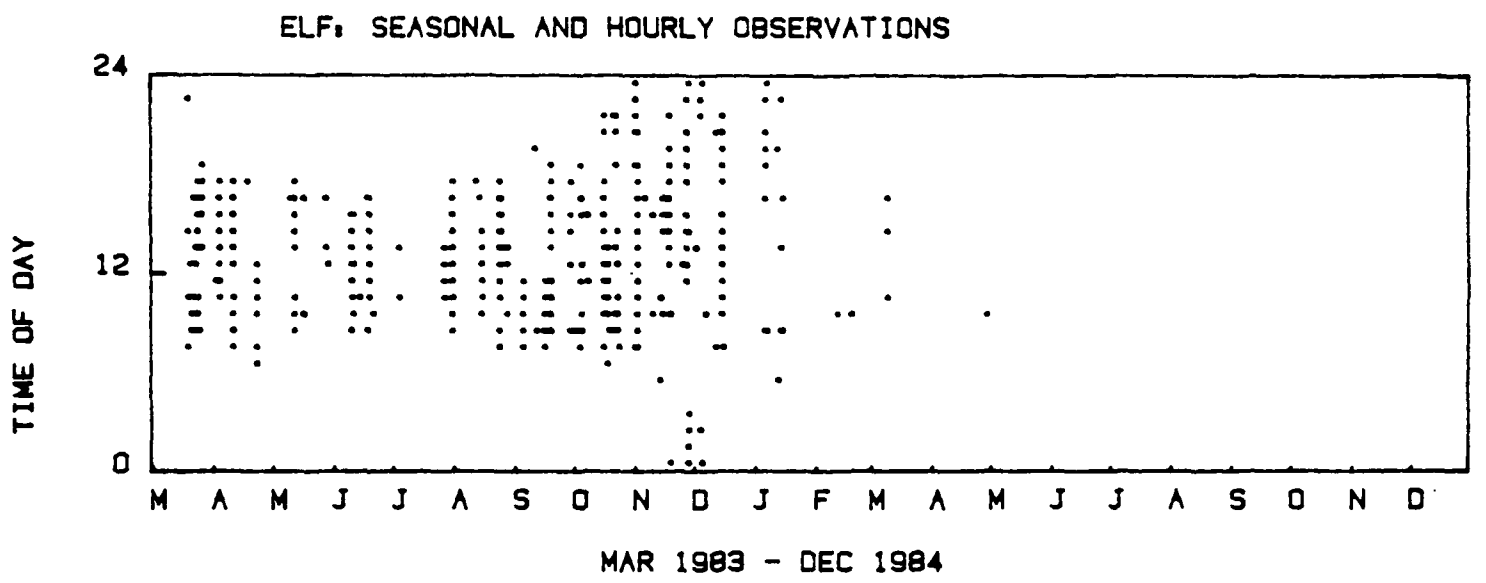
Table 3.2.--The distribution of sightings of the nine radio-tracked maras over time. X's signify that at least one location was recorded for the mara during that month.

	-Radio Collared Maras-								
Dates	ENF	ELF	PAM	GCM	LEM	SYF	WOF	TIF	TUM
-1983-									
Mar	X	X							
Apr	X	X	X	X					
May	X	X	X						
Jun	X	X	X						
Jul	X	X	X						
Aug		X	X						
Sep		X	X	X					X
Oct		X	X	X	X	X	X	X	X
Nov		X	X	X	X	X	X	X	X
Dec		X	X	X	X	X	X	X	
-1984-									
Jan		X	X	X	X	X	X	X	
Feb		X	X		X	X	X	X	
Mar		X				X			
Apr			X			X	X		
May		X				X			
Jun									
Jul									
Aug			X			X		X	
Sep			X			X		X	
Oct			X			X		X	
Nov			X			X		X	

Figure 3.1 (3 pages).

Tracking record plots for each of the 9 radio-collared maras. The plots show both the date and time of day maras were tracked. One point is plotted for each hour in which location data, either through observations or radio fixes, were obtained.


ENF: SEASONAL AND HOURLY OBSERVATIONS
TIME OF DAY
24
12
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984


ELF: SEASONAL AND HOURLY OBSERVATIONS
TIME OF DAY
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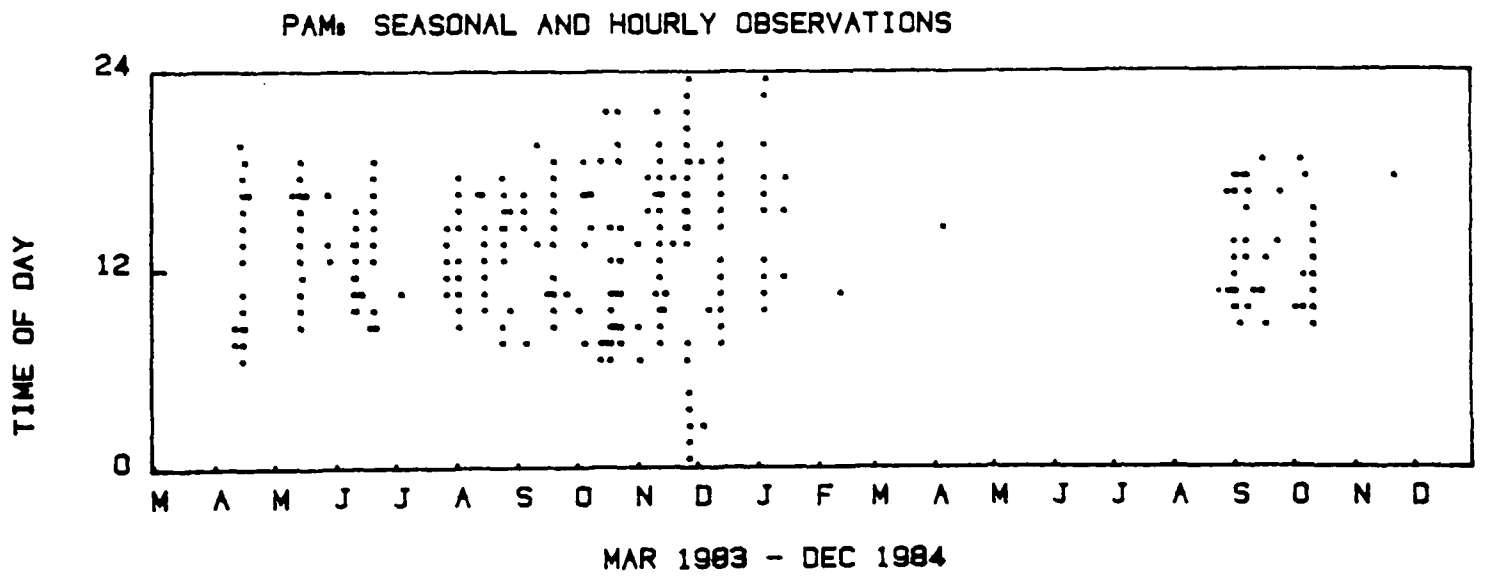
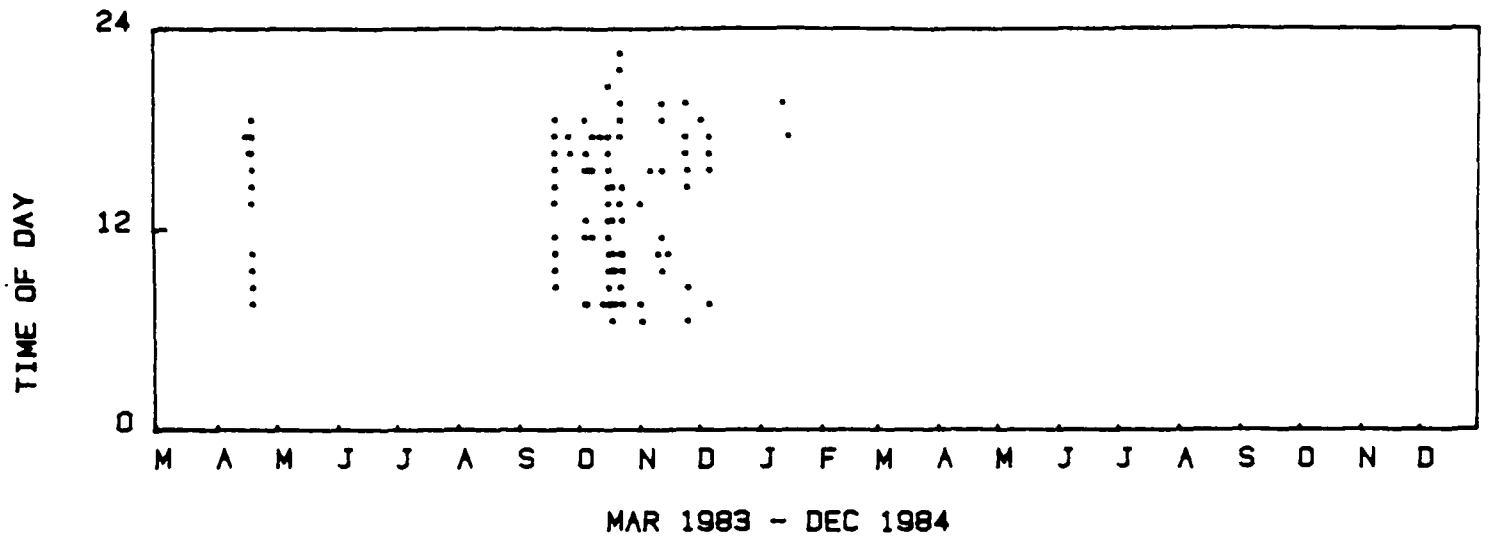
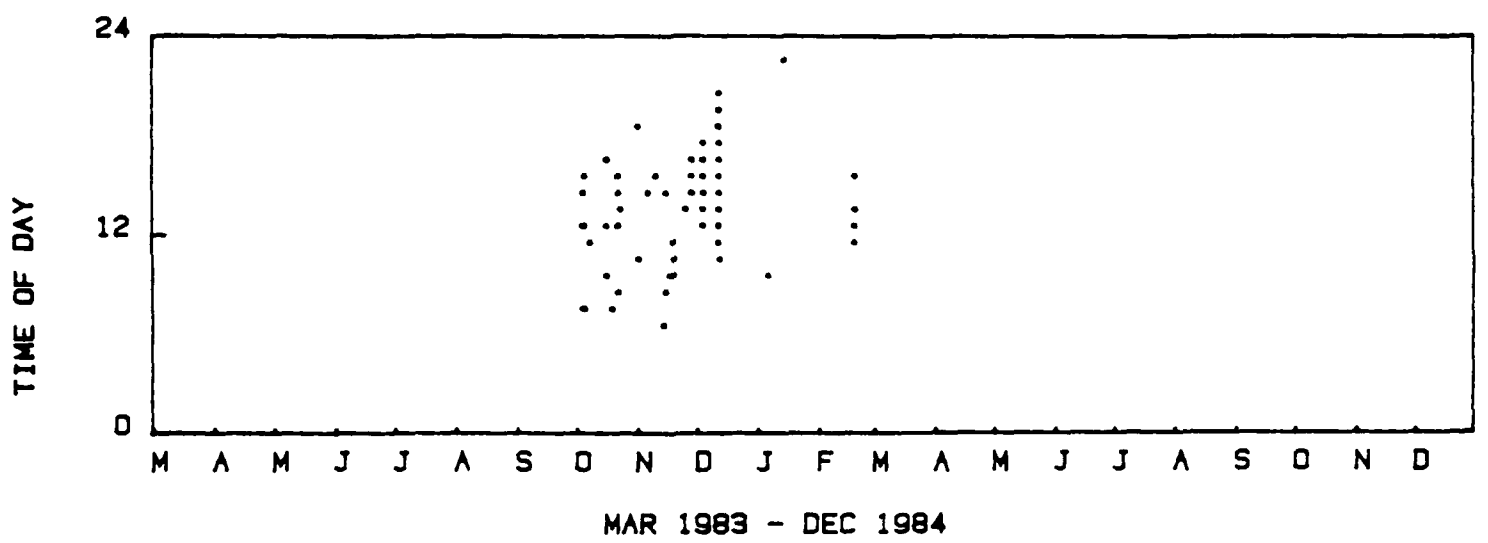
12
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984


PAM: SEASONAL AND HOURLY OBSERVATIONS
TIME OF DAY
24
12
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984

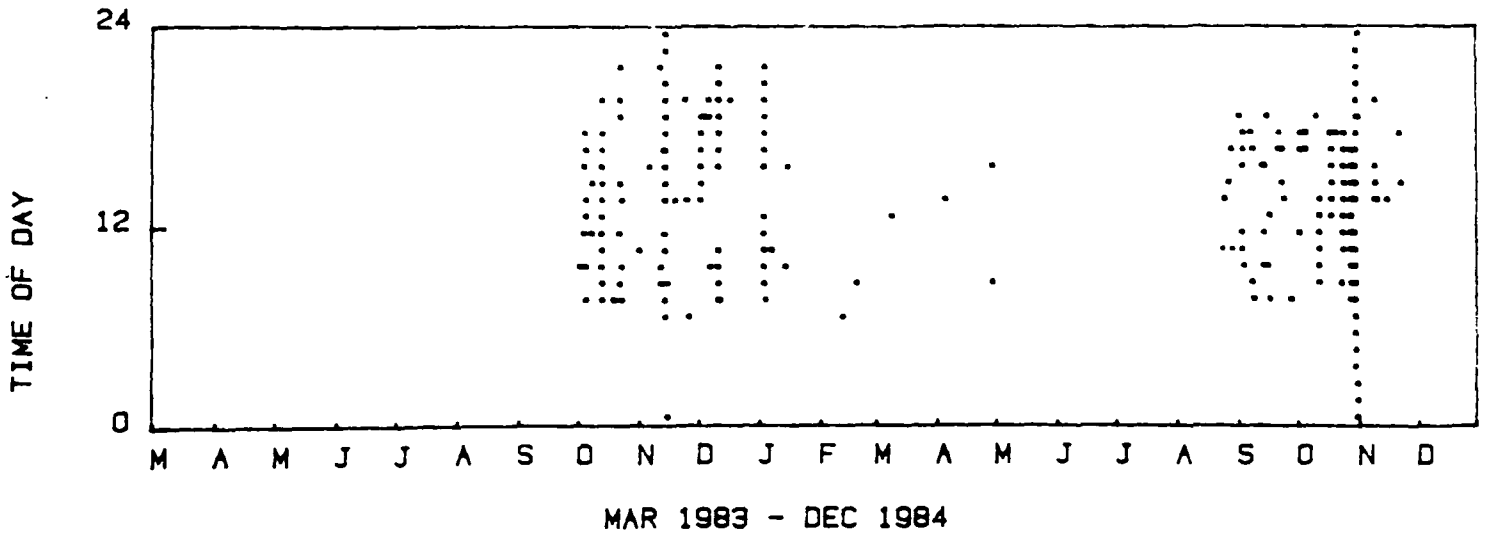
GCMs SEASONAL AND HOURLY OBSERVATIONS

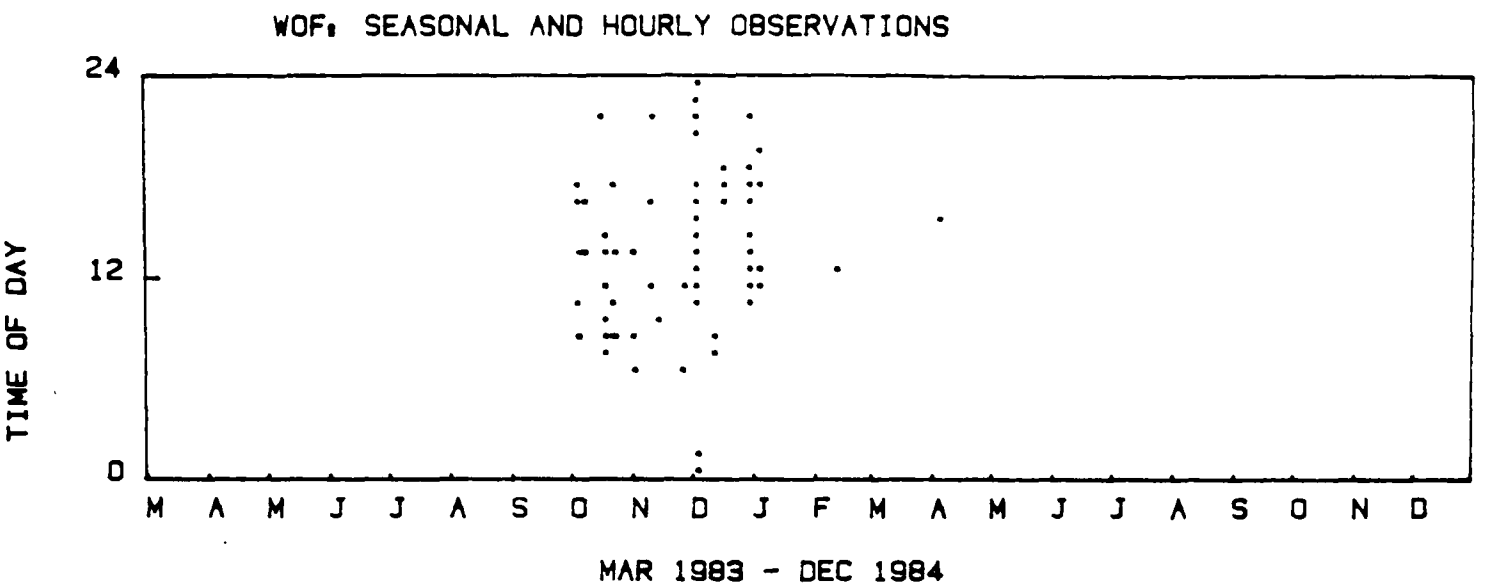


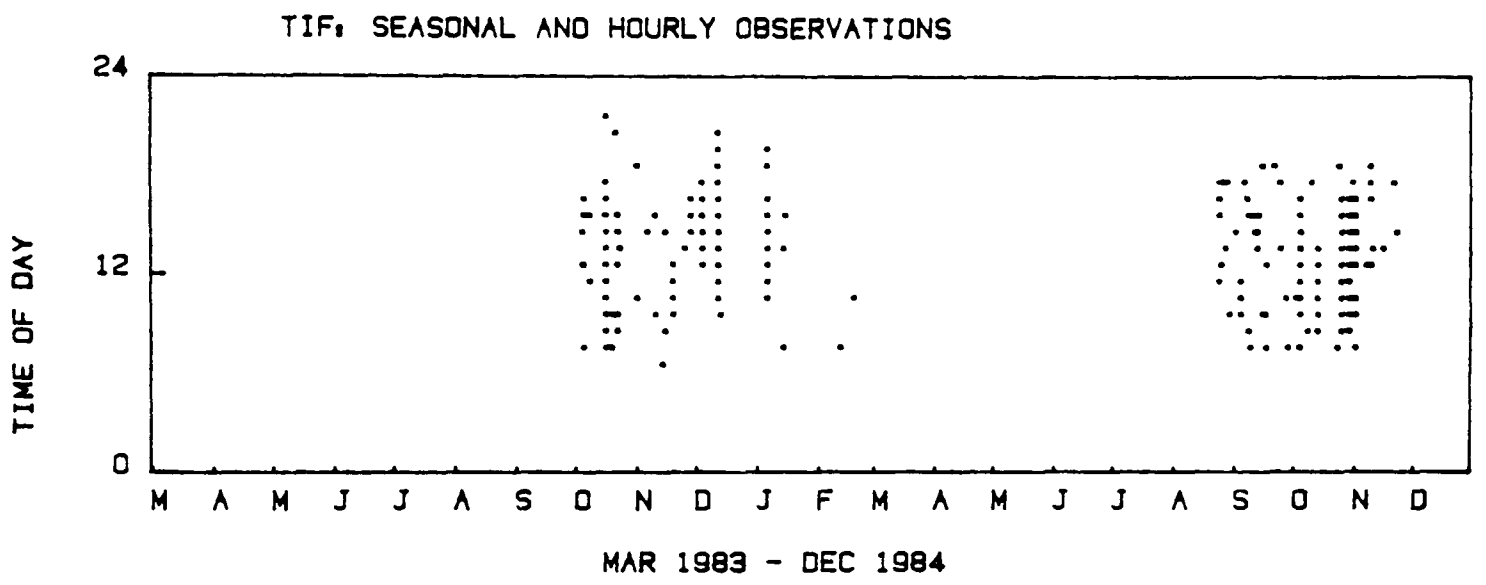
LEMs SEASONAL AND HOURL OBSERVATIONS

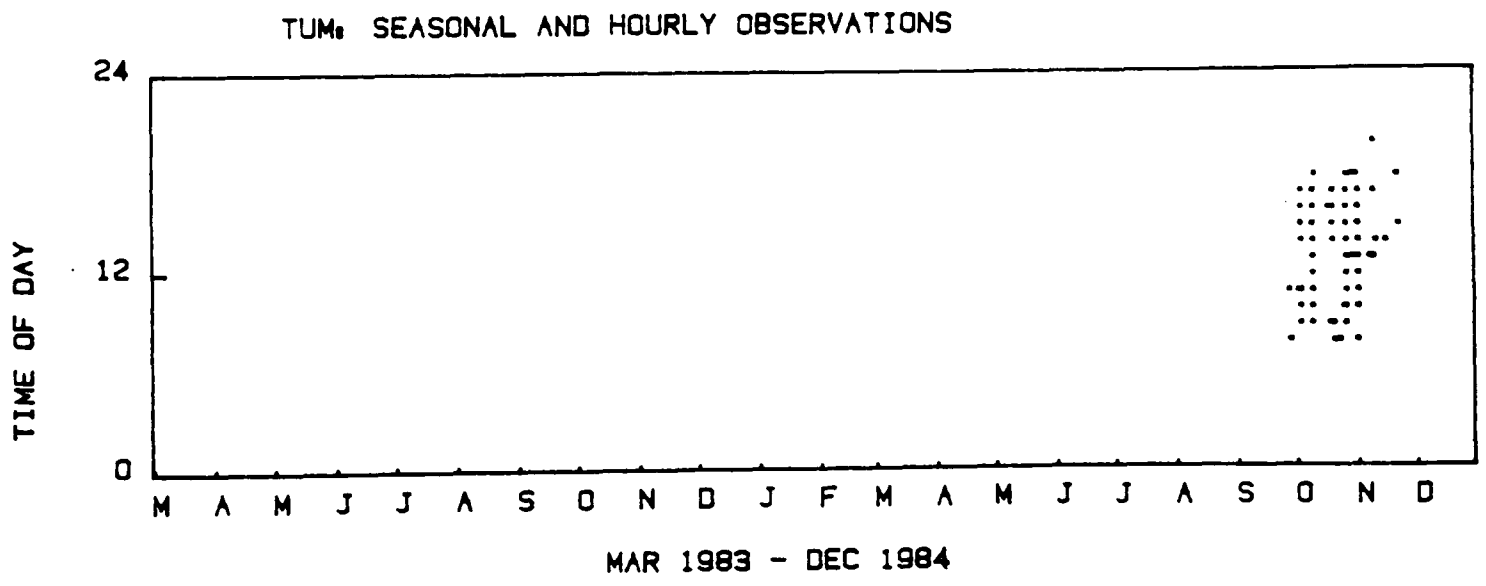


SYFs SEASONAL AND HOURLY OBSERVATIONS




WOF: SEASONAL AND HOURLY OBSERVATIONS
TIME OF DAY
24
12
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984


TIF: SEASONAL AND HOURLY OBSERVATIONS
TIME OF DAY
24
12
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984


TUM: SEASONAL AND HOURLY OBSERVATIONS
TIME OF DAY
24
12
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984

3.2.3 Behavioural Observations

Data were also collected on mara behaviour. Whenever maras, either collared or uncollared, were in sight while radio-tracking I recorded their behaviour every 15 minutes as instantaneous scans (see Chapter 2 for description of sampling technique). Depending on visibility in the habitat that the tracked mara was using, I was able to record several hours of behavioural as well as positional data on some days, while on other days I only recorded a few behavioural observations.

3.2.4 Habitat Data Collection

Before analyzing patterns in mara habitat use the habitat must be described. Here I will build on the description of the La Blanca study site already made in Chapter 2. Two independent methods were used to categorize the vegetation at the La Blanca study site: (i) visual assessment, and (ii) vegetation cover values. These methods are described below.

Visual Assessment

The habitat was divided into 14 habitat types, lumped into 4 general categories, according to various vegetation parameters which could easily be identified by eye (see Table 3.3). While radio-tracking the habitat category an animal was in was recorded along with its location. These locational and habitat data were then used to plot habitat boundaries, and thus to create a vegetation map of the study area (see Figure 3.2).

Table 3.3.--Habitat codes (used in data collection) with corresponding habitat category. In every habitat category roughly half of the ground cover was bare earth.

Habitat Code	Habitat Category	Description
1	Open	Grass and herbs
2	Open	Grass and herbs, few shrubs
3	Scrub	Mixed shrub, grass and herbs
4	Scrub	Dense shrub cover
10	Other	Bunch grass
11	Other	Bunch grass, some shrubs
20	Lagoon	Edge of water on lagoon
21	Lagoon	Dry lagoon--no vegetation
22	Lagoon	Grassy lagoon
23	Lagoon	Edge of lagoon and scrub
30	Other	Inside den
31	Other	In den mouth
40	Other	Dirt Road

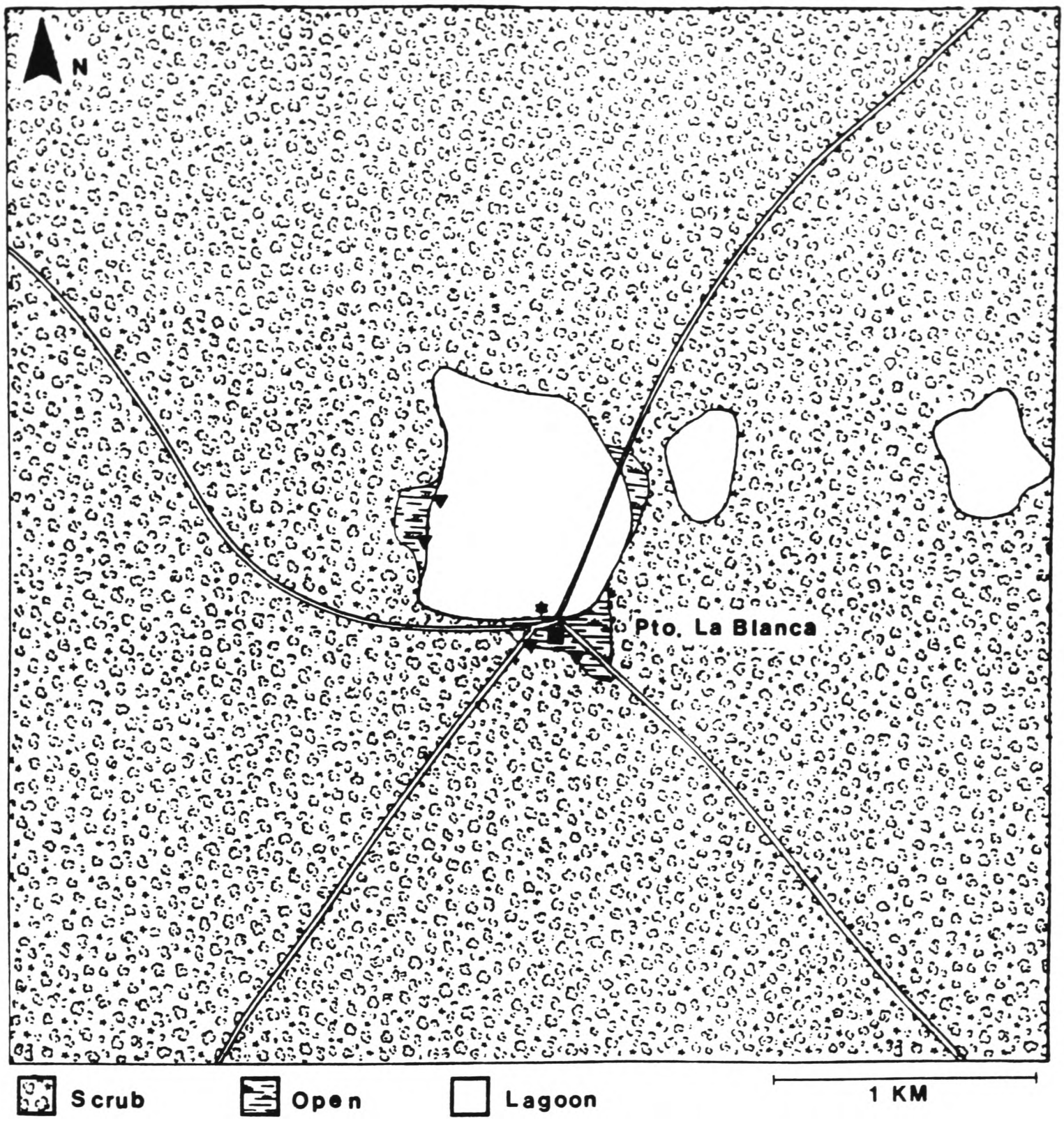


Figure 3.2.--Habitat map of the La Blanca study site. The habitats were classified by visual assessment. Triangles mark the four dens used by pups during the period of field research. The square at the junction of the four tracks marks the location of the main house. The map is oriented on magnetic north rather than true north (magnetic declination in 1963 was 6° 45' E). All subsequent plots of the La Blanca study area cover the same area as this map: 4 km wide, magnetic north to the top, and the bottom edge of the lagoon located in the map center.

Vegetation Cover Values

The goal of this analysis is to determine the structure of the vegetation within the La Blanca study site. Vegetation analysis is a complex field with a large range of sampling techniques available (see review in Goldsmith, Harrison, and Martin, 1986). A systematic sampling method using Braun-Blanquet cover values (Braun-Blanquet, 1932) was chosen since it allows a rapid yet comprehensive inventory of the vegetation cover of an area to be made (Goldsmith, Harrison & Morton, *Op cit*). The vegetation sampling was conducted in the following manner:

- Plots were spaced systematically to give an even sampling of the vegetation cover over the study area. A total of 99 vegetation plots were distributed on a 300 x 300 m grid, with one plot located in the center of each grid. Systematic sampling can lead to biases in a patchy environment, but since the habitat of the La Blanca study site was strikingly uniform in appearance this was not deemed a problem. Plots were located using a 100 m line following a compass bearing. Each plot measured 16 x 16 m (256 m^2) and was subdivided into 4 sub-plots each measuring 8 x 8 m (16 m^2). This sub-plot size falls within the minimum area size for plots in Chaparral shrubland of 10-100 m^2 (Goldsmith, Harrison and Morton, *Op cit.*). Thus 0.25% of the study area was contained within vegetation plots, a percentage similar to that used in comparable habitats elsewhere (see Greig-Smith, 1983).
- In each sub-plot the vegetation cover for the 6 vegetation types were estimated visually using the Braun-Blanquet cover values (see Table 3.4). Cover is defined "as the proportion of the ground occupied by a

Table 3.4.--The Braun-Blanquet cover value scale as used in the vegetation analysis. Cover is defined as the proportion of the ground occupied by a perpendicular projection of the aerial parts of individuals of the species, or group of species, under consideration.

Code	Percent Cover
0	Absent
1	0 - 1 %
2	1 - 4 %
3	5 - 24 %
4	25 - 49 %
5	50 - 74 %
6	75 - 100 %

Table 3.5.--The following vegetation cover categories were devised for the analysis of the La Blanca study site using systematic plot sampling and the Braun-Blanquet cover value scale. See Table 3.6 for a listing of the plant species in each category.

Bare Ground	No vegetation cover--bare earth
Herbs	Short herbaceous plants
Grass	Non-bunch grasses
Bunch Grass	Bunch grasses
Shrub	Woody plants with heights less than 1.5 m
Monte	Woody plants with heights of 1.5 m or more

perpendicular projection of the aerial parts of individuals of the species, or group of species, under consideration" (Greig-Smith, *Op. cit.*). The vegetation types were: bare ground, herbs, grass, bunch grass, and shrubs (see Table 3.5 for a description of each type). A collection was made of the plants in the study site, and Table 3.6 lists the species recorded in each vegetation type. The cover values obtained for each sub-plot were combined to give one value for each vegetation type per plot.

- With sampling at the 0.25% level there is a risk of incorporating biases in the vegetation description since plots were so widely spaced. To verify the reliability of the sampling, 72 ha were sampled at the 5% level, covering 8 of the plots made on the 300 x 300 m grid. To do this, one 25 x 25 m cover value plot was made in the middle of each hectare. These results were then compared with the 8 sample plots (on the 300 x 300 m grid) covering the same area. Results of this comparison are discussed below.

Vegetation Data Verification and Other Sampling Problems

The aim of comparing the sample plots with the verification plots was to test whether sampling at the 0.25% level gives an accurate representation of vegetation cover as revealed by 5% sampling. Cover values should be treated as an index of vegetation cover (Goldsmith, Harrison and Morton, 1986), thus the important thing is that the cover values for the sample plots correlate positively with the more accurate values obtained for the verification plots covering the same area. For each cover type the following method was used to make these correlations:

Table 3.6.--Plant species encountered at the La Blanca and El Salitral study sites. Species are divided into three categories: herbs, grasses, and shrubs.

Family	Genus	Species
	HERBS	
Equisetaceae	?	?
Caryophyllaceae	*Cardionema*	*ramosissimum*
	Cerastium	*funcen*
Cruciferae	*Sisymbrium*	*altissimum*
	Cardaria	*sp.*
Leguminosae	*Hoffmanseggia*	*trifoliata*
Geraniaceae	*Erodium*	*circutarium*
Malvaceae	*Sida*	*leprosa*
Scroph.	*Mecardonia*	*montevidensis*
Umbelliferae	*Torilis*	*sp.*
Convolvulaceae	*Dichondra*	*repens*
Verbenaceae	*Acantholippia*	*seriphioides*
Plantaginaceae	*Plantago*	*sp.*
	Plantago	*patagonica*
	Plantago	*myosorus*
Compositae	*Gamochaeta*	*sp.*
	Facelis	*retusa*
	Perezia	*recurvata*
	Senecio	*filaginoides*
	Grindelia	*tehuelches*
	Baccharis	*pingraea*
	Baccharis	*triangularis*
	Baccharis	*rufescens*
	GRASSES	
Gramineae	*Bromus*	*brevis*
	Bromus	*sp.*
	Hordeum	*murinum*
	Hordeum	*sp.*
	Poa	*ligularis*
	Vulpia	*myorus*
	Vulpia	*sp.*
	Piptochaetium	*napostaense*
	Stipa	*ambigua*
	Stipa	*speciosa*
	Stipa	*tenuis*
	SHRUBS	
Ephedraceae	*Ephedra*	*ochreata*
Rosaceae	*Tetraglochin*	*alatum*
Leguminosae	*Prosopidastrum*	*globosum*
	Prosopis	*alpataco*
	Prosopis	*denudans*
Anacardiaceae	*Schinus*	*polygamus*
Umbelliferae	*Mulinum*	*spinosum*
Solanaceae	*Lycium*	*chilense*
	Lycium	*ameghinoi*
Compositae	*Chuquiraga*	*avellanedae*
	Chuquiraga	*erinacea*
	Gutierrezia	*solbrigii*

- For each of the sample plots in the verification plot coverage area, the mean was calculated for the eight verification plots surrounding the hectare in which the sample plot was made. These central verification plots were not included in these calculations because the values obtained would not have been independent since they cover exactly the same areas used in the sample plots.
- These means were then correlated with the corresponding central plots' cover values. For the central plots, the verification cover values were used instead of the sample plot values. This is because the sample plots covering this area were made at a different time of year from the verification plots, so any differences found could have been a result of seasonal changes in vegetation cover. Although the verification plots were larger (25 x 25 m) than the sample plots (16 x 16 m), in practice the size differences would not have affected the estimated cover values.

The results of these analyses are shown in Table 3.7. In all cover types (bare ground, herb, grass and shrub) there was a significant positive correlation showing that the sample plots did, indeed, give an adequate representation of the actual cover as revealed by sampling at the 5% level.

One problem with the vegetation cover values arose because logistics dictated that the plots could not be sampled simultaneously: 46 of the 99 plots were described in April, while the other 53 were described in January. There are climatic differences between these months (see Chapter 2), and the vegetation cover could have varied accordingly. To test whether there were significant differences in vegetation cover the Mann-Whitney test was used to compare the values obtained in each month for each vegetation type (see Table 3.8). The only difference found was that herb cover had significantly higher coverage levels in April than in December. Because of this difference, it will be prudent

Table 3.7.--Means and standard deviations of the verification plot and sample plot cover values. Also shows Pearson product moment correlation coefficients for the sample and corresponding verification plots' cover values for each cover type.

	PLOTS					
	-Sample-		-Verification-			
Cover	$\bar{x}$	SD	$\bar{x}$	SD	r_s	Significance
Ground	5.12	0.64	5.17	0.51	0.957	$P < 0.01$
Herbs	1.5	0.76	1.71	0.57	0.788	$P < 0.05$
Grasses	2.38	1.51	2.28	0.85	0.913	$P < 0.01$
Shrubs	2.38	1.51	2.45	1.26	0.877	$P < 0.01$

Table 3.8.--Results of Mann-Whitney Tests comparing the distribution of vegetation cover values in different month for the bare ground, herb, grass, and shrub cover types.

Cover Type	-Median Cover Values- March	December	W	Significance
Bare Ground	4	4	2188.5	P = 0.4361
Herb	3	2	2961.5	P = 0.0000
Grass	3	3	2359.5	P = 0.6789
Shrub	4	3	2440.5	P = 0.3260

to consider as provisional any conclusions drawn about mara habitat use patterns as a function of herb cover.

3.2.5 Habitat Description

Figures 3.2 (above) and 3.3 show maps of the La Blanca area made through, respectively, visual assessment and vegetation plots. The habitat map based on visual assessment (Figure 3.2) shows that, with the exception of the area around the lagoons, the area is dominated by an apparently uniform and featureless scrub. On the other hand, the vegetation cover maps show that the vegetation of the area is actually highly variable and follows no easily recognizable pattern. This irregularity will later be shown to be of great importance in understanding the movement and ranging patterns of maras.

3.3 Home Range Size

The goal of this section is to describe mara ranging patterns. In following sections, I will expand on these results to answer specific questions about how the mara's ranging behaviour is affected by habitat features and by the movements of other maras.

To illustrate the nature of a species' ranging ecology the following 3 features of its movements need to be described:

1. The sizes and configurations of home ranges.
2. The usage patterns across ranges.
3. The continuity of 1 and 2 above over time.

Wilson (1975) defined home range as the area an animal knows thoroughly and patrols regularly; and defined a territory as a special kind of home range which may or may

Figure 3.3 (2 pages).

Braun-Blanquet cover value contour plots for each of the vegetation categories. The contours are obtained by joining cells with the same cover value with some smoothing done by the contouring routine (CONTRA of the GHOST80 graphics library). The plots are 4 km wide, with north to the top. These plots cover the exact same area as Figure 3.2 (above). The northern and southern parts of the plots, outside the contour lines, were not surveyed.

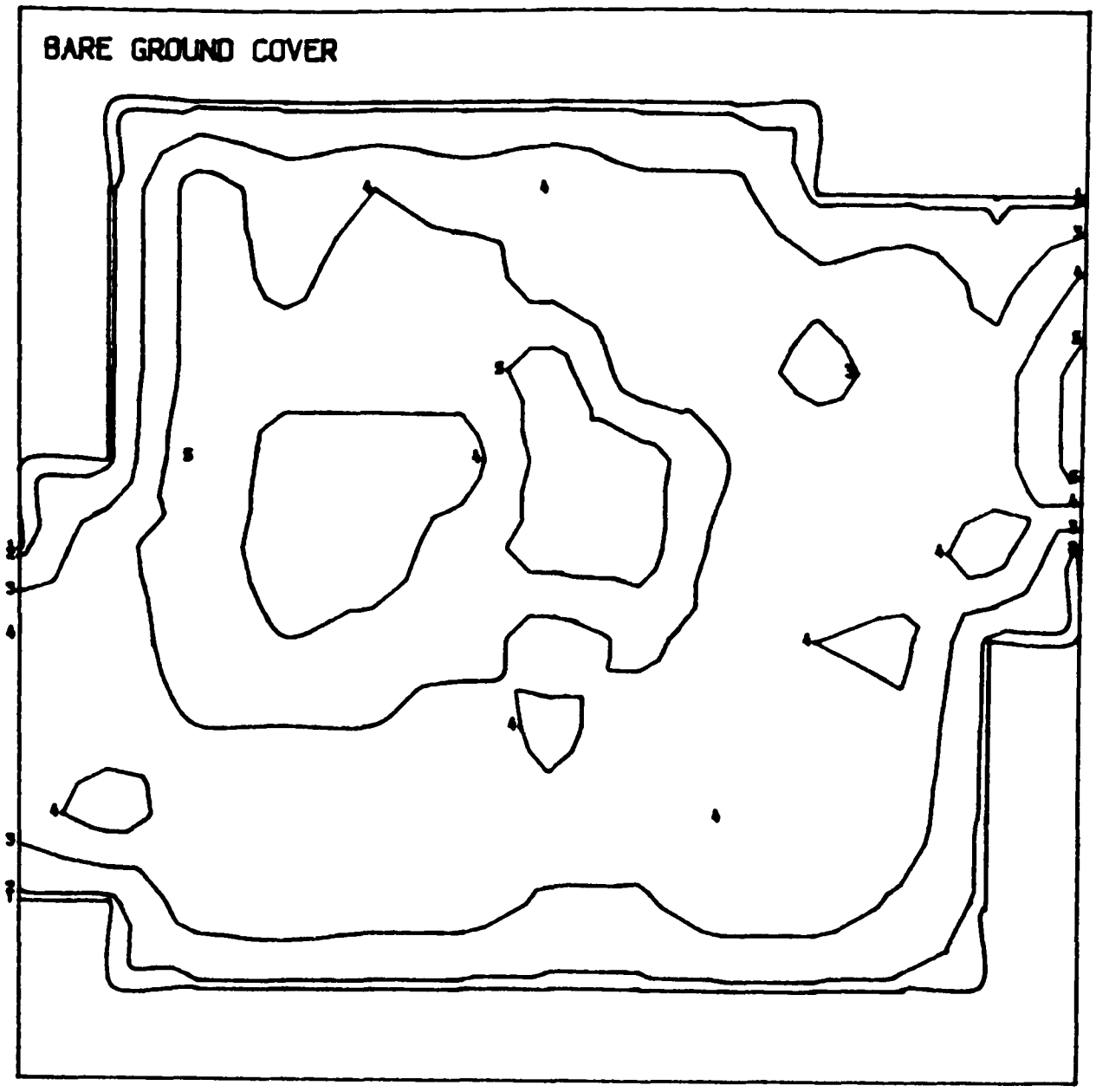
a. Bare Ground Cover

b. Herb Cover

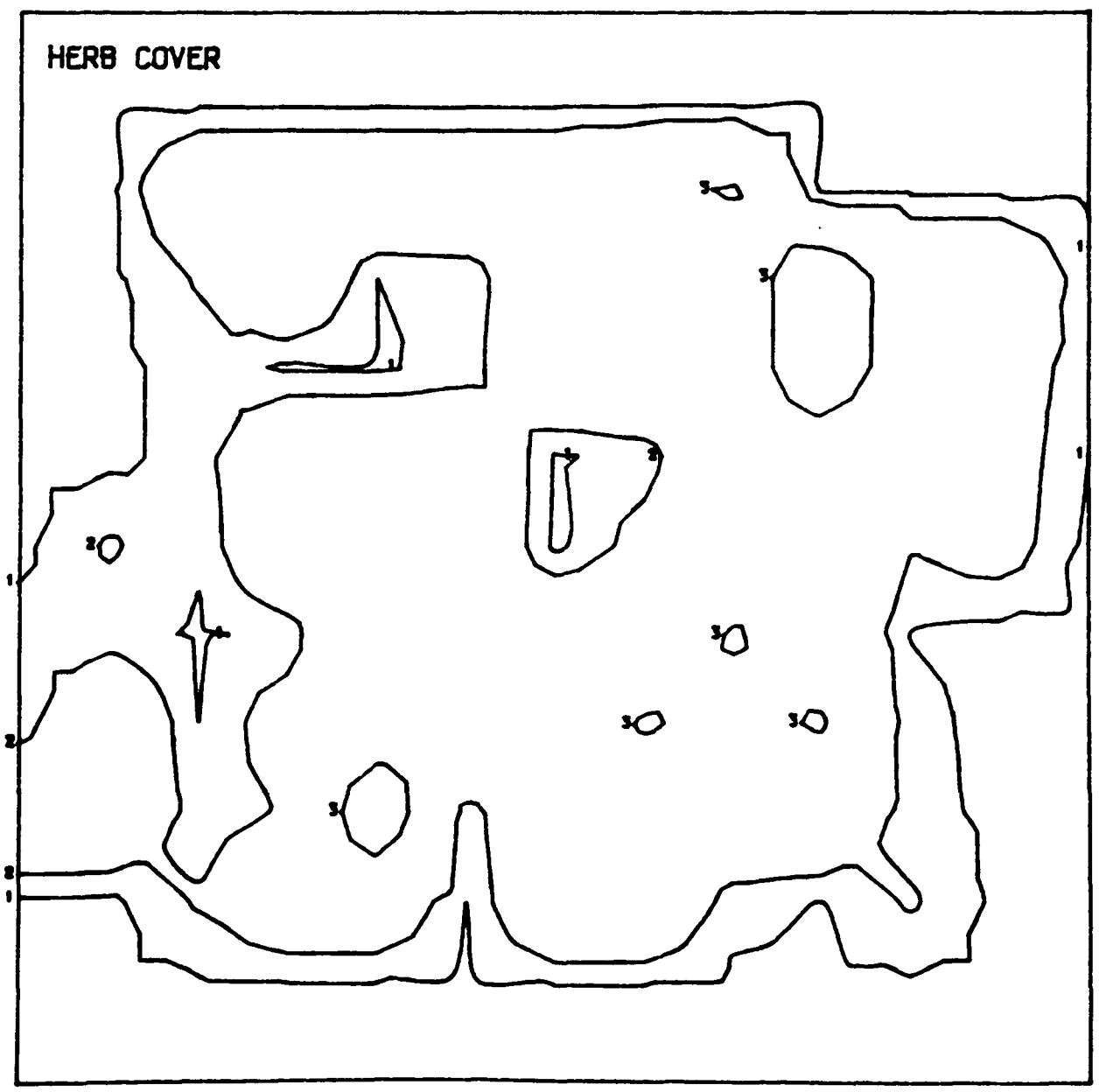
c. Grass Cover

d. Shrub Cover

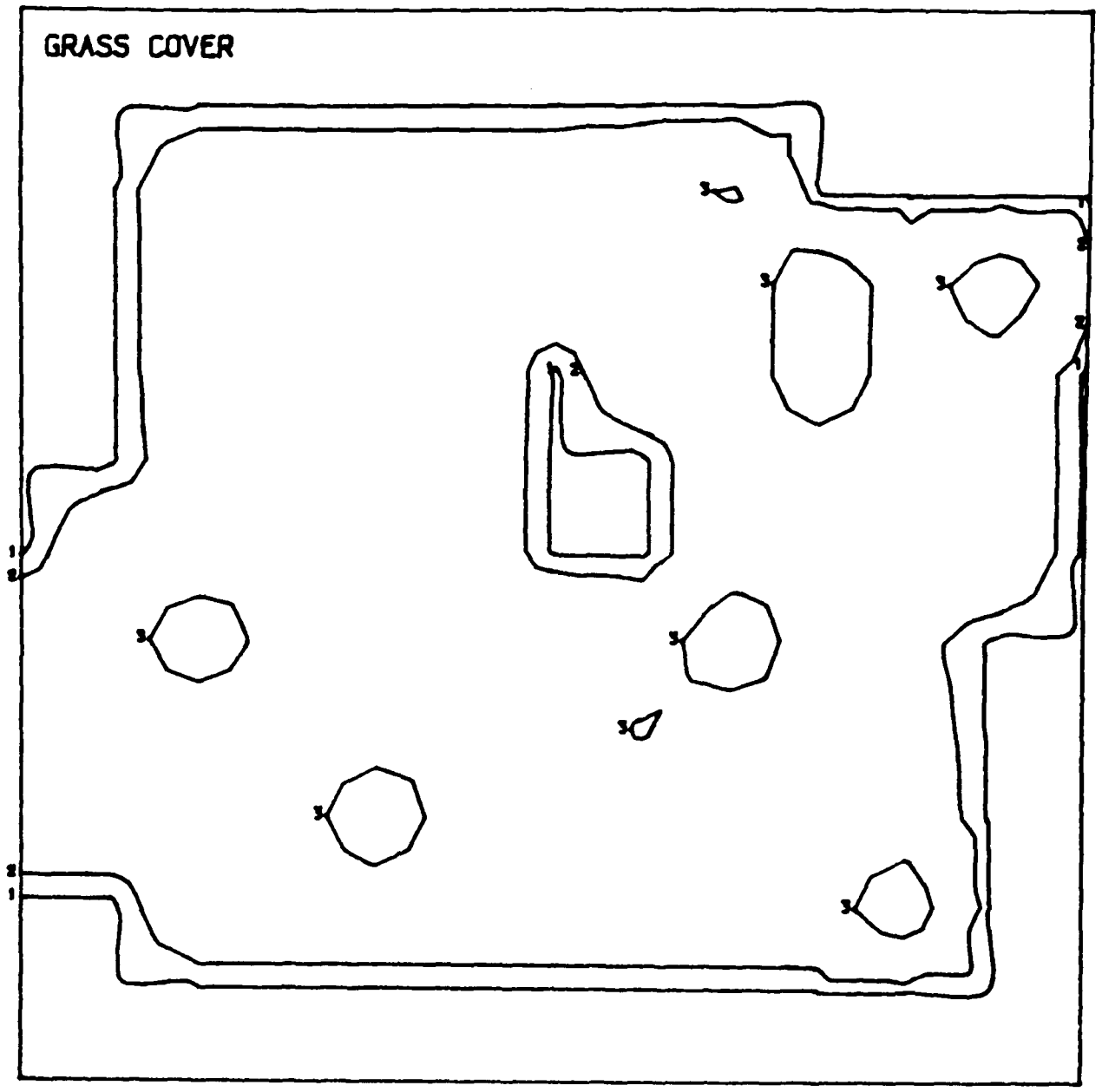
a.



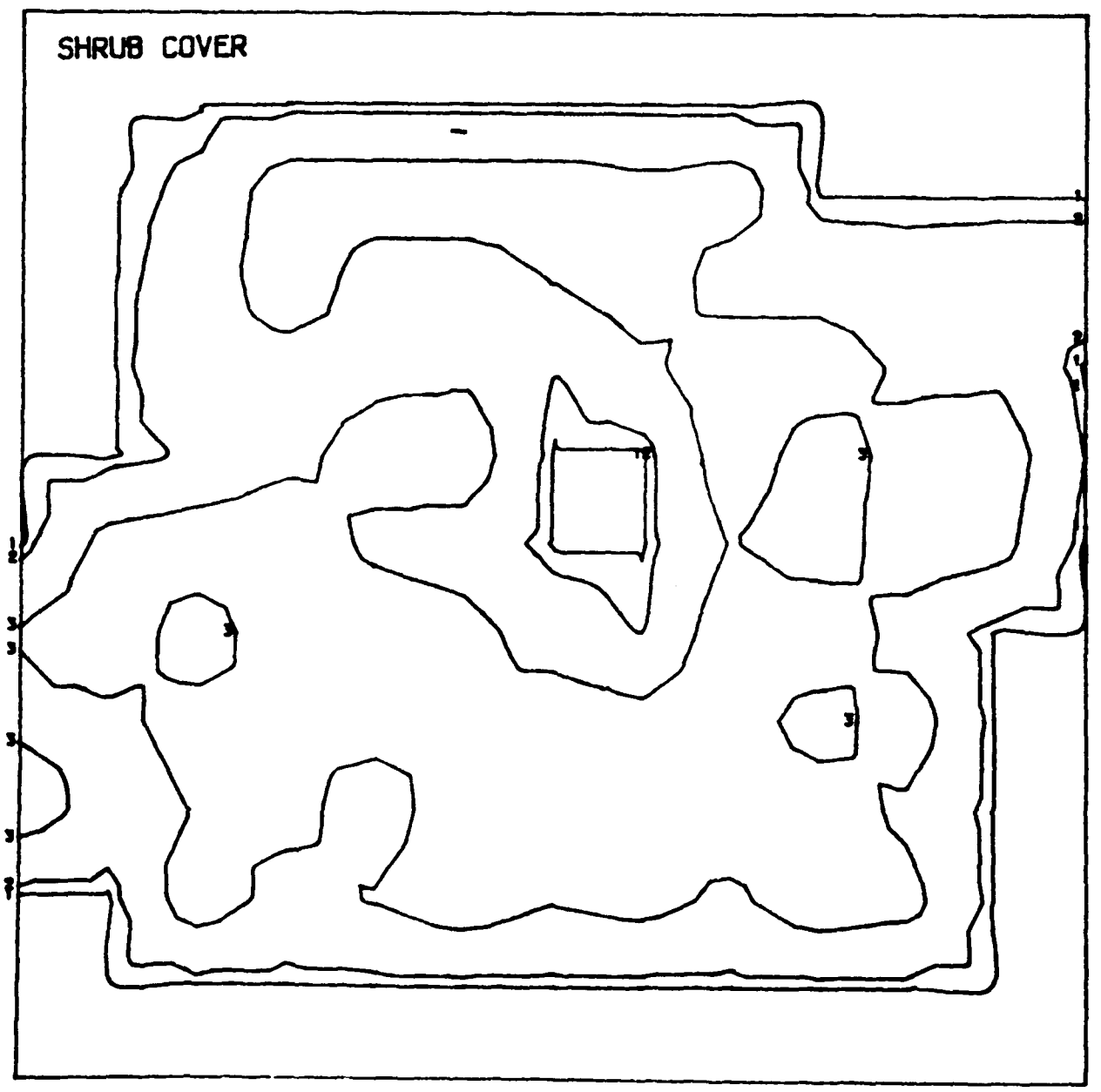
b.



c.



d.



not be defended but are usually used exclusively by one animal, or group of animals, to the exclusion of others. Davies (1978) defined a territory, less rigidly, as applying to circumstances where individual animals or groups are spaced out more than expected from a random occupation of suitable habitat. Here we will consider the home range as the area within which a mara lives. The question of whether the range is a territory, by either of the two definitions, will be addressed in Subsection 3.6.3.

3.3.1 Home Range Analysis Methods

The analysis of home range size and usage is complex, and so far no single method has proved sufficiently powerful to deal with all questions. A large number of methods have been devised to illustrate the configuration and intensity of use of home ranges (see reviews in Dunn and Gipson, 1977; Macdonald, Ball and Hough, 1980; and Don and Rennolls, 1983). I have chosen to use 4 methods here, each of which is appropriate to illustrate different aspects of the way maras use the area in which they live. These methods are: grid cells (Voigt and Tinline 1980), convex polygons (as in Hough, 1980), the Population Utilization Distribution (Ford and Krumme, 1979), and the Prevailing Range (Doncaster, 1985). The use of each of these methods will be discussed below.

The Grid Cell

This method has the advantage of being one with which we in Oxford are very familiar (see Newdick, 1983; Doncaster, 1985; and Hofer, 1986). In addition, a comprehensive computer program named ICELL has been written by Malcolm Newdick (*Op. cit.*) to analyze range data using grid

cells. It is a non-parametric method which accounts well for a patchy environment, an uneven intensity of usage across a range, and convoluted range boundaries. It does, though, require large data sets since it does not rely on mathematical distribution models. The principal features of this method are reviewed below:

- The study area is divided into a grid of cells of a set size. For each location obtained for an animal, through observation or radio triangulation, the grid cell into which the location fell is tagged as part of that animal's range. Each of the eight surrounding cells are tagged as influence cells except that, at the range boundary, influence cells on the outer edge are not counted.
- The size of the grid cells is predetermined as that which gives the highest boundary resolution while maintaining continuity between frequented cells comparable to that suggested by a simple range-estimate made from "eye-balling" a plot of radio locations. If the cell size is too small the range revealed by this method will appear as a series of apparently disconnected islands, making no allowance for the animal's movements between cells. Too large a cell size will reduce the method's power of resolving boundary configurations, and the sum of unused areas included in the boundary cells will become unacceptably large.
- Home range configuration is revealed by following the lines of boundary cells. These take account of indentations, islands and holes in the range (all of which are ignored by the convex polygon method). The size of the range enveloped by these boundaries is calculated by summing up all fix and influence cells.
- The pattern of utilization of the home range can be estimated from the frequency of fixes and influences,

set at 8 and 1 for these purposes, within each home range cell.

Figure 3.4 illustrates the development of this technique (using data on mara ELF) showing respectively: a grid cell plot using 100 x 100 m cells, a grid cell plot using 50 x 50 m cells, and a plot of the locations only. It is clear that the 50 x 50 m cell size plot shows the highest resolution of relative intensity of use of different cells while also having a well defined boundary. Hence, for all analyses using grid cells done in this chapter a 50 X 50 m cell size was used.

The Convex Polygon

The convex polygon method defines the range as the area delineated by connecting all the outlying points with straight lines such that all internal angles are less than 180 degrees. This is shown for ELF in Figure 3.4.d. Through comparing this plot with the 50 m grid cell plot of the same range the limitations of this method can be seen: the area lying between the points at the north edge of the lagoon and the body of ELF's locations to the south, an area in which ELF was never seen, are included in the range. The convex polygon may thus give a misleading measure of range size and configuration. Furthermore it shows nothing about the pattern of usage within a range. This method is useful graphically, however, for showing the general area which a mara inhabited. Thus, it can be used to show spacing between mara's ranges, as well as changes in range location for an animal in different seasons.

Figure 3.4 (2 pages).

These plots show the range of mara ELF, throughout the period she was tracked, using four different methods. The grid cell plots use the darkness of the symbol to show the relative intensity of use of each cell.

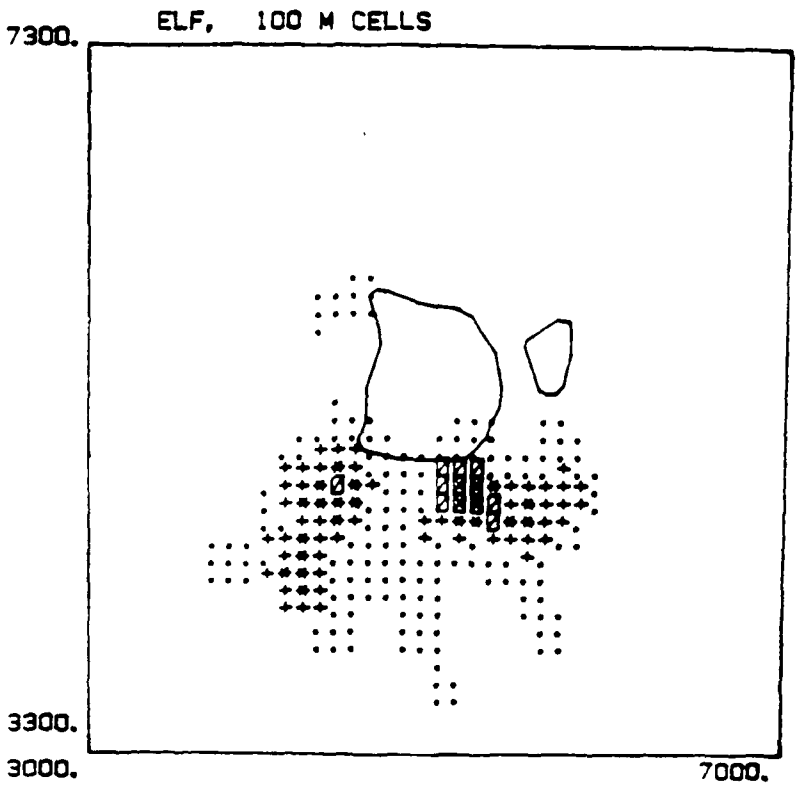
a. Grid cell plot using 100 x 100 m cells

b. Grid cell plot using 50 x 50 m cells

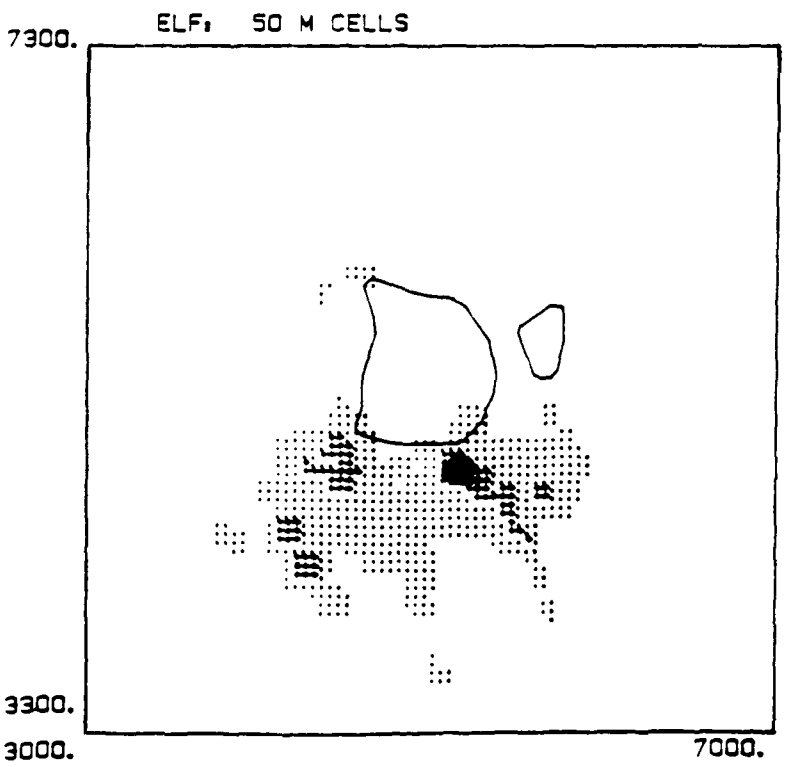
c. Plot of locations of fixes only

d. Convex polygon plot

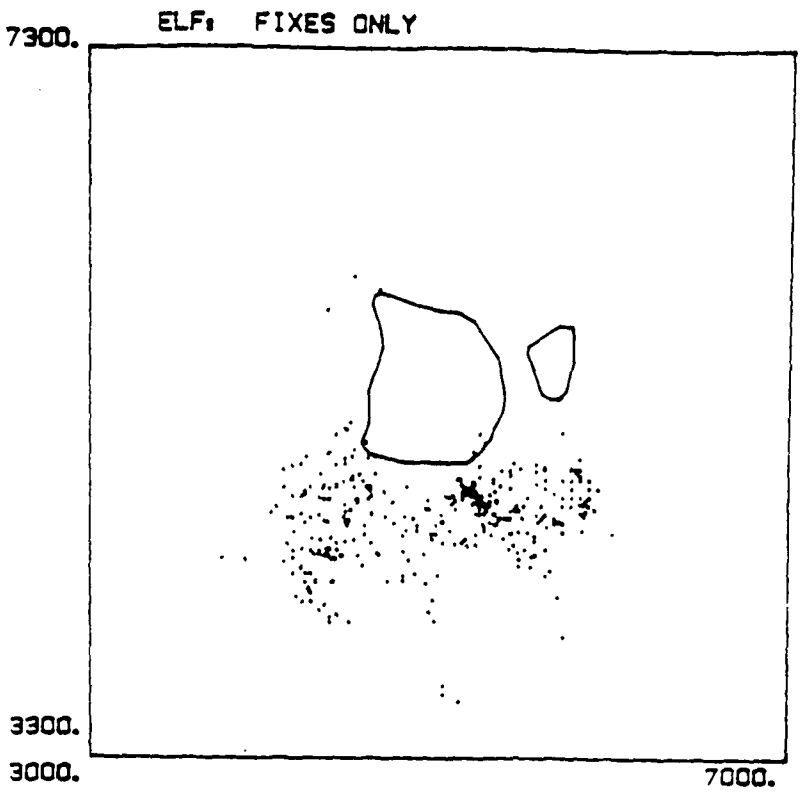
a.


ELF, 100 M CELLS
7300.
3300.
3000.
7000.

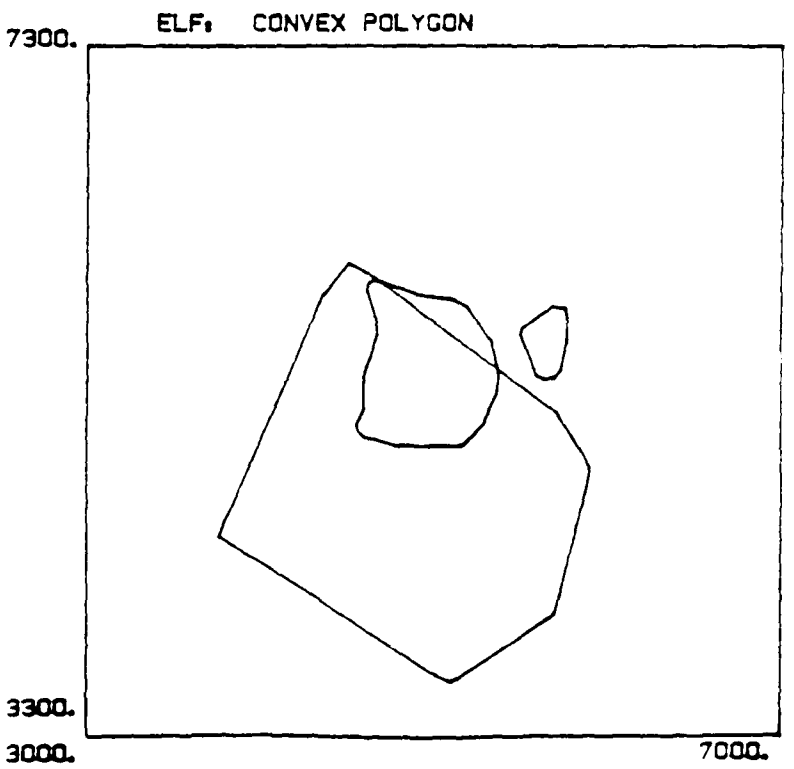
b.


ELF: 50 M CELLS
7300.
3300.
3000.
7000.

c.


ELF: FIXES ONLY
7300.
3300.
3000.
7000.

d.


ELF: CONVEX POLYGON
7300.
3300.
3000.
7000.

The Population Utilization Distribution

This method, developed by Ford and Krumme (*Op. cit.*), derives a range utilization distribution (UD) without making any prior assumptions about either its shape or the statistical properties of the data (such assumptions have limited previous probabilistic methods: e.g. Jennrich and Turner, 1969), and uses the distribution to calculate the minimum areas containing fixed proportions of all observations. The resulting Minimum Area Probability (MAP) function (see below) provides a means of describing range size that takes into account irregular shape and is relatively unaffected by uneven sampling of data on different animals. It is a probabilistic method, and hence is more amenable to statistical testing for variation in range size than the grid cell, convex polygon, or prevailing range methods; as such I have treated it as an index of range size rather than as an actual measurement. I have used it here to test whether there were significant changes in mara range size between seasons. The FORTRAN program PUDNAG2 (provided by Ford and Krumme) was used to carry out this analysis. A brief description of the methodology is given below.

PUDNAG2 derives a UD for each animal by first establishing the frequency distribution of distances between all possible pairs of locations. This is termed a Relocation Distance Function, or RDF. Because it only considers the distance between pairs of observations, the RDF allows the direct combination of data from several individuals. Ford and Krumme call this combined UD the Population UD, or PUD. So long as sampling intervals are approximately similar, any pair of observations are of equivalent significance in revealing distance moved, so the RDF is unaffected by differences in the number of

observations from each contributing individual. Because the RDF considers only the distance between observations without reference to their relative position, the function is not confounded by effects of differing orientation in the original data, as is likely to occur using cartesian coordinates to combine range parameters. The resulting PUD cannot, however, be mapped back to the environment directly. Also, for the results to retain biological meaning it is important that data sets from defined timescales be compared.

The PUDNAG2 program works as follows:

- Prior to running the program all the location data (in x-y coordinates) for each animal to be analyzed are scaled to fit onto a 7 X 7 grid. The grid size is set for all animals such that the individual with the maximum range in either x or y coordinates will fit on the grid (a 400 X 400 m grid size was used here). The 7 X 7 grid dictates (and reduces) the number of possible distances between pairs of observations, thus reducing the system of simultaneous equations that describe the relationship between the RDF function and the UD set out on the grid.
- If the sample sizes are similar for each individual, a UD and MAP function is computed for each. If there are large differences in sample size from contributing individuals, the program combines data from different animals so that sample sizes are more balanced, and the number of successfully fitted UD's making up the PUD (see below) will be accordingly fewer.
- Analysis commences by generating the RDF from an arbitrarily chosen standard initializing UD and comparing the results with the actual RDF generated by the data for each individual (or combination of individuals). In one run the program iterates 250 times, continually modifying the initial UD, and hence RDF, employing an optimiser to select the least squares

fit between the RDF of the original data and the RDF of the derived data. In this way the initial UD is sequentially modified to produce an RDF which matches the RDF of the original data.

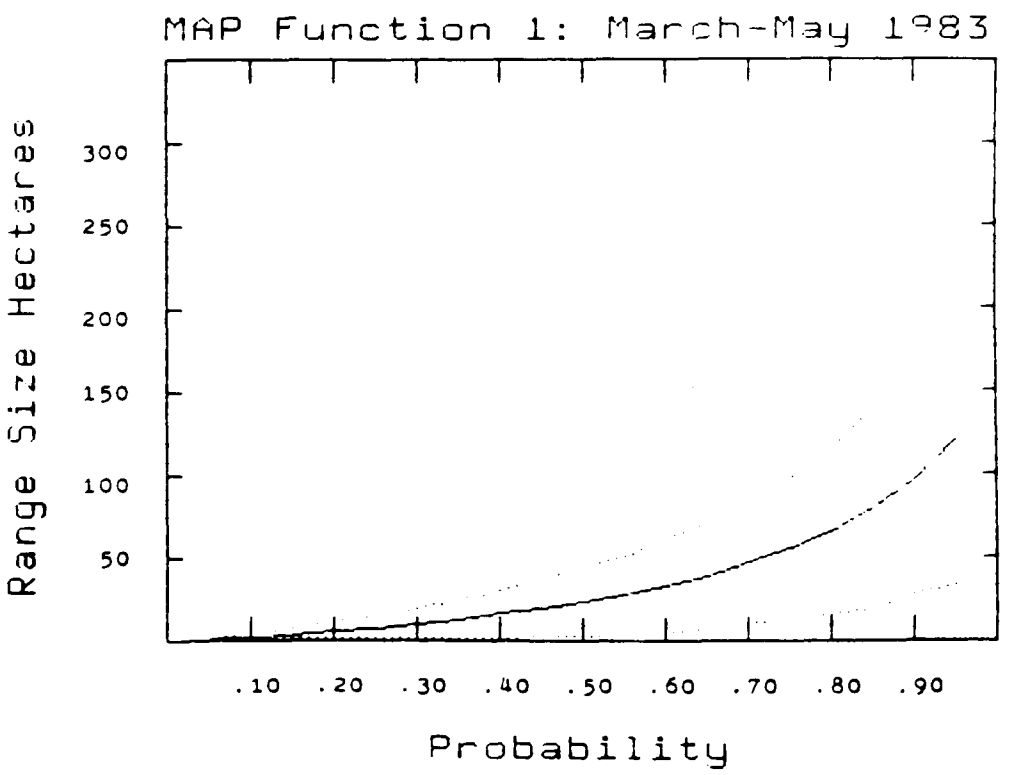
- The optimiser employs a random element, with the consequence that there is variability in the solution according to the random seed number used. For this reason the mean results of 5 runs of the program, each seeded with a different random number, were used to arrive at a best estimate of the PUD.
- The results for each individual (or combination of individuals) are combined to make a PUD by taking the mean areas at equiprobability of occurrence (see below).

The resulting PUD is analyzed by considering the minimum areas that contain known proportions of the locations (the PUD MAP function). These areas are determined by interpolating between the gridded probabilities to locate contours of equiprobability. PUDNAG2 outputs the minimum areas encompassing 5 - 95% (in 5% increments) of the locations (see Table 3.9). Figure 3.5 shows a plot of a sample MAP function. The variability between individual estimates (for one or a combination of animals) gives the combined mean estimate and associated standard deviation. Because the final estimate is derived from five separate runs of the program the mean area at each probability level is taken as the mean of the five estimates generated in the separate runs, and the standard deviations are obtained by converting the standard deviations to variances, taking the mean variance and reconverting to standard deviations. Ford and Krumme show that the mean estimates for a data set may be compared at each probability level with similar estimates for other data sets using a conventional t-test.

Table 3.9.--Sample MAP index showing the minimum area containing increasing proportions of the composite population's utilization distribution: i.e. in this sample, 95 % of the locations would be found within an area of 118.88 ha. This index is calculated for maras ENF, ELF, PAM, and GCM during the fall (March to May) of 1983.

Probability	$\bar{x}$ Range Size (ha)	St. Dev.
0.10	1.28	1.76
0.20	4.64	5.28
0.30	9.28	9.44
0.40	15.52	14.56
0.50	23.20	20.64
0.60	32.16	27.68
0.70	46.72	36.96
0.80	64.96	49.92
0.90	95.20	68.64
0.95	118.88	85.60

Figure 3.5.--Sample MAP function for the fall ranges of maras ENF, ELF, PAM, and GCM. Figure also plots ± the standard deviation at the different probability levels.



The Prevailing Range

This method, devised by C.P. Doncaster (1985), is based on a grid cell system but calculates an animal's range size as the number of cells in 'use' (the Prevailing Range) at any one time. The Prevailing Range on a given day is calculated by summing the cells the animal was known to frequent that day with those cells which were visited previously and would be visited at a later date. This excludes all cells that were neither visited on the day the prevailing range is being calculated nor would be frequented again although they had been used previously. The Prevailing Range can be calculated for each day an animal was tracked and is best summarized in a plot. Figure 3.6 shows the Prevailing Range plot for maras ELF and PAM. From looking at the range size as measured across the top of the plot one can see how the Prevailing Range may remain unchanged over several weeks or months during a time of range stability, or may change from day to day if the range is drifting or undergoing a catastrophic change in location. It is an especially useful method for exploring a pattern of shifting range usage. However, this method requires substantial data sets so I was only able to use it on maras ELF and PAM.

3.3.2 Results

Finding answers to questions about the nature of a species' ranging patterns is no easy task. What at first sight seems straightforward is often found to be extremely complicated. To start, I will summarize data on the first two points made at the start of the section: (i) the description of range size and configuration, and (ii) the pattern of range usage. Then I will examine seasonal

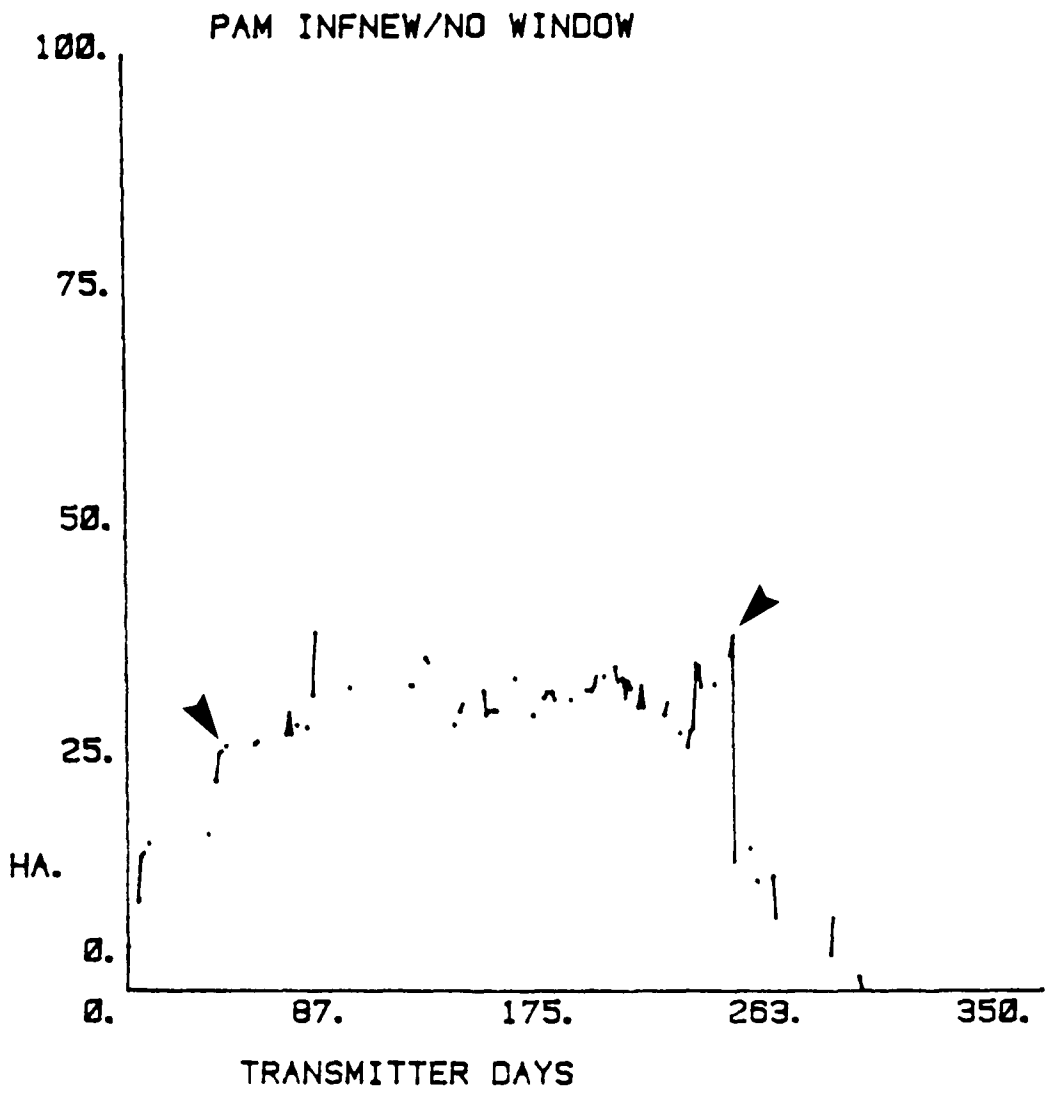
Figure 3.6 (overleaf).

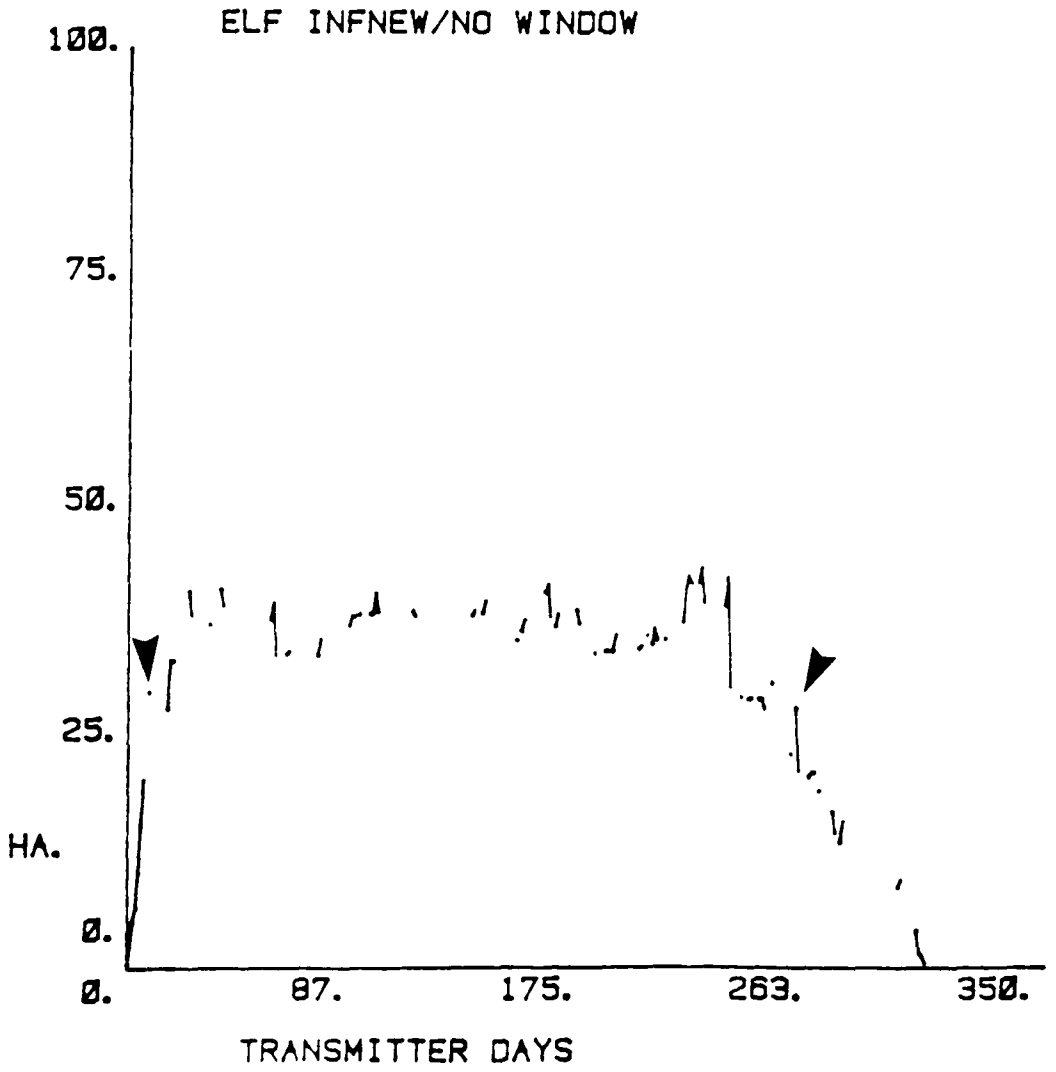
Plots of variation over time in prevailing range size, produced by program INFNEW (Doncaster, 1985) for maras ELF (a) and PAM (b) between March 1983 and February 1984. Transmitter days are the number of days since the mara was first radio-collared. The line mapping prevailing range size joins consecutive days of tracking, so gaps in the line reveal gaps in the tracking record of at least one day. The calculation of area is made for each transmitter day on which data were collected by summing the area of all cells (and influences) the mara visited on the day, plus, those cells which the animal frequented in the past and will use again in the future. Prevailing range graphs shows excursions as steep peaks, and periods of stable range size as plateaus. The INFNEW program also calculates the mean prevailing range size, for a set time period, by integrating the area under the plot of range size and dividing it by the number of days. The problem in interpreting these plots is to decide where to start and end the integration because of the steep rise at the beginning, and fall at the finish, of the plots. The solution to this problem are discussed below:

- When an animal is first radio-collared, depending on the intensity of tracking, several days pass before sufficient radio locations have been obtained to reconstruct an accurate picture of the area the animal is using. Doncaster has defined the point where the first reliable estimate of the prevailing range size is obtained as the day at which the range size first ceases to climb despite the fact that data collection continues.

- The rapid decline at the end of the plots exist because the prevailing range includes areas an animal visits in the future. As the amount of data on the 'future' movement of an animal declines at the end of the study period the plotted range size declines as well. Finally, on the last day an animal was tracked the range includes only the cells the animal was recorded visiting that day. Thus, to determine the cut off point for the integration period I choose to use the last day on the plot where the range size climbed from the previous day.

In practice, delineating the period over which to integrate range size is quite obvious when one views the plots. On both plots I have marked the start and cutoff points.


PAM INFNEW/NO WINDOW
100.
75.
50.
25.
HA.
0.
0.
87.
175.
263.
350.
TRANSMITTER DAYS


ELF INFNEW/NO WINDOW
100.
75.
50.
25.
HA.
0.
0.
87.
175.
263.
350.
TRANSMITTER DAYS

patterns of range usage before, finally, presenting an estimate of range size which incorporates the main features of the mara's ranging behaviour.

General Description of Ranges

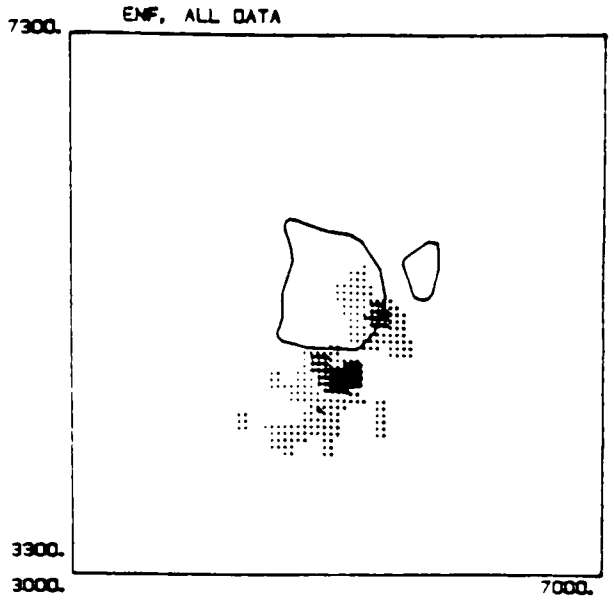
The clearest way to show the general pattern of size and configuration of an animal's range is through graphical representation of the data. Figure 3.7 shows grid cell plots of the ranges of the 9 radio-collared maras during the entire period for which each animal was tracked. From examination of these plots and Table 3.10, where other features of these ranges are detailed, the following characteristics of all the ranges can be seen:

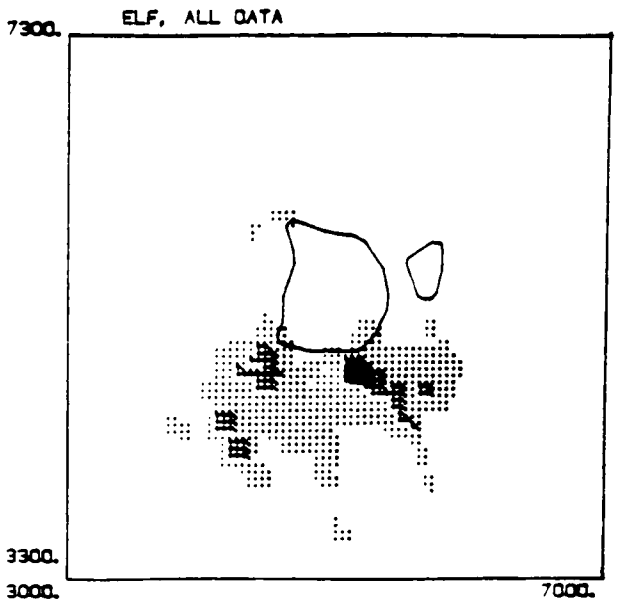
1. Range boundaries are highly convoluted.
2. There is considerable individual variation in home range size. Ranges varied, as calculated from the grid cells, from 81.75 ha for ENF to 243.25 ha for TIF (see Table 3.10).
3. In each range there are several areas of intensive use.
4. A few small islands of unvisited areas occur in most ranges.
5. There are numerous satellite areas outside each range. Satellite areas are small aggregations of a few grid cells disconnected from the main part of an animal's range.

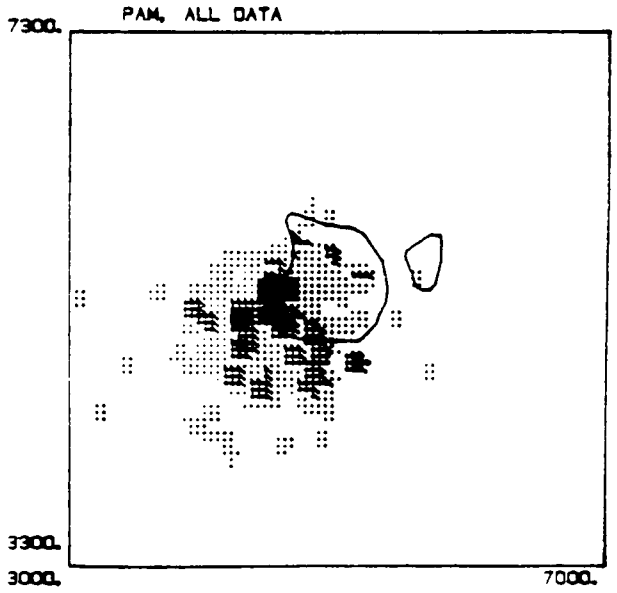
There is considerable variation in the number of fixes (136 to 841) and the span of days (56 to 590) over which maras were tracked (see Table 3.10 (above). To see how these variables might affect range size, the number of fixes and the span of days tracked for each mara were correlated with range size. The following results were obtained:

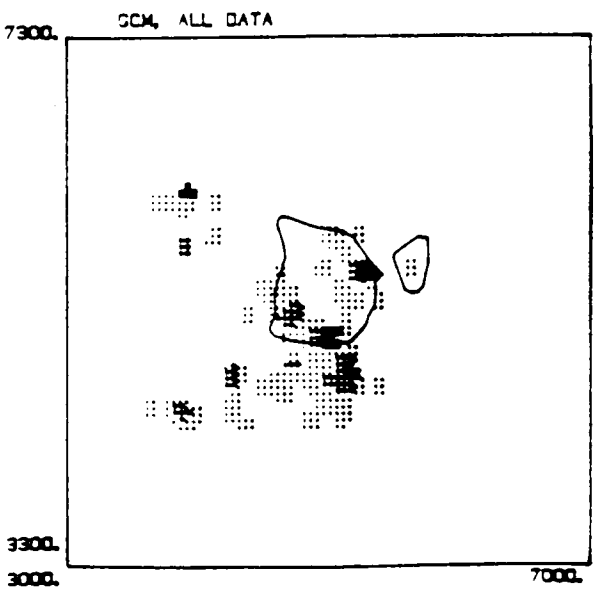
Figure 3.7 (2 pages).

Grid cell plots of the ranges of nine radio collared maras throughout the period each animal was tracked. Ranges were plotted using the program ICELL with a 50 x 50 m cell size. Each range plot shows the La Blanca lagoon as a means of orienting the ranges relative to each other.


ENF, ALL DATA
7300.
3300.
3000.
7000.


ELF, ALL DATA
7300.
3300.
3000.
7000.


PAM, ALL DATA
7300.
3300.
3000.
7000.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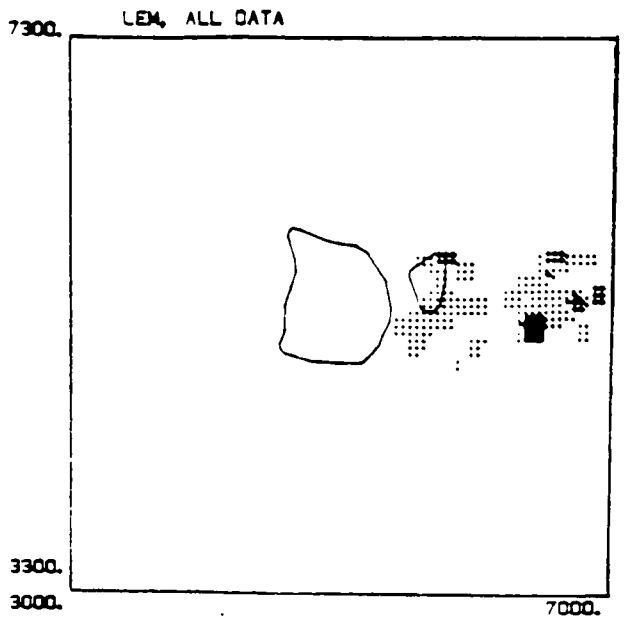
3000.
7000.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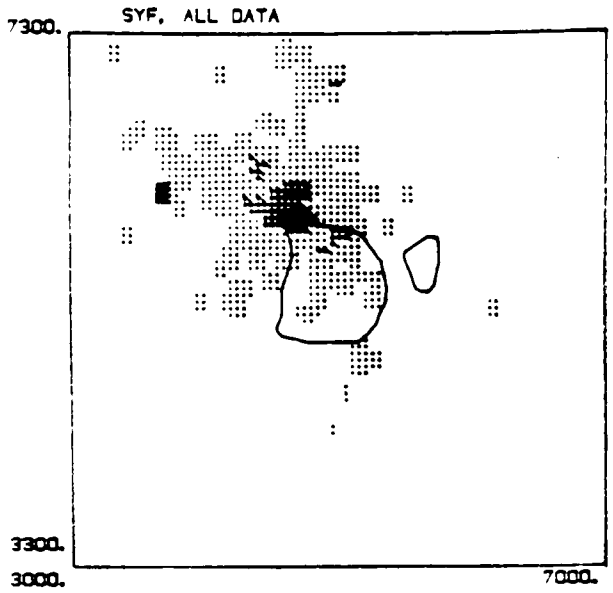
3300.
3000.
7000.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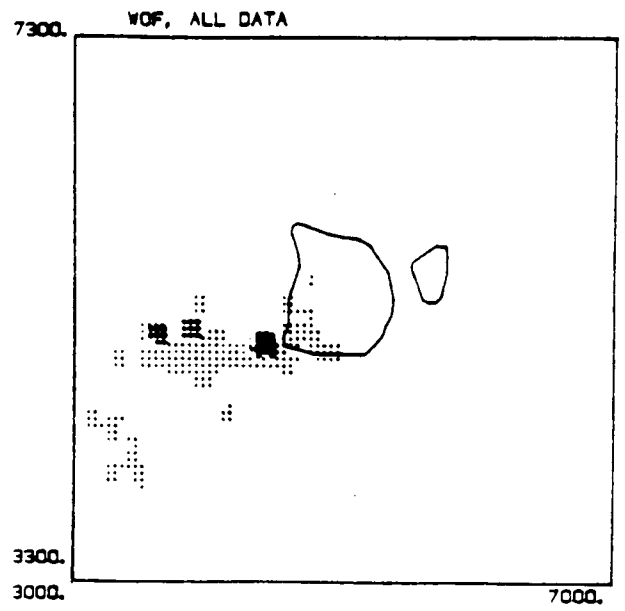
3000.
7000.


WOF, ALL DATA
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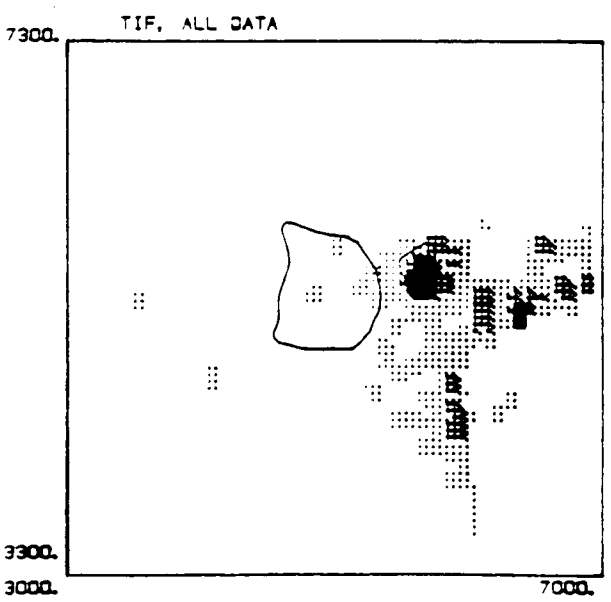
3300.
3000.
7000.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3300.
3000.
7000.

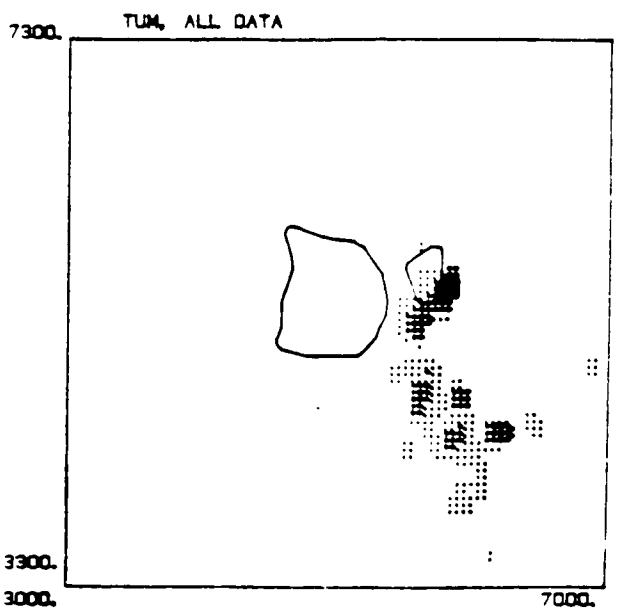

TUM, ALL DATA
7300.
3300.
3000.
7000.

Table 3.10.--Estimates of range size (in hectares), using the grid cell and convex polygon techniques, for 9 radio-collared maras. All location data on each mara were used. Two different grid cell range estimates are given: (i) the number of cells (fixes and influences) which the animal was recorded occupying during the study period; and (ii) the total range, which counts additional cells connecting non-adjoining cells by the shortest possible line. In future, only the total range estimate will be used. For time period each animal was tracked see Table 3.1.

Mara Name	Number Fixes	Span Days Tracked	-Grid Cell- Occupied Area	Total Range	Convex Polygon
ENF	649	108	64.75	81.75	102.09
ELF	841	409	158.75	212.25	312.36
PAM	797	590	166.75	227	352.68
GCM	181	276	104.5	171.25	390.41
LEM	122	139	55.5	88	94.56
SYF	531	416	191	284	515.44
WOF	136	185	59.25	90	153.44
TIF	401	414	151.75	243.74	452.42
TUM	136	56	67.25	90.5	197.23

Statistical findings on above data:

1. Spearman rank correlation of the number of fixes with the total range per mara was not significant ($r_s = 0.4268$, $N = 9$).

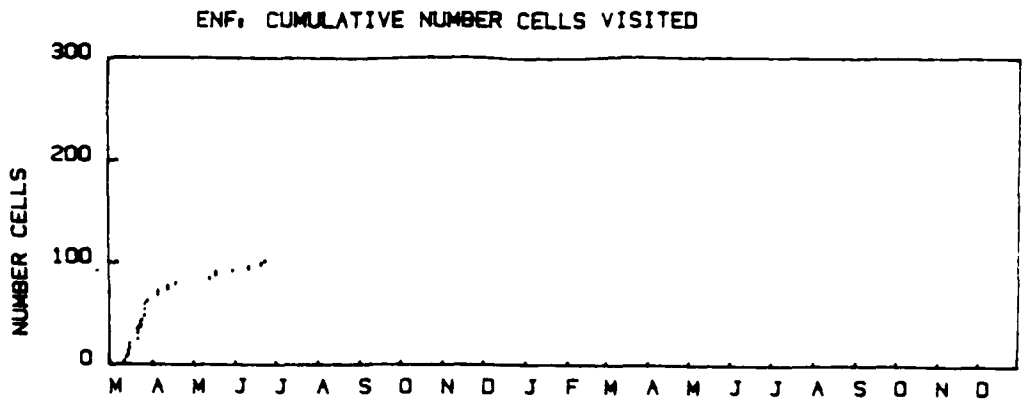
2. Spearman rank correlation showed a positive significant correlation between the span of days over which a maras was tracked and the total range size ($r_s = 0.85$, $N = 9$, $P < 0.01$).

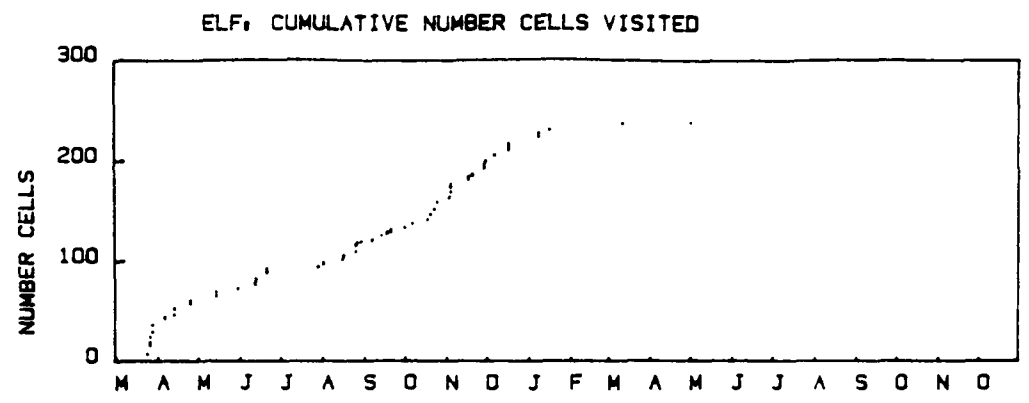
- Although the correlation coefficient was positive there was not a significant correlation between the number of fixes and the maras' range sizes (r_s = 0.427, N = 9, N.S.).
- There was a highly significant correlation between the span of days over which a mara was tracked and the final range size (r_s = 0.85, N = 9, P < 0.01).

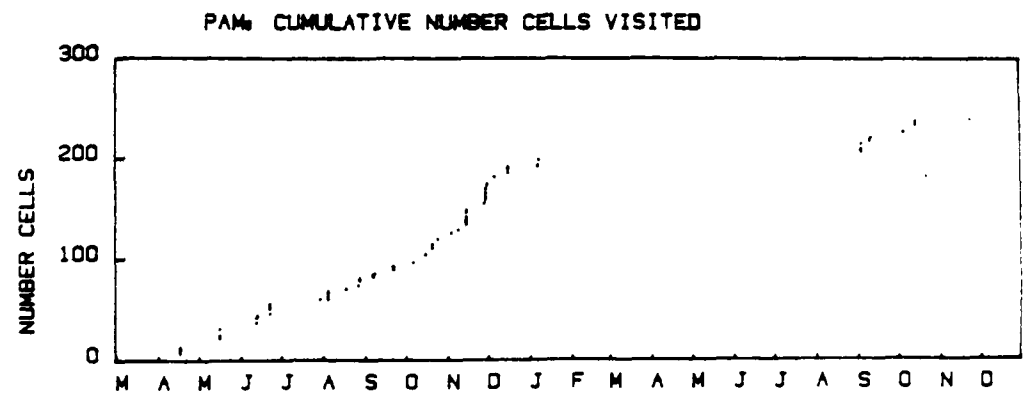
With these results it is apparent that range data on different animals are not directly comparable unless the animals have been radio-tracked for equivalent lengths of time. This is further illustrated in Figure 3.8 where the curve of the cumulative number of cells visited for each mara (in 10 fix increments to account for tracking intensity) are plotted against the research period. From these plots one sees that maras were continually visiting new cells. In species which have ranges which are stable in size and location a different pattern is seen in these kinds of plots. At first, as the number of fixes recorded climbs there is an increase in the number of cells visited. This climb is followed by a leveling off, and then a plateau as the number of cells which an animal has been known to visit equals the number of cells in the animal's range (see, for example, data on foxes in Ables, 1969). With maras, the few level areas in these curves invariably coincide with periods where few fixes were obtained. These results show that there is considerable instability in the location of individual mara's ranges. They are also consistent with the convoluted range boundaries and large number of satellite cells--signs that ranges are in a steady state of flux as maras continually move into new areas.

Figure 3.8 (2 pages).

Plots of the cumulative number of cells visited against time for each of the radio tracked maras. One point is plotted for every 10 fixes recorded; thus the plots also show the intensity of tracking effort on each mara over time.


ENF: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D


ELF: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D


PAM: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
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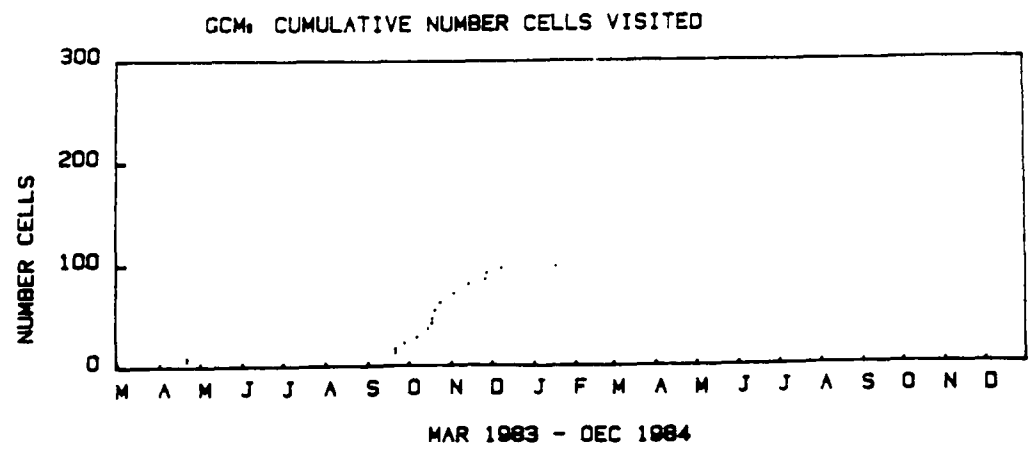
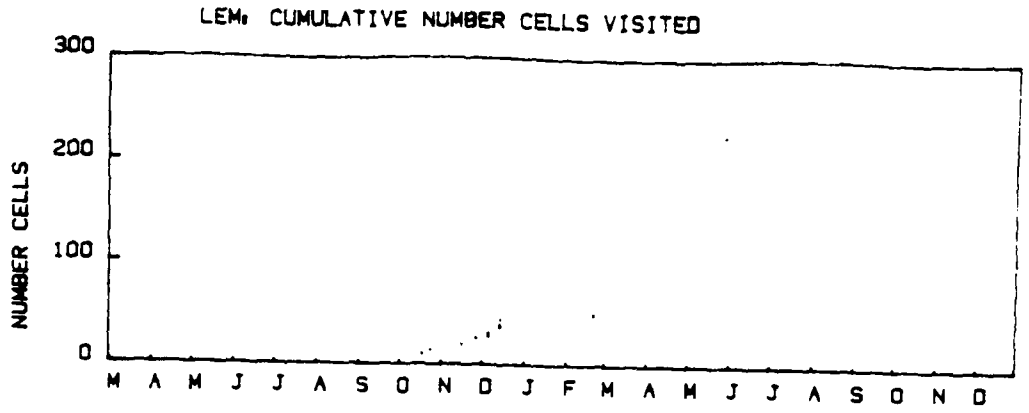
200
100
0
M A M J J A S O N D J F M A M J J A S O N D


GCM: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984


LEM: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
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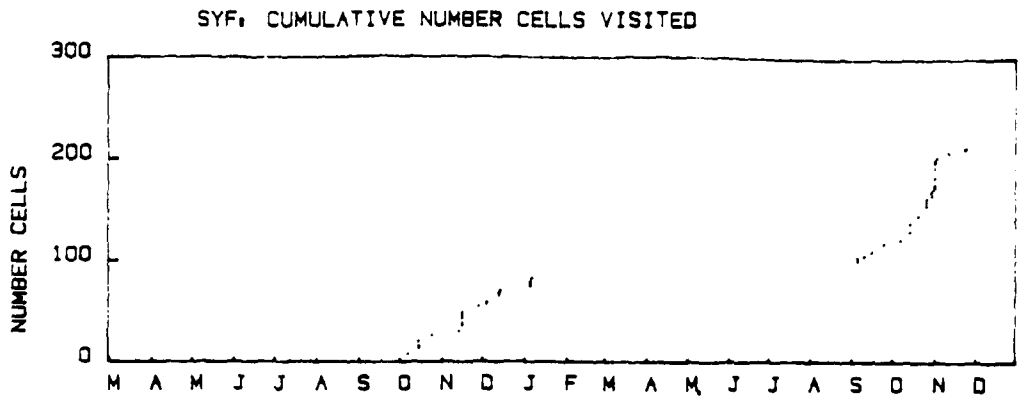
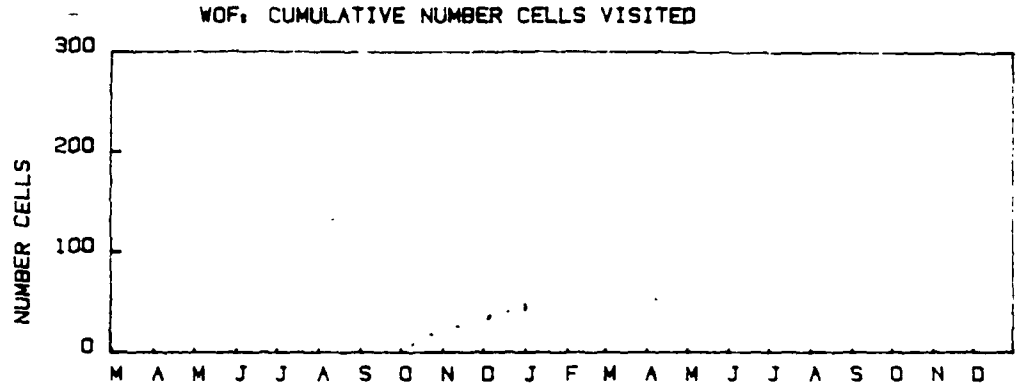
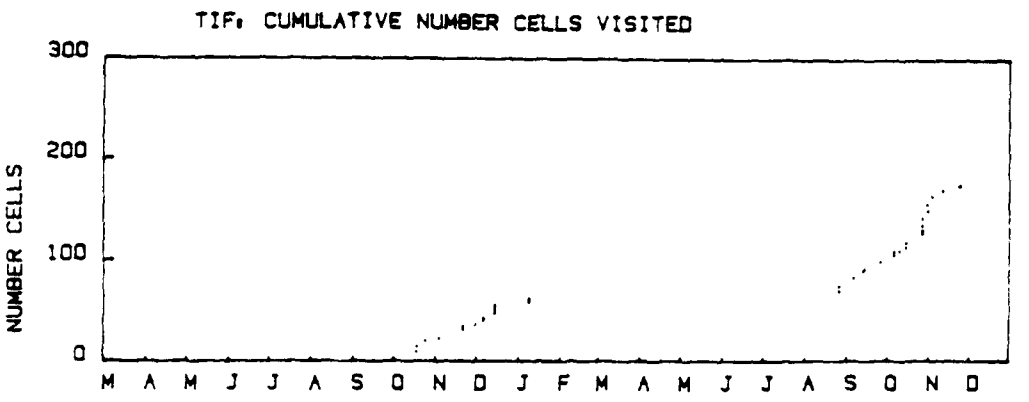
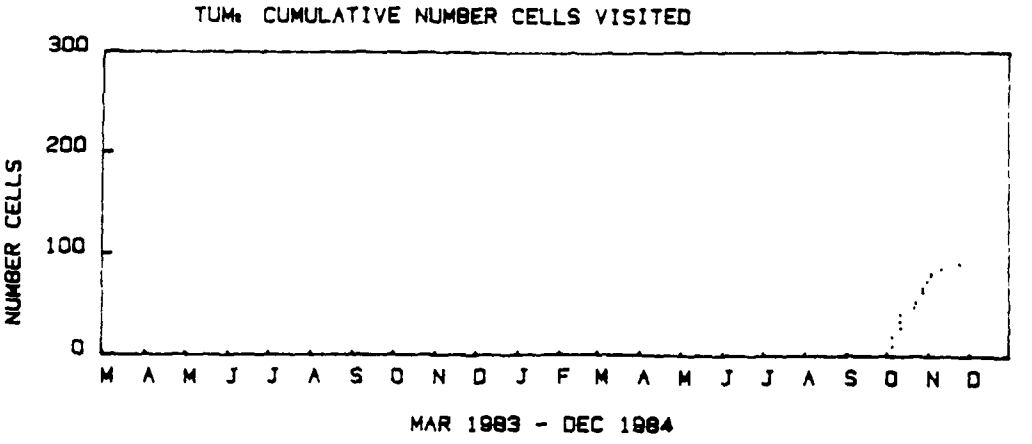
100
0
M A M J J A S O N D J F M A M J J A S O N D


SYF: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D


WOF: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D


TIF: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D


TUM: CUMULATIVE NUMBER CELLS VISITED
NUMBER CELLS
300
200
100
0
M A M J J A S O N D J F M A M J J A S O N D
MAR 1983 - DEC 1984

Seasonal Ranges - Patterns of Usage

As a means of comparing how the pattern of range usage changes through time, the data sets were divided into seasonal blocks. Looking at the data by seasonal blocks is an artificial division since, as shown in Figure 3.8 (above), maras were continually visiting new cells. However, a seasonal division of the data can be seen as a window onto the animals' continual movements. As such, a seasonal analysis allows comparison between different maras' ranging patterns, as well as an examination of how ranging patterns fluctuate during the year. This is because maras could be selected for analysis within seasons so that: (i) the problem of correlation between range size and the number of days over which data were collected is reduced since animals would have been tracked over roughly the same number of days, and (ii) the amount of location data for different animals are more nearly equal. To eliminate animals on which I had limited data within seasons I used the following criteria:

1. Full days of at least 9 hrs of tracking must have been collected on the animal in at least 2 of the 3 months in each season.
2. At least 80 fixes must have been recorded during the season.

Table 3.11 shows the range sizes, and the number of hours in which fixes were obtained, for each animal in each season during which I had adequate data.

To test whether the problem of varying sample sizes had been adequately dealt with; the size of seasonal ranges (obtained from ICELL) were correlated with the number of hours in which fixes were obtained for the radio-collared animals in each season. There was not a significant

Table 3.11.--Seasonal range sizes for 8 maras. For each seasonal range the (i) total range size (from grid cells counts), and (ii) the number of hours during which fixes were obtained, are given. Seasonal range size $\bar{x}$ = 97.71 ha, ± 42.53.

	-Seasons of the Year-					
	1983			1984		
Mara	Mar-May	Jun-Aug	Sep-Nov	Dec-Feb	Sep-Nov	Mean
ENF	75.25 133					
ELF	144.25 66	75.00 63	101.50 121	82.25 45		100.75 74
PAM		85.75 58	118.00 98	48.50 29	71.50 39	80.94 56
GCM			120.50 75			120.50 75
SYF	91.25 59	84.50 41	175.75 97	117.17 66		
WOF		33.25 33				33.25 33
TIF		68.50 35	197.50 60	133.00 48		
TUM				90.50 60		90.50 60

correlation (r_s = 0.3769, N = 17, N.S.) so seasonal ranges of different maras may be seen as roughly comparable.

Two main features of seasonal mara ranges will be investigated: (i) changes in size (which more accurately reflects changes in rate of visiting new cells), and (ii) changes in location. Each of these will be dealt with in turn below.

Seasonal Changes in Range Size

The Maras' seasonal ranges varied in size from 33.25 ha to 197.5 ha, with a mean range size of 97.87 ha (± 13.59, see Table 3.11). As a means of accounting for unequal sample sizes the Population Utilization Distribution (PUD) was used to compare range sizes between seasons. All available data for each animal were included to create MAP probability functions for each season (Table 3.12). The results of these analyses are summarized in Figure 3.9 where the range size at the 95% probability level is plotted with the standard deviation for each month. Using the t-test formula in Ford and Krumme (*op. cit.*), no significant differences were found between the range sizes at the 95% probability level between any of the seasons.

Seasonal Changes in the Location of Ranges

Because of the complexity of the data, the easiest way to illustrate changes in the location of maras' ranges is through range plots. Figure 3.10 shows convex polygons of the individual maras' ranges in different seasons of the year. Only seasons were used where I had enough data to satisfy the requirements as laid out above, so I was only

Table 3.12.--Comparison of MAP function home range size estimates at the 95% probability level for maras in different seasons of the year. No significant differences were found between range sizes in the different seasons using a T test (formula in Ford and Krumme, 1979).

Seasons	Mean Range Size (ha)	St. Dev.
Fall 1983	118.88	85.60
Winter 1983	171.40	95.04
Spring 1983	174.08	38.08
Summer 1984	135.84	39.36
Spring 1984	218.56	91.68

Figure 3.9.-- Plot of mean range size (error bars mark standard deviations) for maras at the 95% probability level in different seasons of the year.

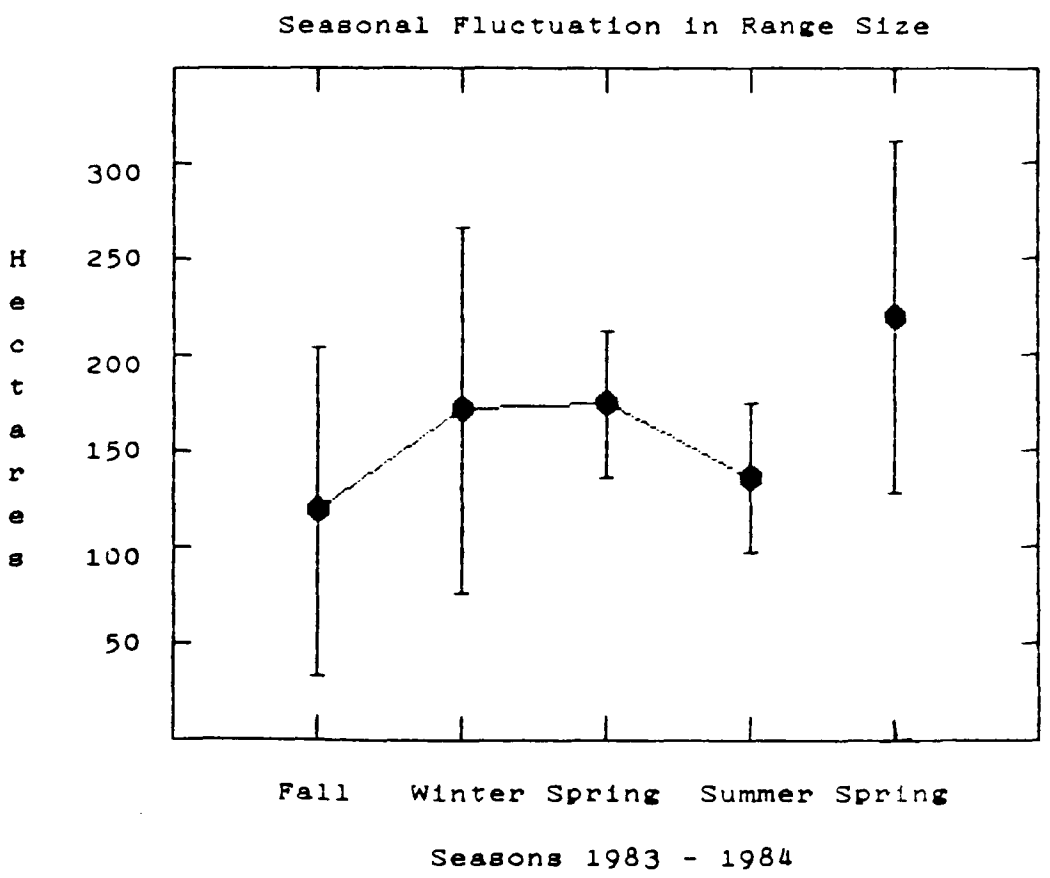
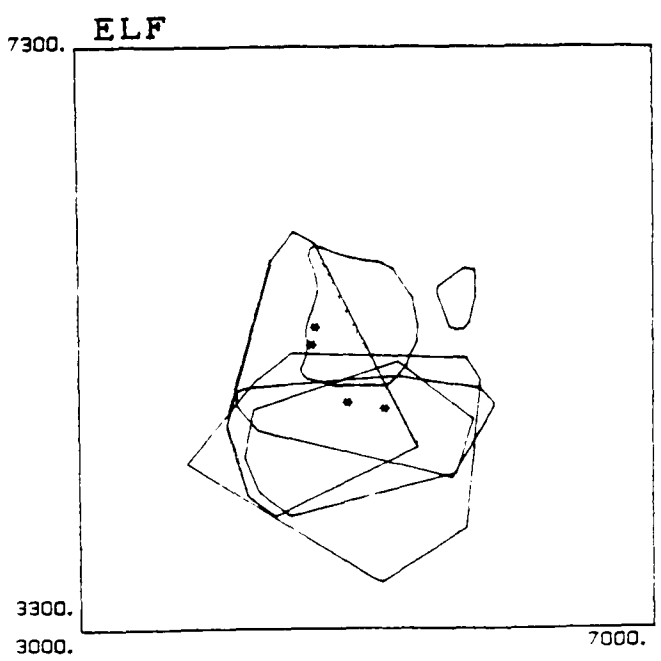
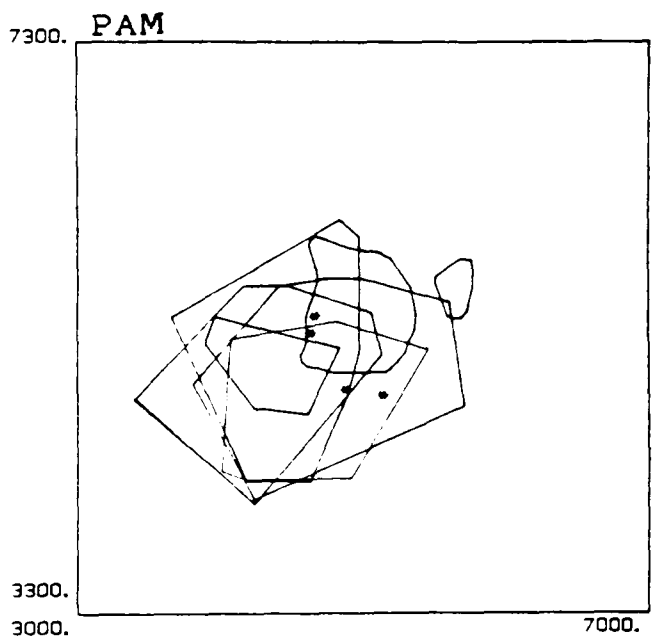
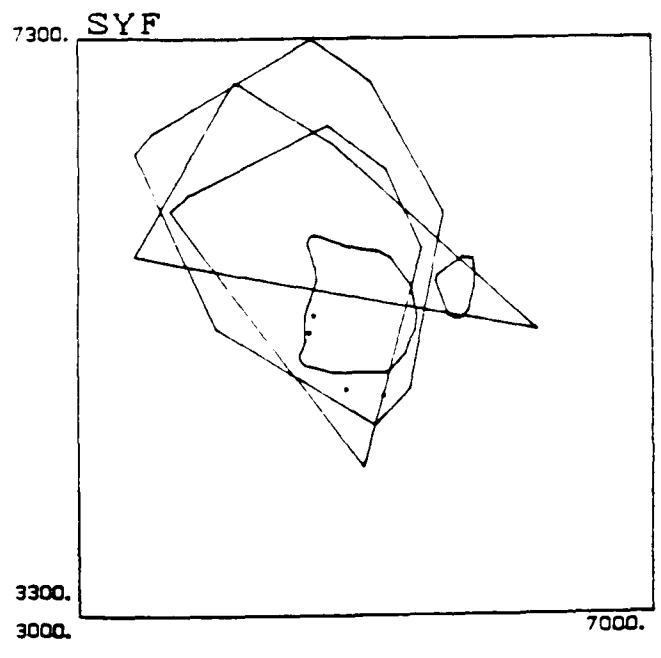
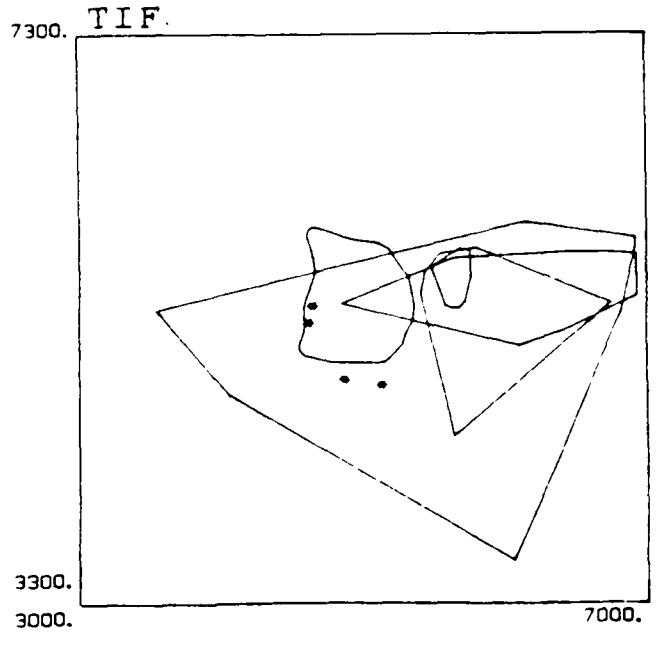


Figure 3.10.--Convex polygon plots for the seasonal ranges of 4 maras (ELF, PAM, SYF, and TIF) who were tracked for more than two seasons. The stars on the plots mark the locations of active den sites; also, the location of the two lagoons are marked on each plot.









able to compare seasonal ranges in maras ELF, PAM, SYF, and TIF. From these polygons the following characteristics of the maras' inter-seasonal ranging patterns can be noted:

1. There is considerable spatial overlap between each mara's seasonal ranges.
2. For each mara there was an area which was contained in its range in all seasons sampled. These 'core' areas seemed to provide a geographic center around which the seasonal ranges revolved.
3. There was no consistent pattern in the inter-seasonal changes in direction, orientation, or location of ranges for any of the maras compared.

Below, these data are examined in more detail in two further analyses investigating (i) the extent inter-seasonal ranges overlapped in space, and (ii) the spatial correlation of ranges between different seasons.

Inter-seasonal Range Overlap

The ICELL program was used to calculate the number of cells which a mara's range shared in two different seasons. The number of hectares shared was then divided by the number of hectares in each seasonal range to obtain an estimate of the proportion of the ranges overlapping. This proportion has to be calculated for both ranges in a comparison since they may differ in size between seasons. The results are shown in Table 3.13. Ranges overlapped from 3 to 33.5 ha with the proportion of the ranges overlapping varying from 0.04 to 0.37. Clearly, individuals' ranges are not stable in space between seasons.

Table 3.13.--Inter-seasonal overlap between ranges. Numbers given are: (i) number of ha in common between seasons, the proportion of the earlier (ii) and later (iii) season's range in the overlap zone, and (iv) the Spearman rank correlation coefficient for the two ranges.

Mara		-Amount of Overlap-		
ELF		Mar-May	Jun-Aug	Sep-Nov
	Jun-Aug	23.25 (0.16, 0.31) -0.375		
	Sep-Nov	25.00 (0.22, 0.25) -0.565	23.25 (0.31, 0.23) -0.430	
	Dec-Feb	13.75 (0.10, 0.17) -0.658	8.75 (0.12, 0.11) -0.696	21.50 (0.21, 0.26) -0.440
PAM		Jun-Aug	Sep-Nov	Dec-Feb
	Sep-Nov	30.73 (0.36, 0.26) -0.370		
	Dec-Feb	7.25 (0.08, 0.15) -0.609	15.75 (0.13, 0.32) -0.361	
	Sep-Nov 1984	17.00 (0.20, 0.24) -0.476	16.25 (0.14, 0.23) -0.556	3.00 (0.06, 0.04) -0.786
SYF		Sep-Nov	Dec-Feb	Sep-Nov 84
	Dec-Feb	18.75 (0.21, 0.22) -0.407		
	Sep-Nov 1984	33.50 (0.37, 0.19) -0.358	20.50 (0.24, 0.12) -0.310	
TIF		Dec-Feb		
	Sep-Nov 1984	10.75 (0.16, 0.05) -0.583		

Inter-seasonal Range Correlation

Correlating two ranges provides one number which allows the comparison of the relative degree of concordance between paired ranges. This technique was developed by C.P. Doncaster (1985). He has shown that, for samples where two ranges overlap and have a similar spread of utilization, range correlation provides a useful assessment of the combination of overlap and concordance in the use of common areas.

To do this analysis the ICELL data output was used for each mara's seasonal range. These data were then fed into the program USE (Doncaster, 1985). This program combines the data for two seasons by matching the proportion of fixes in each season for every grid cell visited in either or both seasons. These utilization values per cell were then correlated with MINITAB using the Spearman rank correlation. Results are shown in Table 3.13. The correlations varied from -0.310 to -0.786. A correlation of 1.0 would be consistent with a perfect overlap with both ranges using the same cells with exactly the same intensity; and a correlation of -1.0 would mean that the maras did not use any of the same cells in the different seasons being compared. These highly negative correlations show that, despite the appearance of a high degree of overlap between maras' seasonal ranges (see Table 3.13 and Figure 3.10 above), the utilization of cells in different seasons varies substantially. Maras may be inhabiting the same areas between seasons, but the actual cells in use change.

To examine whether there was a consistent cycling in usage patterns I compared the correlation coefficients between ranges 1, 2, 3, 4, and 5 seasons later (see Table 3.14). An increasingly negative correlation would have been consistent with animals leaving one area and moving on to another. This is clearly not happening as, although there may be a weakening of the correlation over the following 2

Table 3.14.--Spearman rank correlations made between the seasonal ranges of the same maras at different seasonal lag intervals. Maras used are ELF, PAM, SYF, and TIF.

-Time Lag in Seasons-				
1	2	3	4	5
-0.375	-0.565	-0.658	-0.556 *	-0.476
-0.430	-0.696	-0.786	-0.358 *	
-0.440	-0.609	-0.310		
-0.370		-0.583		
-0.361				
-0.407				

* Correlation of seasonal ranges made between two breeding seasons when animals used the same den site.

seasons, the range correlations do not continue to decline.

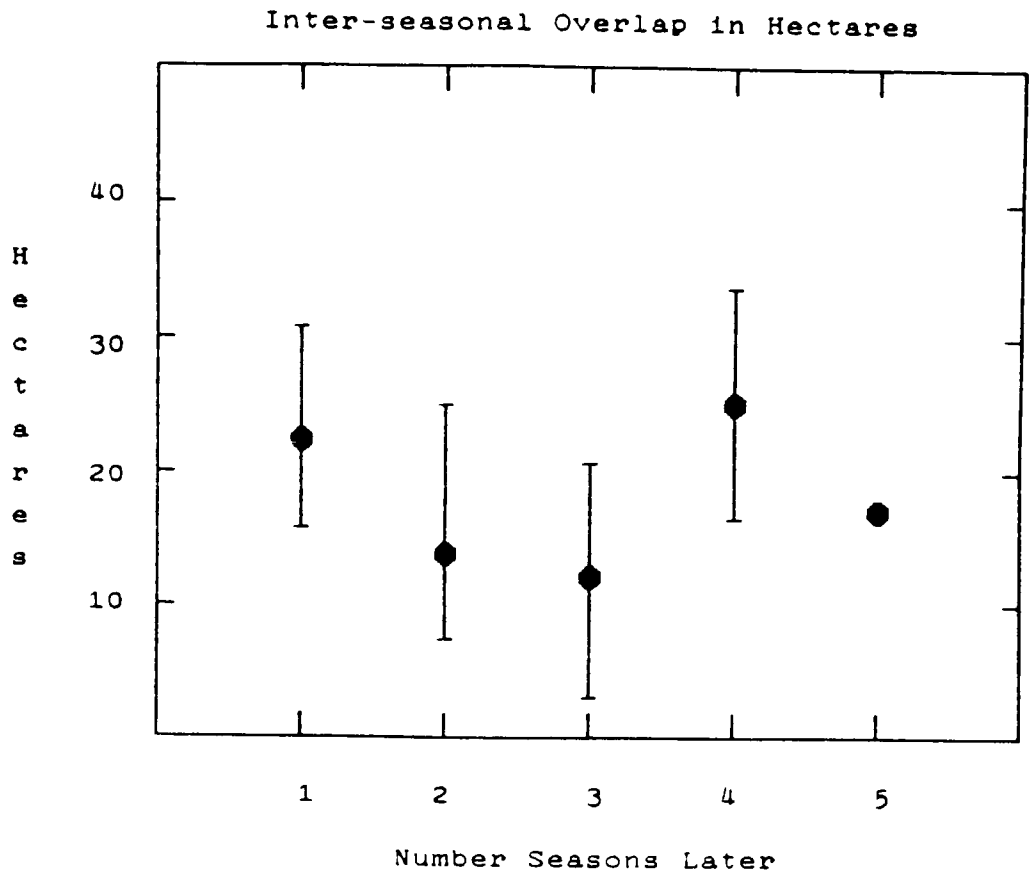
The range overlap values in ha, and the proportion of the ranges overlapping, at different seasonal lag intervals were plotted (Figure 3.11) to further examine the data for evidence of cyclicity in range usage. There is a hint of a yearly cycle, since in these plots and the correlations above, there was a rise 4 seasons later. In both cases where overlap data covered a 4 season spread, the ranges being compared were breeding season ranges when animals would be drawn into the area around the den (see Chapter 5). Therefore, any hint of cyclicity in inter-seasonal range use must be taken as preliminary. However, this result does make the point that the movements of maras are limited by the need to return to the same den site (or adjacent den, see Chapter 5) each spring during the breeding season.

Towards a Meaningful Estimate of Range Size

I was able to obtain fixes in approximately equal numbers for maras ELF (835 fixes) and PAM (714 fixes) spanning a whole year (1 March 1983 to 1 March 1984). The total areas based on cell counts for these animals' ranges were, respectively, 174.75 ha and 210.75 ha (see Table 3.15). The range size based on the convex polygon method for this period was 282.71 ha for PAM and 312.01 ha for ELF. On the basis of these two animals one can tentatively conclude that annual home ranges are on the order of 200 ha. However, as we have shown that ranges are in a continual state of flux it is doubtful that an annual range size has much biological meaning.

Another way of estimating range size is through the use of the Prevailing Range. This method has been tested and reviewed in Doncaster (1985) and its implementation is shown

Figure 3.11.--Number of hectares, and proportions of ranges, overlapping for individual maras at different seasonal lag intervals. Error bars mark the maximum and minimum numbers obtained, not the standard errors.



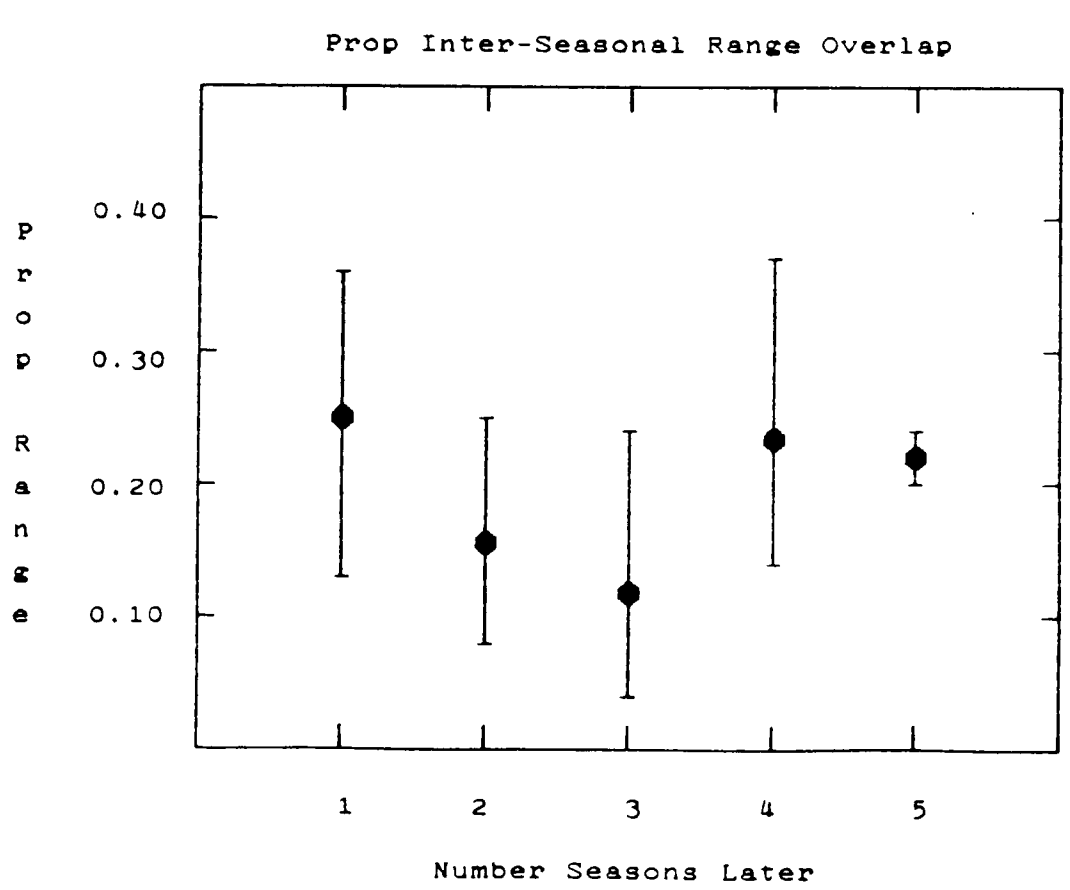


Table 3.15.--Estimates of yearly range size for two maras tracked from 1 March 1983 to 1 March 1984. Estimates made based on grid cell and convex polygon methods.

Mara Name	Number of Fixes	Total Area (ha)	Convex Polygon Area (ha)
ELF	835	210.75	312.01
PAM	714	174.75	282.71

in Figure 3.6 (see Subsection 3.3.1, above). I was only able to use this technique on two animals on which I had sufficient data: PAM and ELF. They showed mean prevailing ranges of respectively 33.33 ha and 36.58 ha. This range size was maintained consistently over time as can be seen by the plateaus in the plots in Figure 3.6 (above). This consistency of prevailing range size is backed up by the lack of any significant differences in range size between seasons as compared using a t-test of MAP functions (see above).

3.4 Behaviour and Range Use Patterns

Results covering the following topics will be presented to examine daily and seasonal mara activity patterns: (i) behavioural time budgets, (ii) diurnal activity patterns and their link with seasonal changes in day length and temperature, and (iii) daily ranging patterns and how they fluctuate in different seasons. In the previous section we looked at the general ranging patterns of maras; here we examine how maras move around in their ranges and partition their time between activities.

3.4.1 Behavioural Time Budgets

Every species must respond to a variety of requirements on it each day: they need to find and eat food, to rest, and to associate with other animals for a variety of reasons. Below I will present results showing how maras divide up their time during the day.

Most of the results presented are based on the analysis of the behavioural scan data (see Chapter 2). Although 60 different behaviour categories were used in collecting the data, I have chosen to lump behaviours into 6

general categories to simplify analysis (see Table 3.16). These general behaviour categories are as follows:

Sitting	Sitting and alert behaviours.
Feeding	Grazing, browsing, and rooting.
Resting	Lying down, sleeping, coprophogy, and grooming.
Moving	Running, trotting, stotting, and standing. Standing is included because it usually precedes movement.
With Pups	All behaviours associated with pups such as nursing, sniffing, or chasing pups. In months where few interactions with pups were observed this is included in the Miscellaneous behaviour category.
Miscellaneous	All other behaviours--none of which were viewed more than a few times.

The Daily Activity Pattern

I analyzed data by monthly blocks to take into account the yearly cycle of changes in day length, and sunrise and sunset times, during the year (see Chapter 2). Only months were used in which at least 400 behaviour scans (adult maras only) were recorded, spread over at least nine hours of the day. For each behaviour category the proportion of the total scans for each hour during the day was plotted for the feeding, resting, moving, and with pups behaviour categories (see Figures 3.12). These histograms also show the mean sunrise and sunset times within each month so that activity patterns can be tracked relative to the sun. As a means of examining these data systematically, the data were further lumped by months into morning (7:00-10:59), midday (11:00-15:59), and evening (16:00-21:00) time blocks. Then, X^2 tests were made on

Table 3.16.--Division of scan behaviour categories into general behaviour categories. See Chapter 2 for a description of each behaviour category.

-General Behaviour Categories-						
Sit	Feed	Rest	Move	Pup	Miscellaneous	
ST	GZ	LI	TR	NS	ND	AA
AL	BR	GM	WK	WC	SG	MS
	RT	CP	SD	SC	SN	CF
		SL	RN	TC	AD	CL
		SR		RC	BE	OT
				CC	RL	FH
				WH	DG	ZZ
					CH	EB
						LS

Figure 3.12 (4 pages).

Histograms of diurnal time budgets, lumped by hours, for each month in which more than 400 behavioural observations were made. These data were taken from all scans of adult maras selected at a one hour independence interval to insure independence of scans. The open and closed circles on each histogram mark the mean sunrise and sunset times for the month. Histograms for the following behaviour categories are shown:

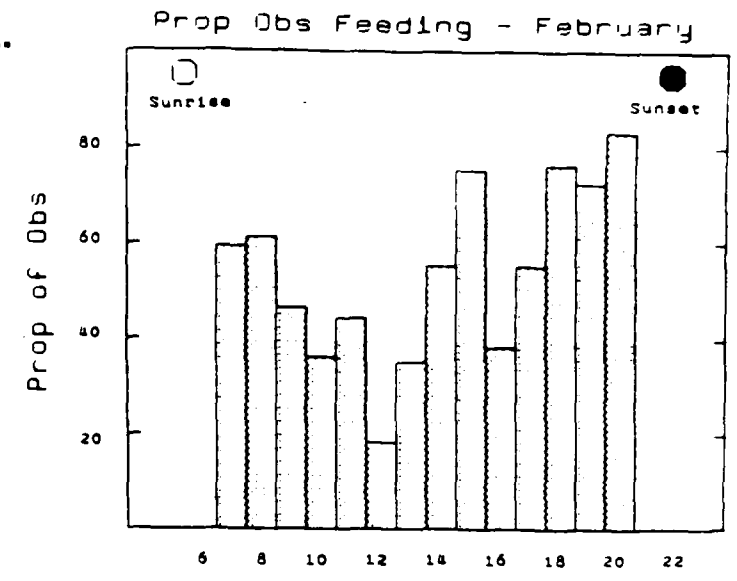
a. Feeding

b. Resting

c. Moving

d. With Pups

a.


Prop Obs Feeding - February
Sunrise
Sunset
Prop of Obs
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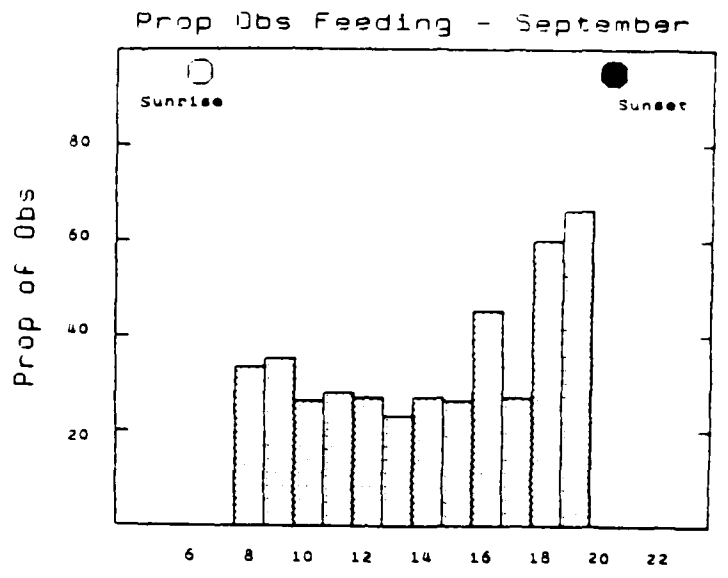
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Sunrise
Sunset
Prop of Obs
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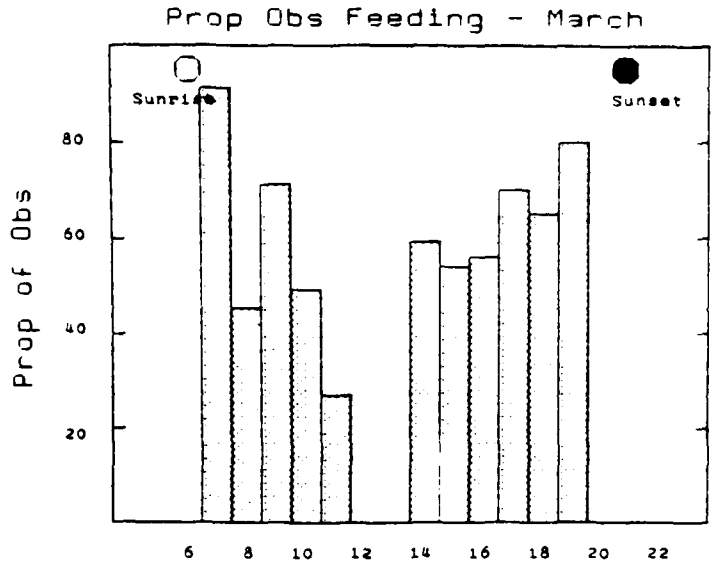
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Sunrise
Sunset
Prop of Obs
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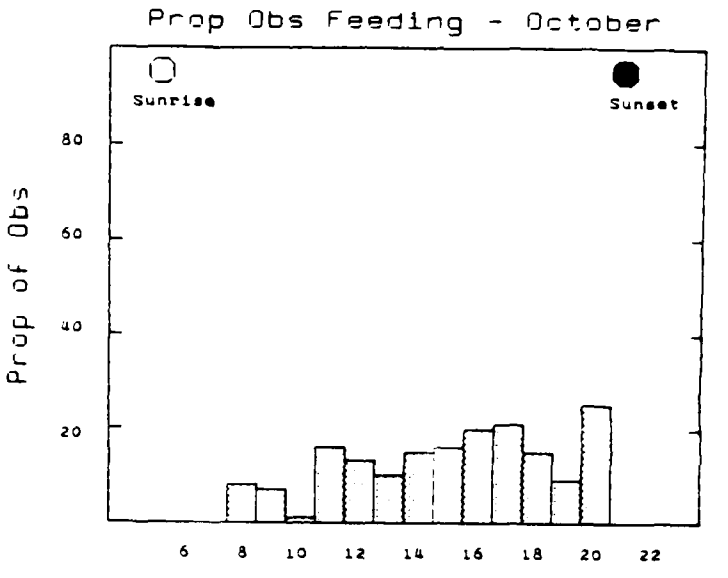
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Sunrise
Sunset
Prop of Obs
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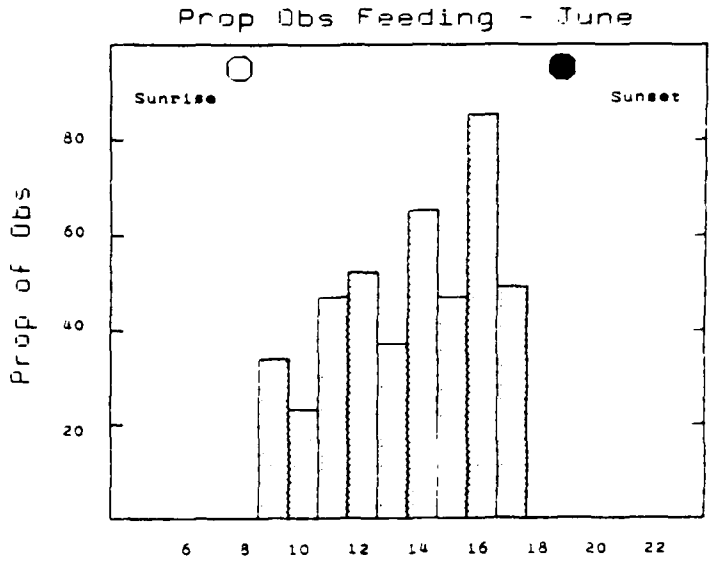
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Sunset
Prop of Obs
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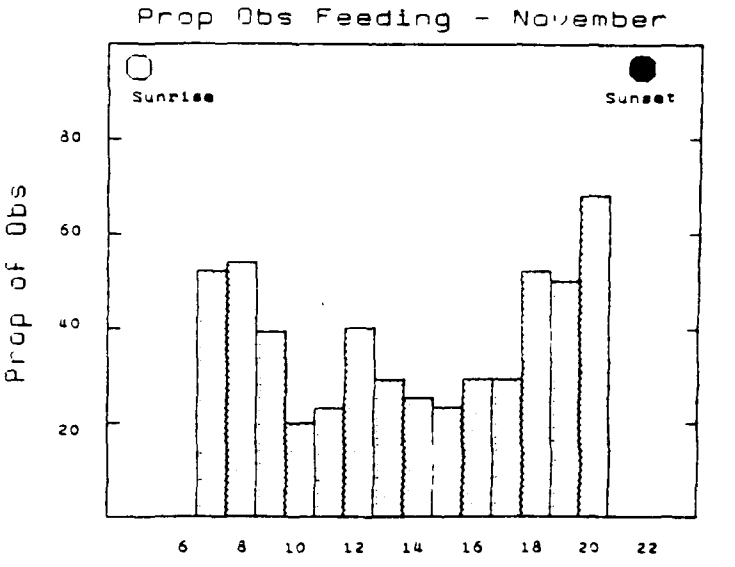
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Sunrise
Sunset
Prop of Obs
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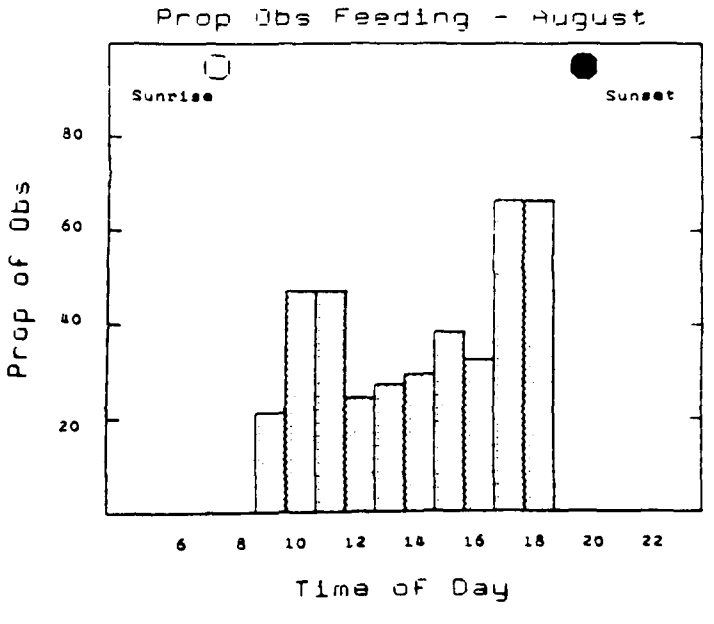
Prop Obs Feeding - August
Sunrise
Sunset
Prop of Obs
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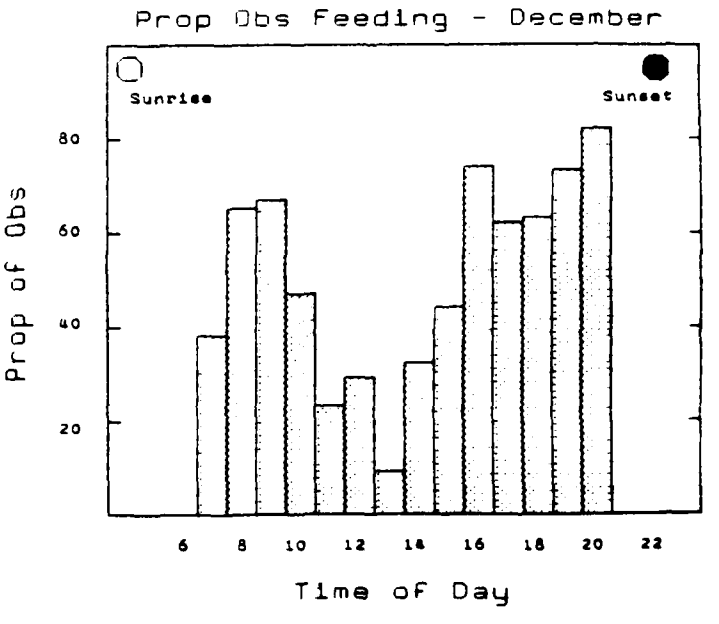
Time of Day


Prop Obs Feeding - December
Sunrise
Sunset
Prop of Obs
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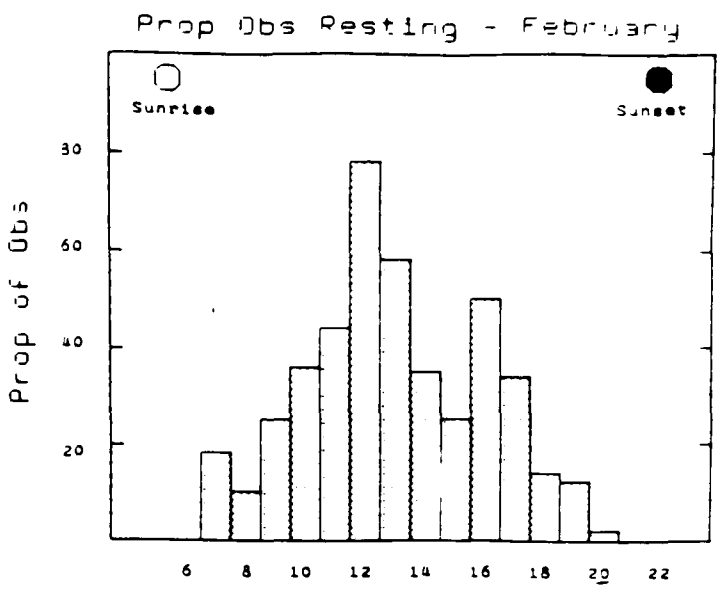
22
Time of Day

b.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Sunrise
Sunset
Prop of Obs
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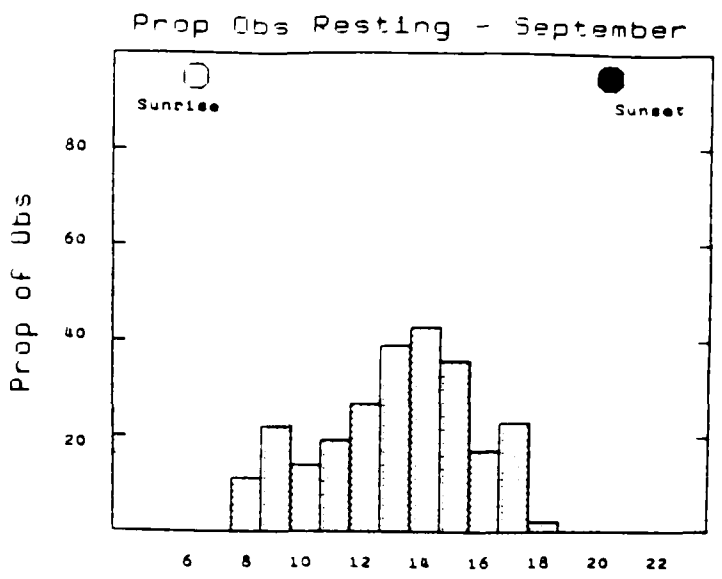
6 8 10 12 14 16 18 20 22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Sunrise
Sunset
Prop of Obs
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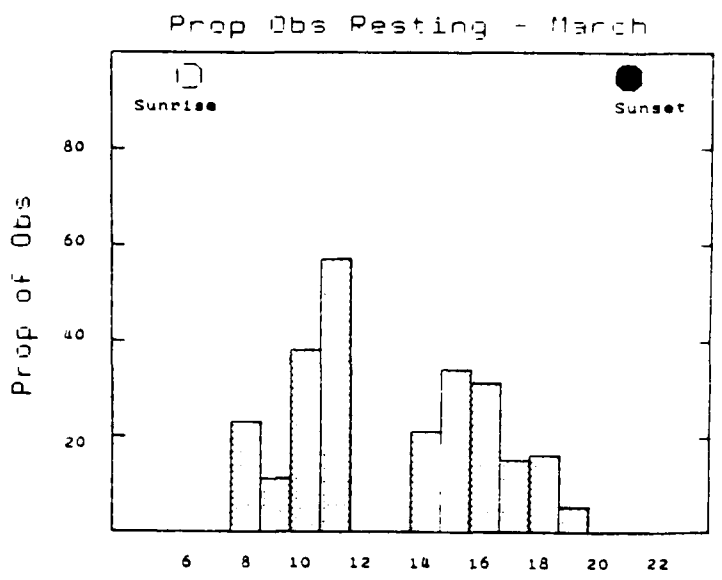
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Sunrise
Sunset
Prop of Obs
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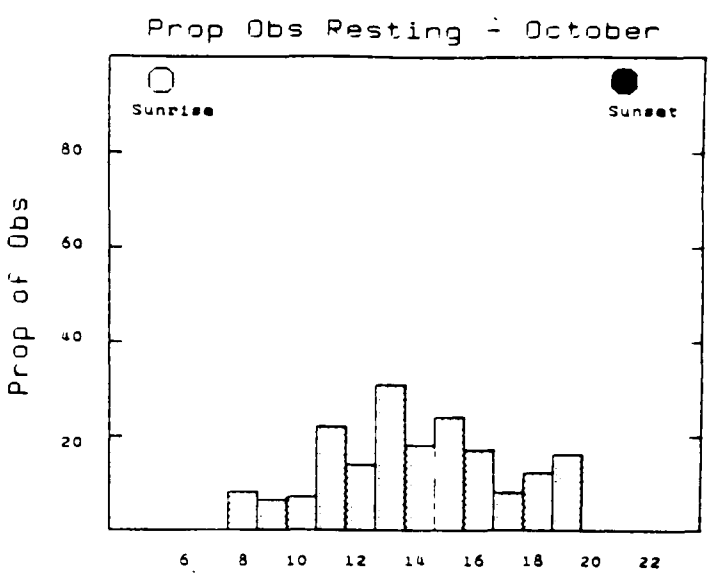
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Sunrise
Sunset
Prop of Obs
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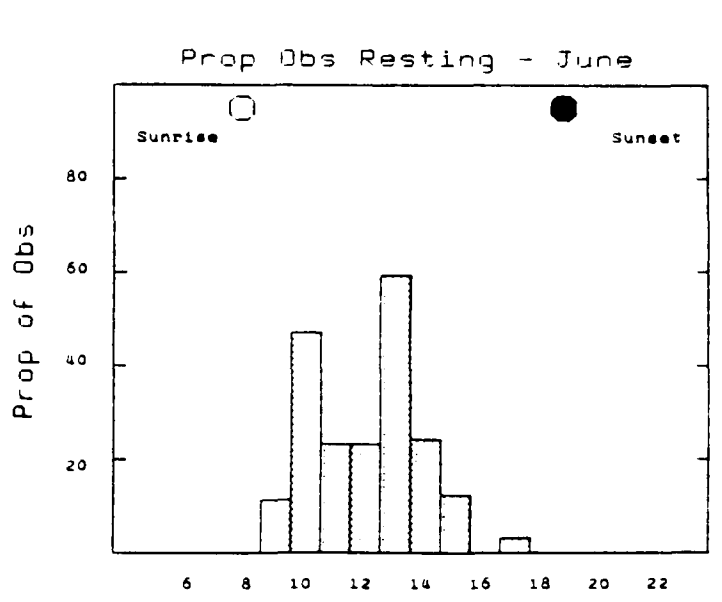
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Sunrise
Sunset
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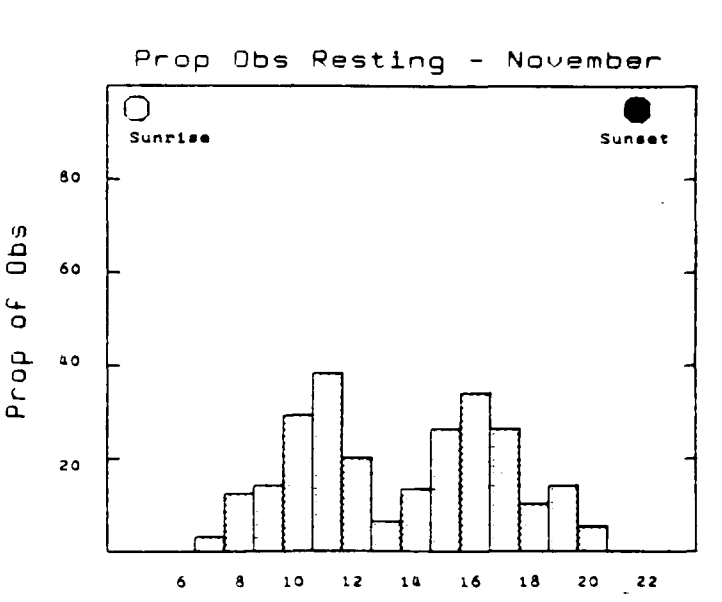
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Sunset
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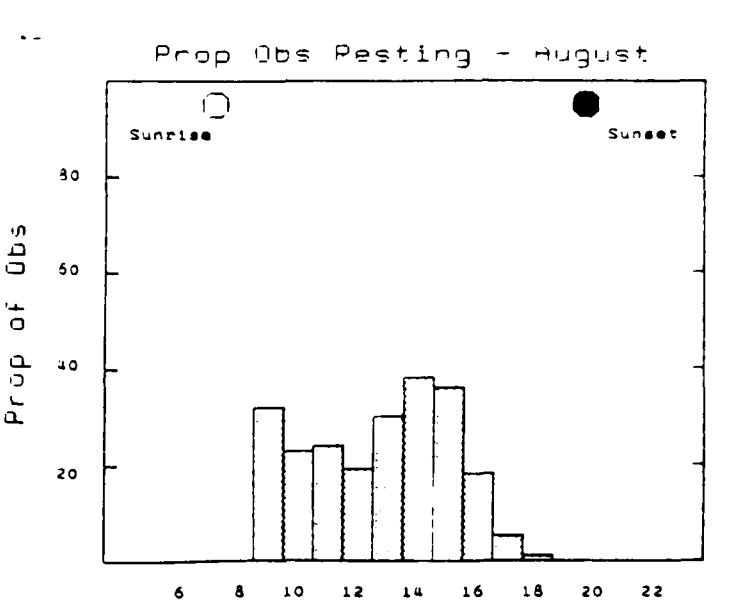
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Sunrise
Sunset
Prop of Obs
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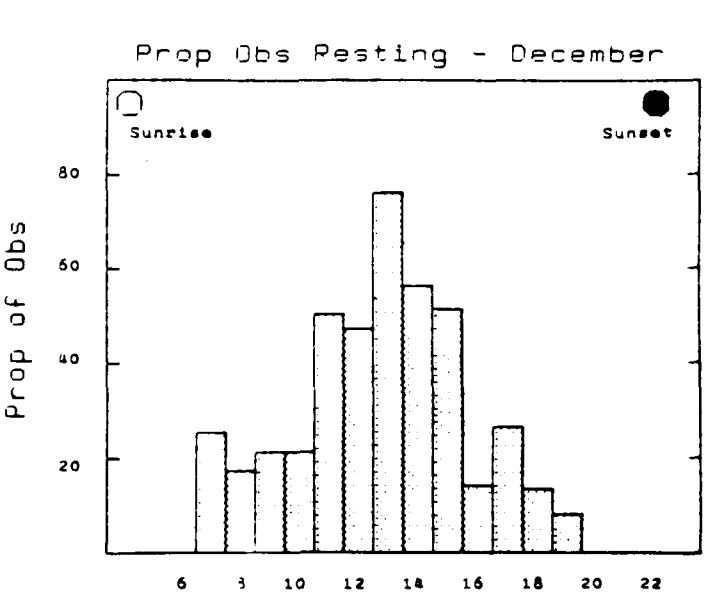
Time of Day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Sunrise
Sunset
Prop of Obs
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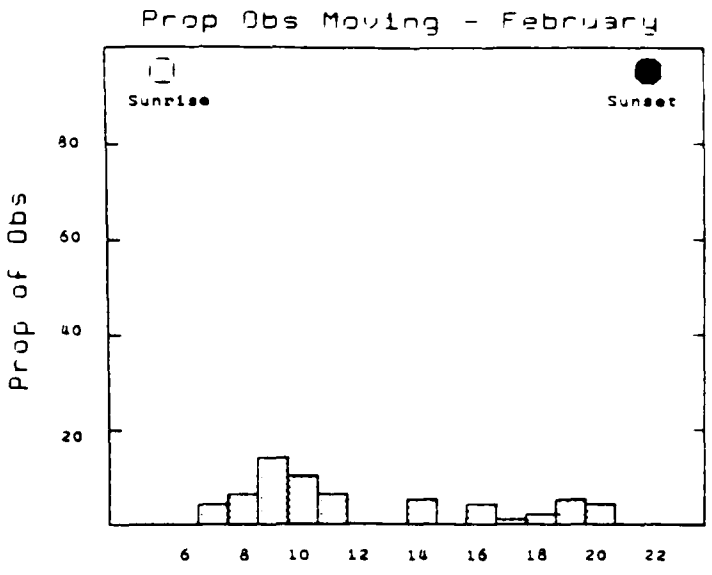
6 8 10 12 14 16 18 20 22
Time of Day

c.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Sunrise
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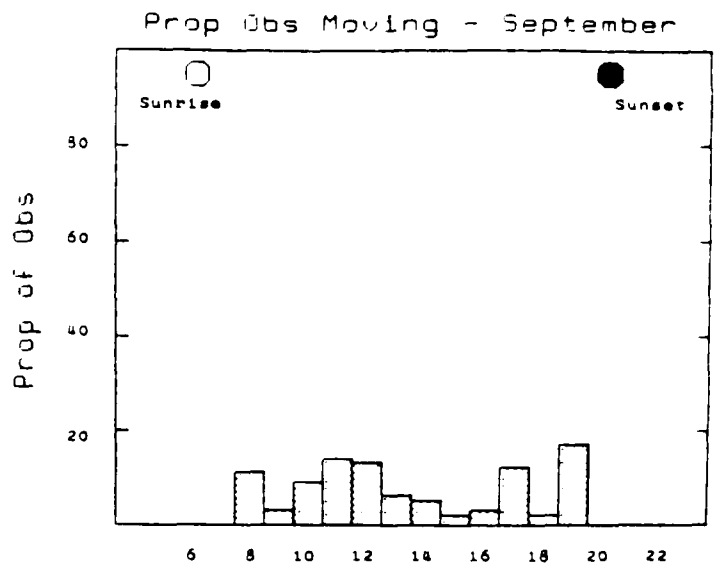
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Sunset
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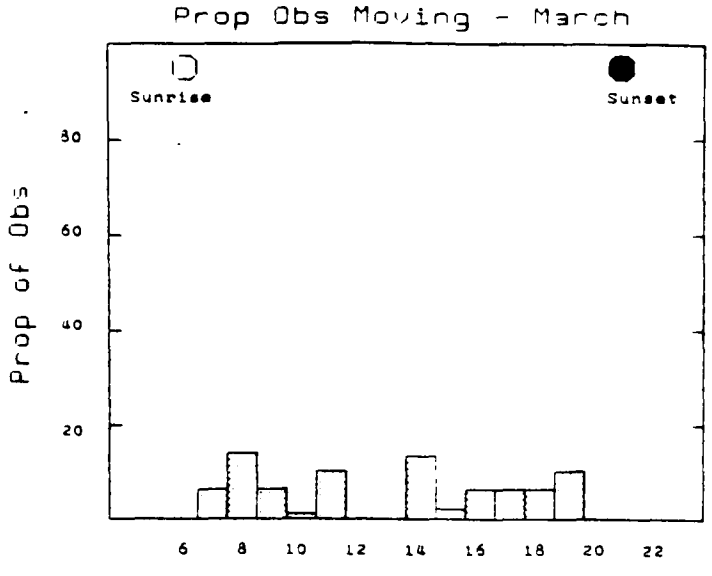
Prop Obs Moving - March
Sunrise
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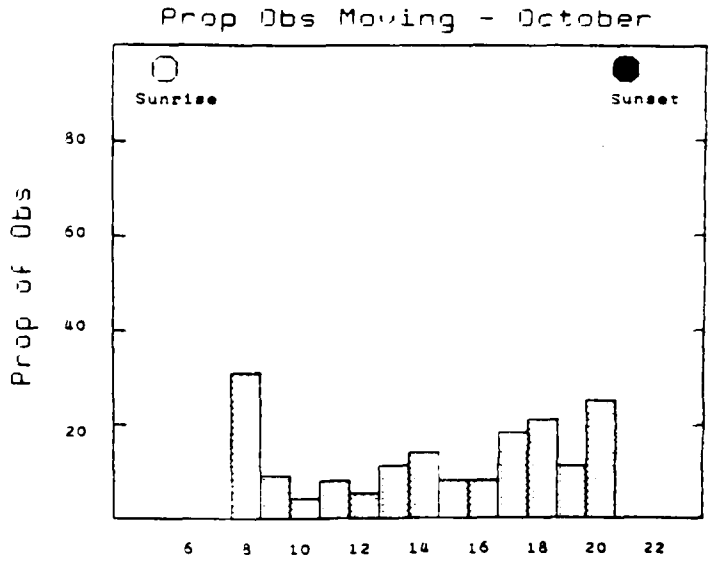
Prop Obs Moving - October
Sunrise
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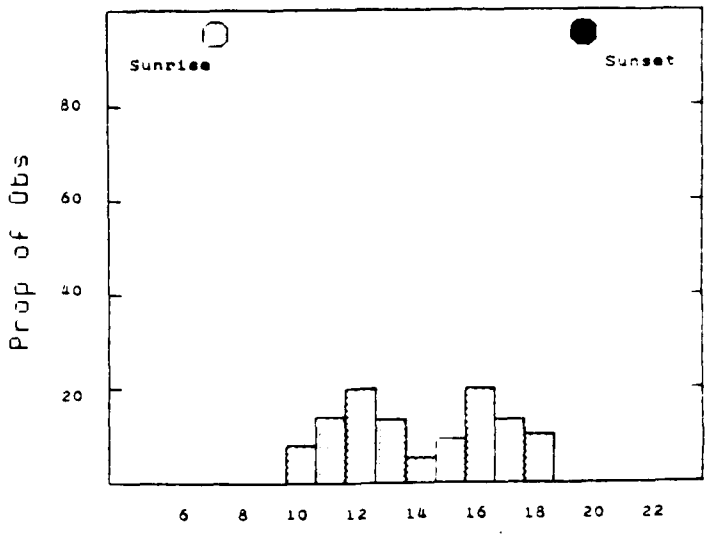
Prop Obs Moving - August
Sunrise
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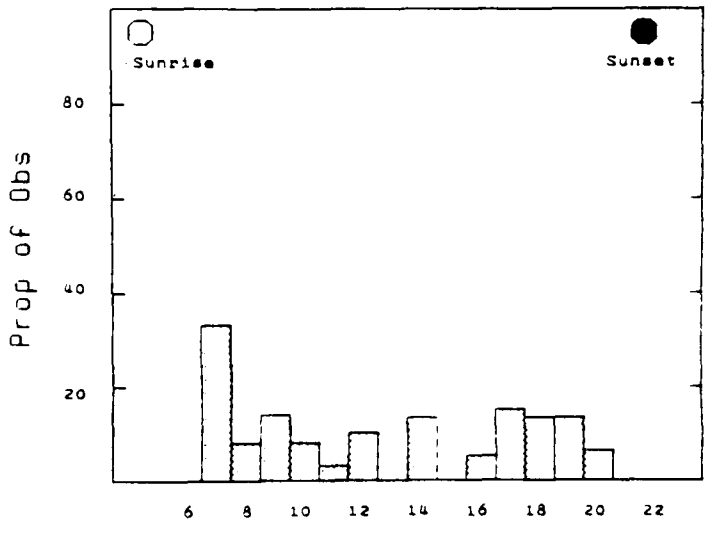
Prop Obs Moving - November
Sunrise
Sunset
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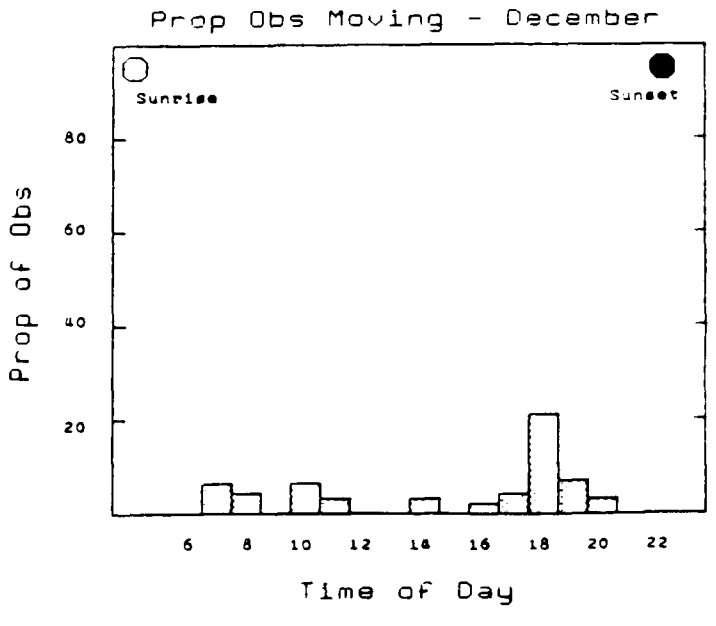
Prop Obs Moving - December
Sunrise
Sunset
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Time of Day

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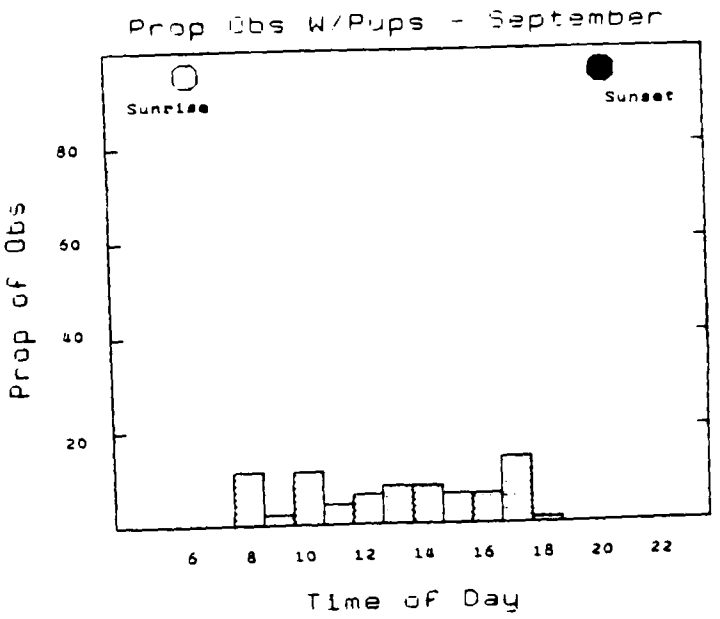
Prop Obs W/Pups - September
Sunrise
Sunset
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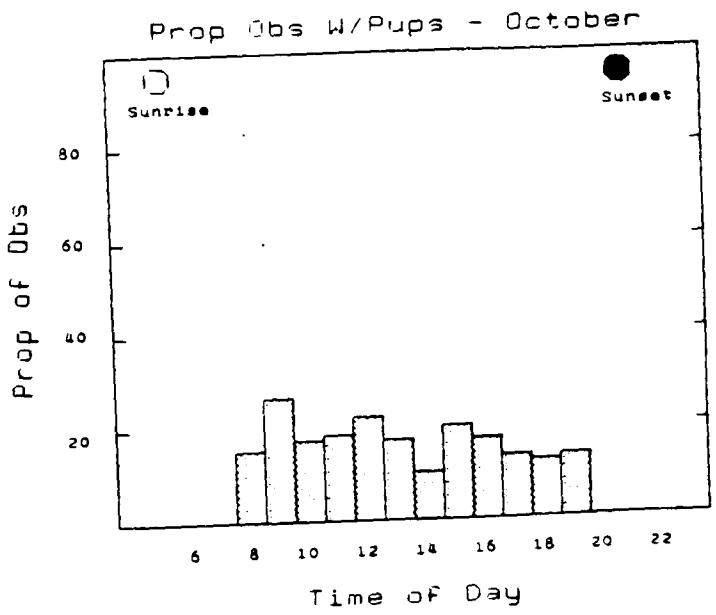
Time of Day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Sunrise
Sunset
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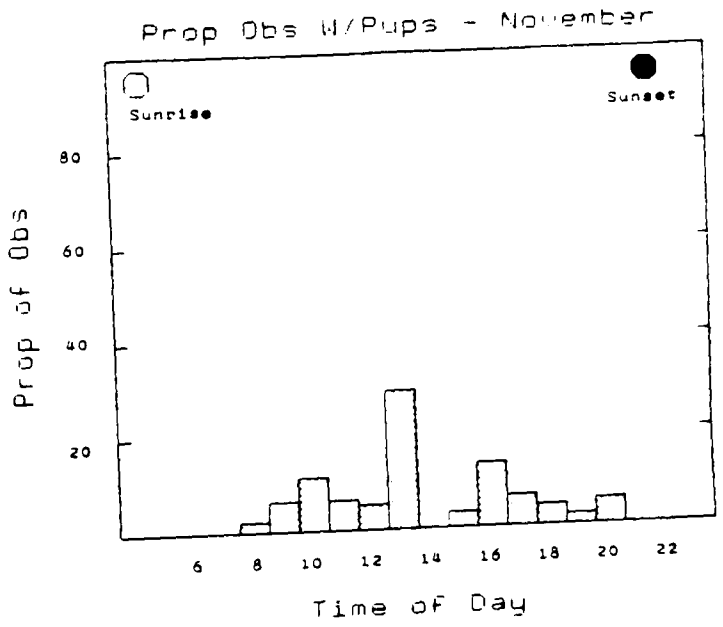
Time of Day


Prop Obs W/Pups - November
Sunrise
Sunset
Prop of Obs
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Time of Day

these data to test if there were significant differences in the amount of time the animals spent engaging in different behaviours in the different parts of the day. Through examining the histograms (Figure 3.12) and Table 3.17 the following patterns are apparent:

Feeding. The proportion of observations of animals feeding fluctuates in different hours of the day. In every month the animals spent proportionally more time feeding in the evening than in the morning and midday. In the months with the most hours of sunlight, December to March, the proportion of observations of maras feeding is markedly lower at midday than in the morning.

Resting. As in feeding, the proportion of observations of animals resting fluctuates at different hours of the day. In every month but June maras spent significantly more time resting around midday than in the morning and afternoon. The histograms also show a pronounced peak in resting around midday during the months with the longest and hottest days (see Chapter 2), December and February.

Moving. Only during the late spring and summer months are there significant differences in the amount of time the animals spent moving in the different parts of the day. In December, November, and February the data shows the opposite pattern from resting with maras moving more in the morning and evening than midday.

With Pups. Histograms are only shown during the breeding season months (September, October, and November), the only times of year when pups are present in any numbers. There were no significant differences in the proportion of observations of mara adults interacting with pups in the different hours of the day in any of the three months.

In general then, maras are active throughout the day with a tendency to be more active in the twilight. This is best shown by the significantly larger proportions of

Table 3.17.--The proportion of observations, by month, of maras engaging in different activities in different parts of the day. X^2 test results also given, which show whether the proportions were significantly different. The X^2 tests were calculated on 2 x 3 contingency tables with the number of observations of animals engaging in each behaviour in one column, the number of observations of animals engaging in other behaviours in the other column, and with the part of the day as the rows.

Month	-Proportion Observations- Morning	Midday	Evening	X^2	Significance
			FEEDING		
Feb	0.53	0.44	0.63	43.79	P < 0.005
March	0.59	0.52	0.66	24.33	P < 0.005
June	0.27	0.49	0.66	27.18	P < 0.005
August	0.39	0.33	0.55	22.21	P < 0.005
September	0.28	0.26	0.45	40.04	P < 0.005
October	0.05	0.14	0.18	15.11	P < 0.005
November	0.36	0.26	0.46	18.33	P < 0.005
December	0.53	0.29	0.69	73.16	P < 0.005
			RESTING		
Feb	0.20	0.48	0.24	93.12	P < 0.005
March	0.22	0.32	0.18	20.42	P < 0.005
June	0.35	0.28	0.02	23.85	P < 0.005
August	0.26	0.29	0.08	27.99	P < 0.005
September	0.16	0.33	0.14	63.38	P < 0.005
October	0.06	0.22	0.14	24.37	P < 0.005
November	0.18	0.28	0.17	7.52	P < 0.025
December	0.21	0.57	0.13	107.80	P < 0.005
			MOVING		
Feb	0.08	0.03	0.03	13.34	P < 0.005
March	0.06	0.07	0.07	0.34	N.S.
June	0.06	0.06	0.10	1.59	N.S.
August	0.06	0.13	0.14	4.37	N.S.
September	0.08	0.08	0.07	0.17	N.S.
October	0.10	0.10	0.13	1.98	N.S.
November	0.13	0.04	0.11	9.16	P < 0.025
December	0.04	0.02	0.09	13.11	P < 0.005
			WITH PUPS		
September	0.09	0.06	0.07	1.63	N.S.
October	0.21	0.17	0.14	3.43	N.S.
November	0.06	0.08	0.05	1.05	N.S.

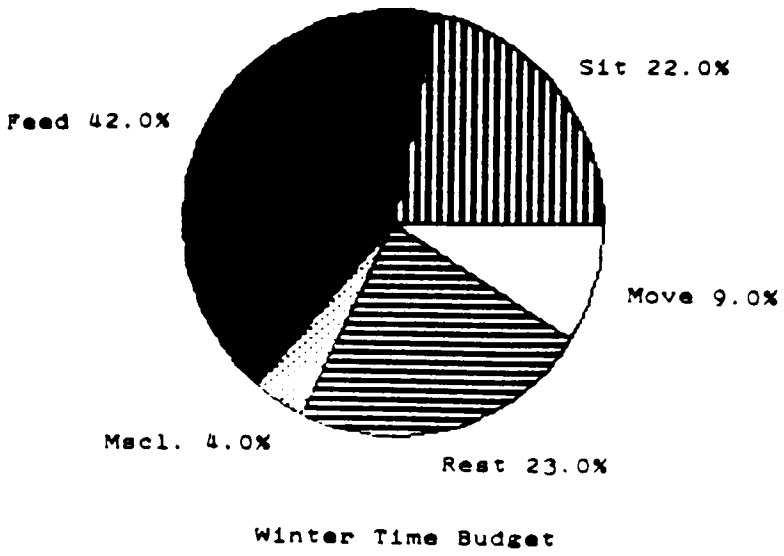
observations of maras resting at midday in almost every month.

Seasonal Time Budgets

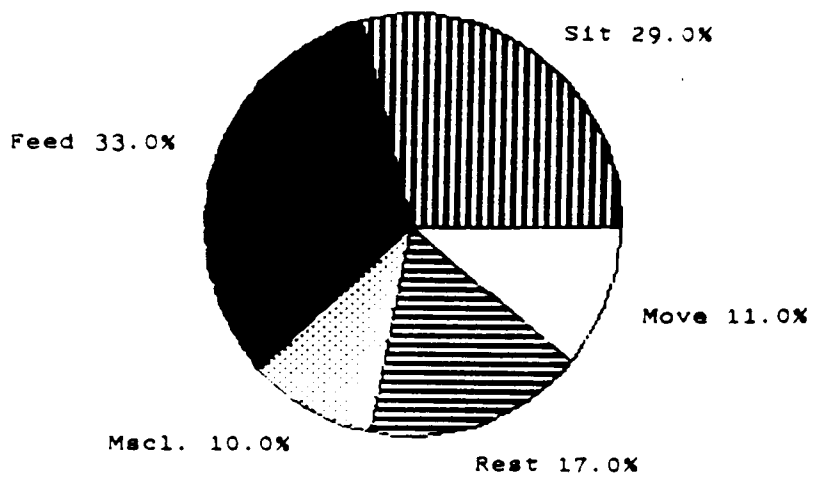
Below I will show that the proportion of daylight hours in which maras engage in different behaviours changes in different seasons. Changes in behavioural time budgets between seasons could reflect the reproductive cycle, changes in food or water availability, or temperature and other climactic factors. These results will be examined to determine what factors could account for this inter-seasonal variation.

To determine the proportion of observations of maras engaging in different behaviours in each season the unequal number of observations collected in each hour of the day must be accounted for. For each season, for all daylight hours in which adequate data were available, the proportion of observations of maras engaging in each behaviour category was found. The means of these hourly proportions were then taken to give a combined proportion of scans of maras doing each of the behaviour categories for each season. The resulting seasonal time budgets are shown in Figure 3.13.

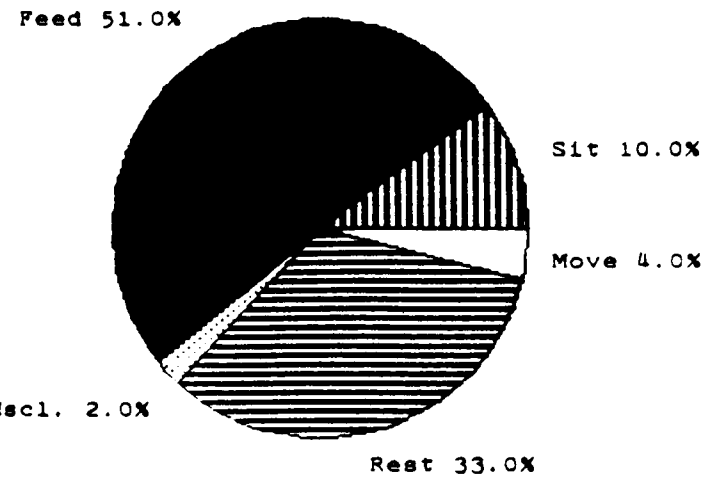
In all seasons feeding occupies the highest percentage of scans (varying from 33.0% to 55.0%). Resting (17.0% to 33.0%) and Sitting (10.0% to 29.0%) come next, followed by moving (4.0% to 11.0%), and then miscellaneous behaviours (2.0% to 10.0%). To test whether differences between seasons were significant a t-test was made comparing these proportions using Equation 3.1 to calculate the standard error, and Equation 3.2 to calculate the T statistic (equations--Pers. comm. F.H.C. Marriot).



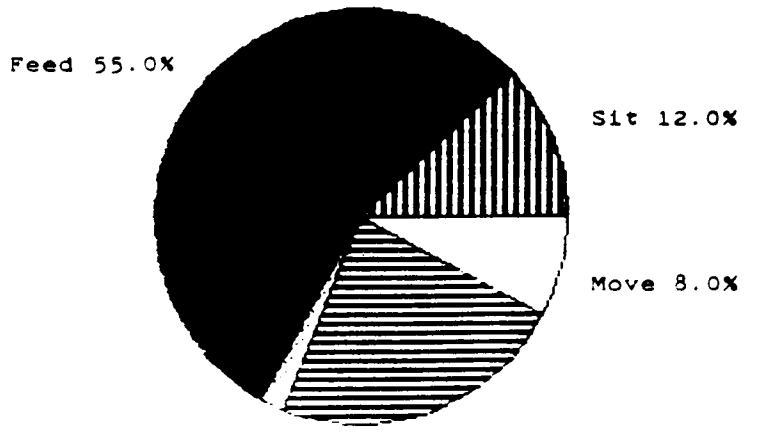
Winter Time Budget



Spring Time Budget



Summer Time Budget



Fall Time Budget

Figure 3.13.--Pie charts of mara time budgets for the winter, spring, summer, and fall seasons. These data were taken from all scans of adult maras, selected at one hour independence intervals to reduce auto-correlation between scans.

Equation 3.1

no = Number of observations of particular behaviour each hou
nh = Number of observations in that hour
k = Number of hours in which data were obtained

$$\text{Standard Error} = \frac{1}{k}\sqrt{\frac{(no\ (nh - no))}{nh^3}}$$

Equation 3.2

n1 = Proportion observations for season 1
s1 = Standard error for season 1
n2 = Proportion observations for season 2
s2 = Standard error for season 2

$$T = \frac{n1 - n2}{\sqrt{s1^2 + s2^2}}$$

The results of these tests are summarized in Tables 3.18 to 3.21 and Figures 3.14 to 3.17.

As a means of investigating the relationship between mara behaviour, climactic variables and yearly cycles, the proportion of scans in which maras engaged in different behaviours was correlated with the amount of rainfall and the mean daylength in each month. For these analyses, data in the months of April, May, and July were not included since too few observations were recorded. The results of the t-tests and Spearman rank correlations are presented below:

Feeding. The histogram in Figure 3.14 shows a yearly cycle in the proportion of time maras spend feeding: the animals spent less time feeding in the winter and spring, and more time in the fall and summer. These results are born out by the t-test results (see Table 3.18) which show a significant decline from fall to winter, and from winter to spring, followed by a climb in the proportion of time spent feeding in summer which was not significantly different from fall. A significant positive correlation was found between the proportion of scans of maras feeding and the amount of precipitation in the month ($r_s = 0.6213$, $N = 9$, $P < 0.05$). There was no significant correlation between the

Table 3.18.--Mean and standard error of the proportion of scans in which maras were feeding in different seasons. Also shows the results of T tests comparing these proportions between seasons. * P < 0.05

Season	Mean	St. Error	Winter	Spring	Summer
Fall	0.55	0.02	4.85 *	9.23 *	1.67
Winter	0.42	0.01		5.27 *	4.73 *
Spring	0.33	0.01			11.96*
Summer	0.51	0.01			

Figure 3.14.--Histogram of the percent of behavioural observations of maras feeding in the 4 seasons of the year.

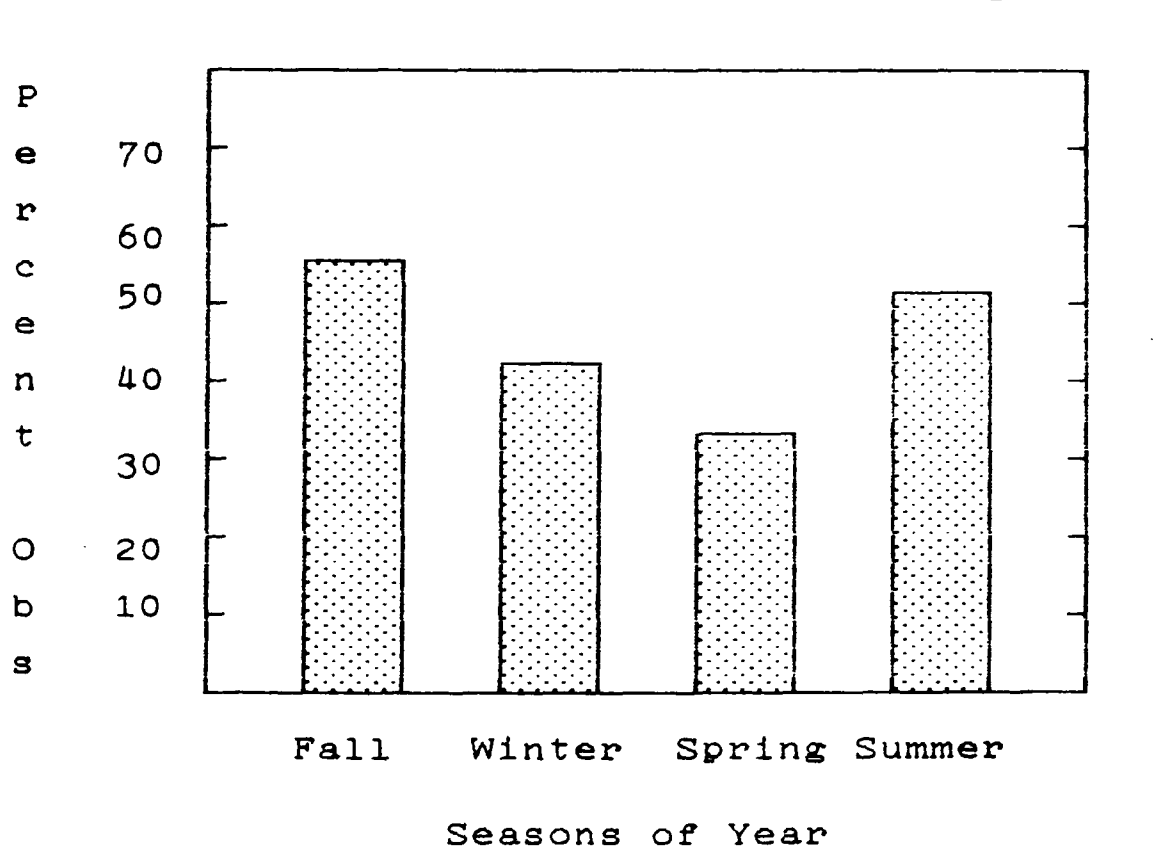


Table 3.19.--Mean and standard error of the proportion of scans in which maras were sitting in different seasons. Also shows the results of T tests comparing these proportions between seasons.

Season	Mean	St. Error	Winter	Spring	Summer
Fall	0.12	0.03	2.69	5.144 *	0.733
Winter	0.22	0.01		4.93 *	7.92 *
Spring	0.29	0.01			17.10*
Summer	0.10	0.01			

Figure 3.15.--Histogram of the percent of behavioural observations of maras sitting in the 4 seasons of the year.

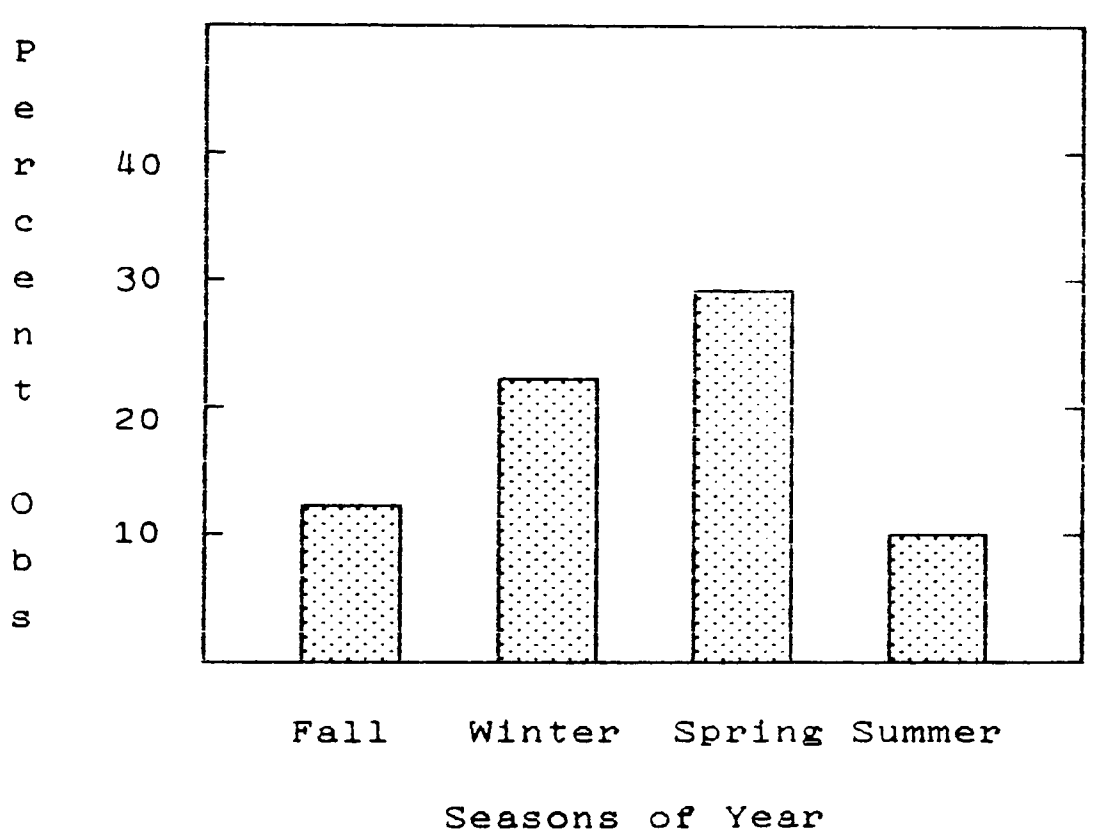


Table 3.20.--Mean and standard error of the proportion of scans in which maras were resting in different seasons. Also shows the results of T tests comparing these proportions between seasons.

Season	Mean	St. Error	Winter	Spring	Summer
Fall	0.23	0.03	0.16	1.68	3.26 *
Winter	0.23	0.01		3.96 *	5.90 *
Spring	0.17	0.01			11.58 *
Summer	0.33	0.01			

Figure 3.16.--Histogram of the percent of behavioural observations of maras resting in the 4 seasons of the year.

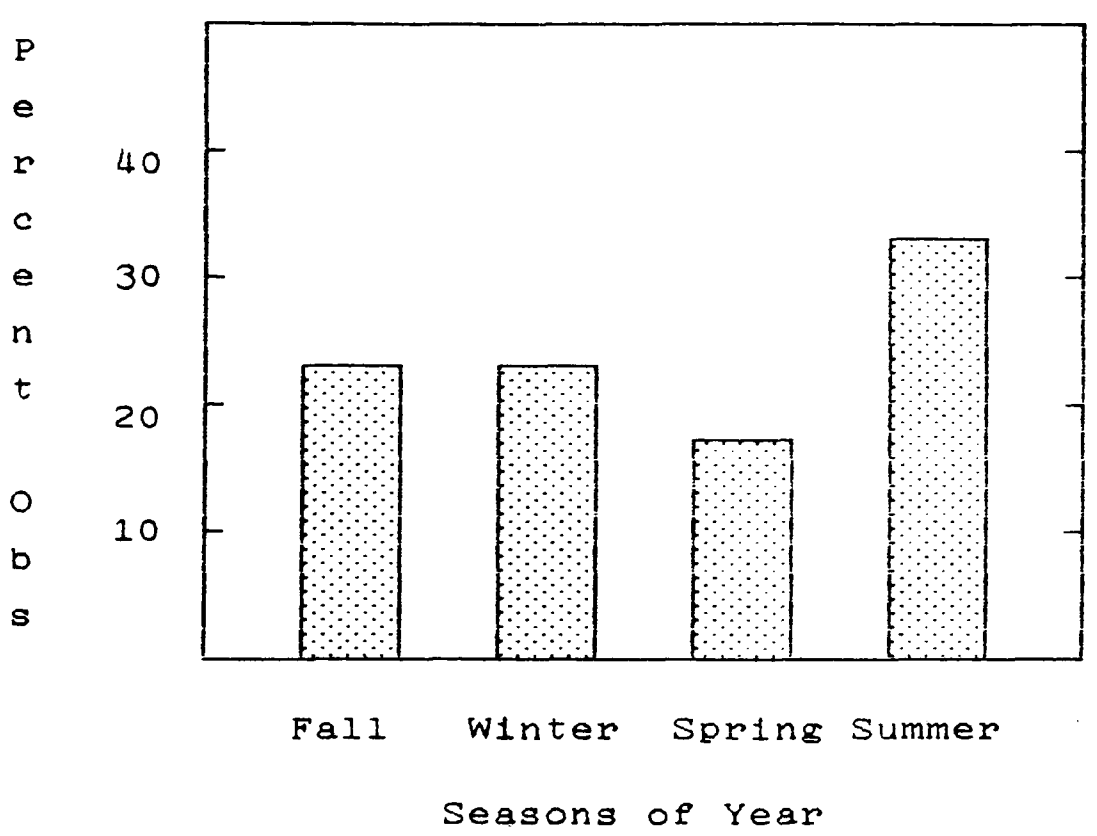
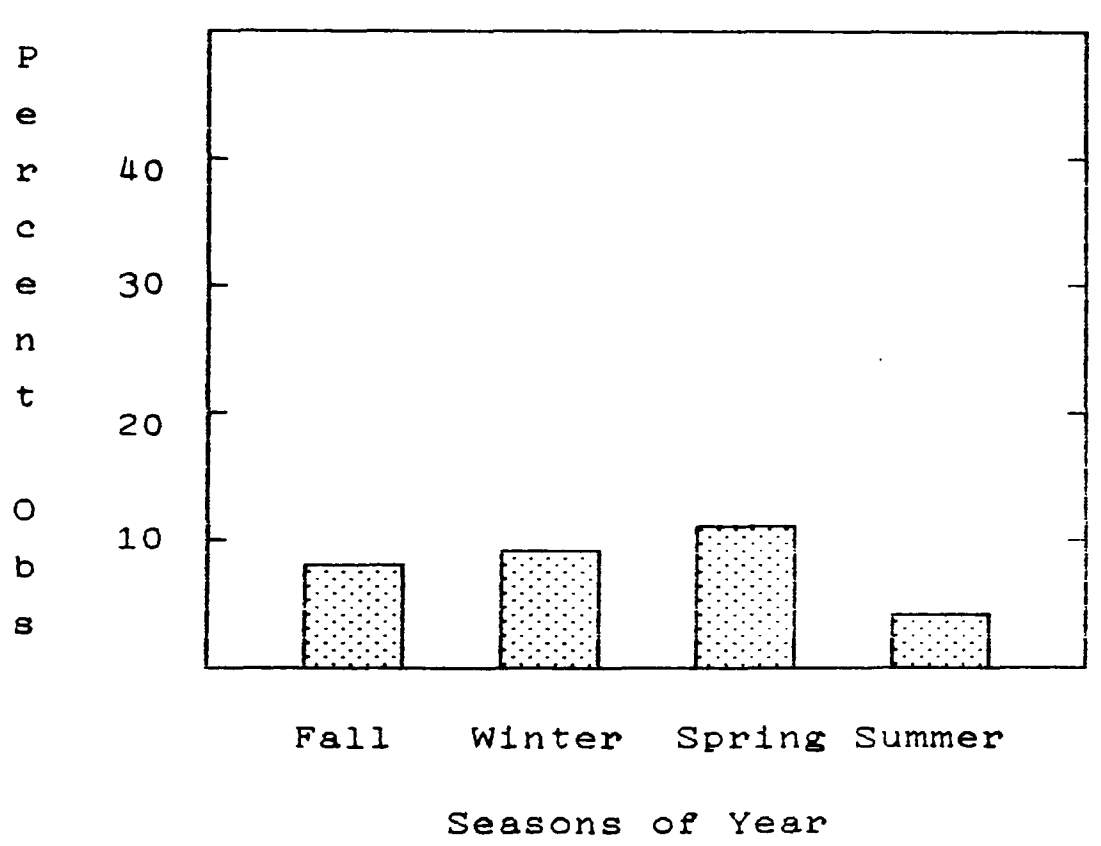


Table 3.21.--Mean and standard error of the proportion of scans in which maras were moving in different seasons. Also shows the results of T tests comparing these proportions between seasons.

Season	Mean	St. Error	Winter	Spring	Summer
Fall	0.08	0.02	0.60	1.68	2.12
Winter	0.09	0.01		1.74	5.18 *
Spring	0.11	0.01			8.05 *
Summer	0.04	0.004			

Figure 3.17.--Histogram of the percent of behavioural observations of maras moving in the 4 seasons of the year.



proportion of time spent feeding and day length (r_s = 0.5292, N = 9, N.S.).

Sitting. Figure 3.15 shows a yearly cycle in the amount of time maras spend sitting. The t-test results (Table 3.19) show a climb in the amount of time (proportion of scans) sitting from fall to winter, and from winter to spring; and then a decline from spring to summer, which was not found to have significantly different sitting rates from the fall. There was not a significant correlation between the proportion of observations of maras sitting and precipitation (r_s = -0.5556, N = 9, N.S.) or day length (r_s = -0.2101, N = 9, N.S.). It seems likely that this increase in the amount of time sitting (predominately predator scanning behaviour) is associated with the presence of pups in late winter and through the spring (see Chapter 5).

Resting. A clear seasonal cycle in the proportion of observations of maras resting cannot be seen in Figure 3.16. There is no change in the proportion of scans of maras resting between fall and winter (see Table 3.20). The proportion drops from winter to spring, perhaps reflecting the increased activity around the breeding season. There is a climb in the proportion of animals resting from spring to summer, followed by a drop from summer to winter. Significant correlations were not found between the proportion of animals resting and rainfall (r_s = 0.1447, N = 9, N.S.) or daylength (r_s = 0.4184, N = 9, N.S.).

Moving. The t-tests results show (see Table 3.21 and Figure 3.17) that the low proportion of moving behaviour during the summer is significantly different from the amount of moving in the other seasons. No significant differences were found between the amount of time maras spent moving in the other three seasons.

Overall Time Budgets

To obtain an overall mara time budget the seasonal time budgets, as shown in Figure 3.13 (above), were averaged to give a composite time budget as shown in Figure 3.18. In this pie chart one sees that during daylight hours maras spend roughly half of their time feeding, followed by a quarter of their time resting, and 18% of their time sitting, followed by a small amount of time moving and engaging in miscellaneous behaviours.

3.4.2 Daily Movement Patterns

In this subsection results covering the following features of mara daily movement patterns will be presented: (i) the size of the daily range, (ii) how far animals travel during the day, and (iii) how long animals stay in one place.

To examine the daily range size, the range an animal covers during one day, only those days were used where data had been collected on a radio-collared mara between 8:45 and 19:30. At least 12 fixes must have been recorded, and there must have been no more than a single hour long gap in the data sequence during this time period. This time interval was chosen to maximize the number of days of acceptable, comparable data for different animals. Since these ranges were not calculated from all daylight hours they should be viewed as minimum range sizes. Table 3.22 summarizes results showing that the daily range varies, as calculated using the grid cell system, from a minimum of 2.25 ha to a maximum of 23.25 ha. The mean range size is 10.25 ha ($\pm$ 5.64).

I further examined range sizes for individual maras over 24 hr periods. The start times and stop times were

Figure 3.18.--Composite behavioural time budget showing the percent of scans in which maras were observed engaging in different behaviours. Averaged from the seasonal time budgets.

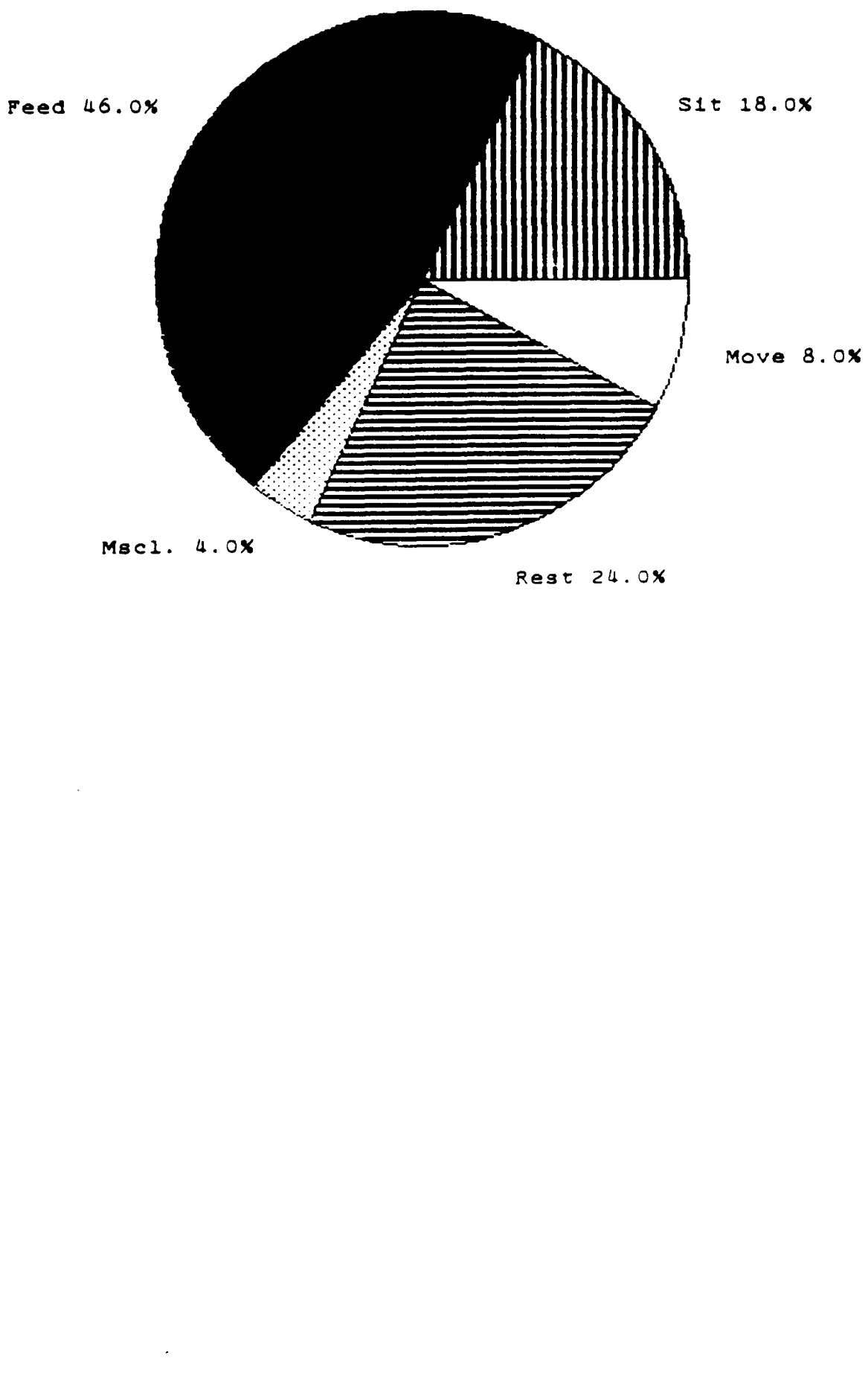


Table 3.22.--The number of hectares visited and distance travelled by radio-collared maras in a day between 8:45 and 19:30. Only days were used where there was no more than a single one hour gap in location records on a mara during this time period. Data is sorted by months. The time period was selected to maximize the number of days in which adequate data were available. SYF (*) was tracked continuously for 24 hours on 841031.

Mara	Date	Number Fixes	Range Size (Ha)	Distance Travelled (m)
SYF	840106	28	8.50	770
ENF	830321	44	8.00	-
ENF	830323	39	5.50	-
ELF	830413	37	13.50	2573
PAM	830417	38	3.25	654
GCM	830421	33	9.50	1532
PAM	830517	38	12.00	1276
ENF	830519	37	2.25	-
ELF	830803	36	7.75	1080
ELF	830827	37	10.00	5873
PAM	830922	26	4.50	711
ELF	830922	25	9.50	1767
GCM	830922	22	19.75	1984
SYF	831016	44	6.50	957
SYF	841031	27	20.25	6326 *
ELF	831105	44	9.75	1397
PAM	831115	73	10.00	1266
SYF	831117	49	11.00	1822
PAM	831216	81	23.25	1263
Mean			10.25 ha	1953 m
St. Dev.			5.64	1697

Statistical findings on the above data:

1. There was not a significant correlation between the number of fixes made and the daily range size ($r_s = -0.35$).

2. Analysis of variance revealed no significant differences between the daily range sizes in each month ($F = 1.01$), or the daily range sizes for the different maras ($F = 0.94$).

3. Using analysis of variance; no significant differences were found between the distance travelled by the individual maras ($F = 0.78$), or between the different seasons ($F = 0.75$).

chosen individually for each of the 19 samples to maximize the number of fixes obtained within the sample period (see Table 3.23). These 24 hr ranges varied from 2.25 ha to a maximum of 60.25 ha ($\bar{x}$ 19.97 ha). When divided by the seasonal range size for each mara in the same season (see Table 3.11 above) the 24 hr ranges varied from 0.03 to as much as 0.55 of the seasonal range ($\bar{x}$ 0.22).

To discover how far animals travelled in a day I plotted the movements, using program LENGTH (Doncaster, 1985), for those days for which I had previously calculated daily range sizes. These daily movement patterns are mapped in Figure 3.19. To determine the distance travelled each day I used a digitizing pad, with appropriate software, on an Apple IIe computer (courtesy of F. Vollrath, Dept. Zool., Oxford). The mean distance travelled in a 10 hr and 45 min day was 1953 m ($\pm$ 1697). The maximum distance travelled was 5873 m (6326 m during one 24 hr period), and the minimum distance travelled was 711 m. It is of interest to note that there is no circling pattern to these daily wanderings: there is no tendency for animals to come back to the same place at the end of the day, as has been shown for maras in captivity where most pairs use the same sleeping spot every night (Dubost and Genest, 1974).

The duration of visits to a given grid cell (50 x 50 m) was computed by program LENSTAY. This program selects data sequences in which fix intervals were no more than 15 minutes, and arrival and departure times for a cell were known to the nearest 15 minutes. The results are shown in Table 3.24. These results are accurate only to 15 minute intervals and so might underestimate a given duration of visit by up to 30 minutes. However it is clear that in the bulk of observations (81%) animals stayed in one 50 x 50 m grid cell for less than 50 minutes.

The pattern of daily movement which emerges from the results presented above is one of an animal constantly on the move: maras may cover up to a half or more of their

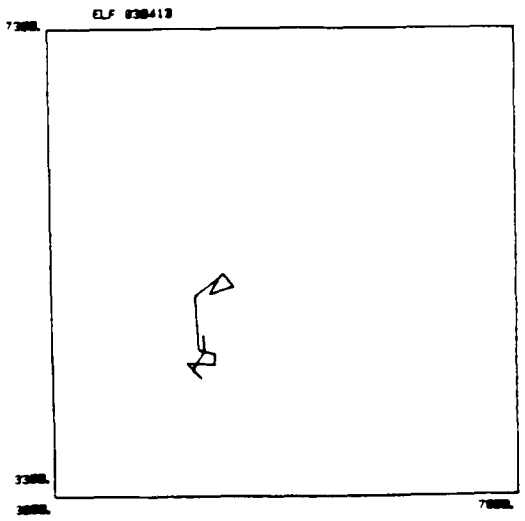
Table 3.23.--Daily range size based on grid cells. Data were selected from days where radio fixes were obtained over at least twelve hours. The time periods for each sample were chosen in each case to maximize the number of fixes within a 24 hour period. Mara SYF was tracked for a full 24 hours on 841031.

Mara Name	Date	Daily Range (ha)	Proportion of Seasonal Range
GCM	831019	13.75	0.11
TIF	831019	32.25	*
WOF	831026	10.25	*
ENF	830321	8.00	0.11
	830514	4.50	0.06
	830519	2.25	0.03
SYF	831016	8.00	0.09
	831117	50.25	0.55
	831214	4.50	0.05
	840106	24.50	0.29
	841031	36.00	0.20
ELF	831019	12.00	0.12
	831104	13.75	0.14
	831130	10.25	0.10
	831219	60.25	0.73
PAM	830416	12.25	*
	831114	20.50	0.17
	831129	33.00	0.28
	831216	23.25	0.48
Mean		19.97	0.22
St. Dev.		16.02	0.22

* Seasonal range size not available.

Figure 3.19 (2 pages).

Paths followed by individual maras from 8:45 to 19:30. Only tracking days were used where there was no more than a single one hour gap in the tracking record for an individual mara during the above time period. The path shown for SYF on 831117 is based on data collected over 24 hours of continuous tracking.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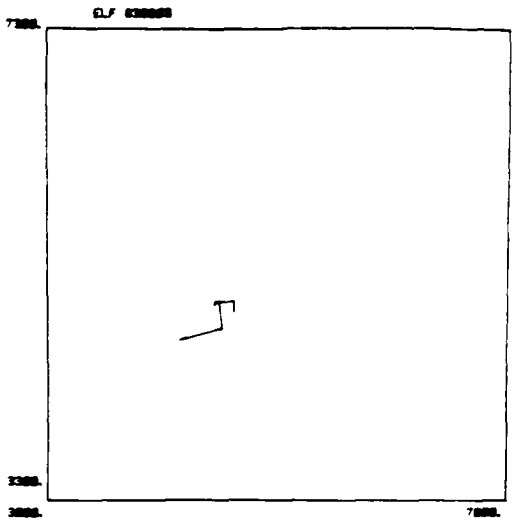
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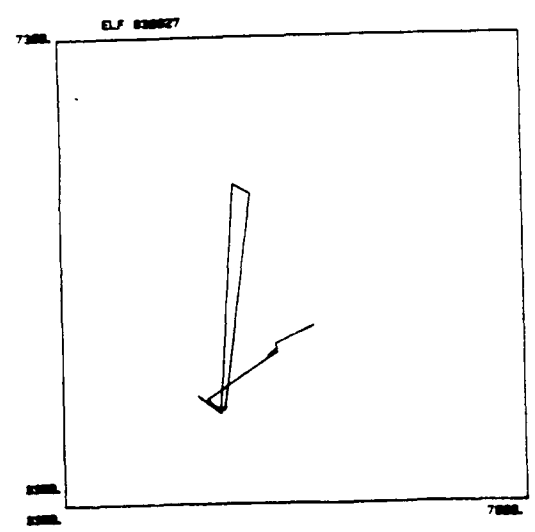
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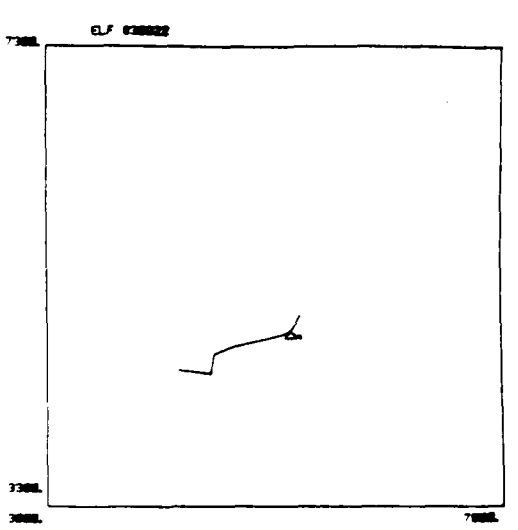
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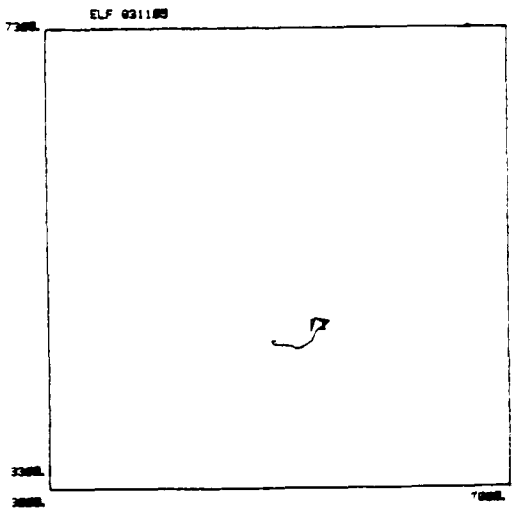
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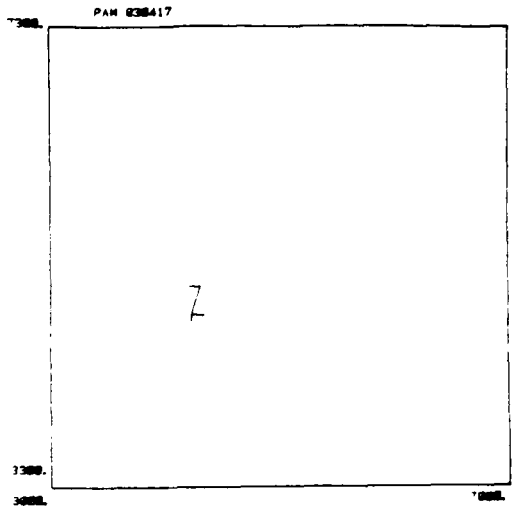
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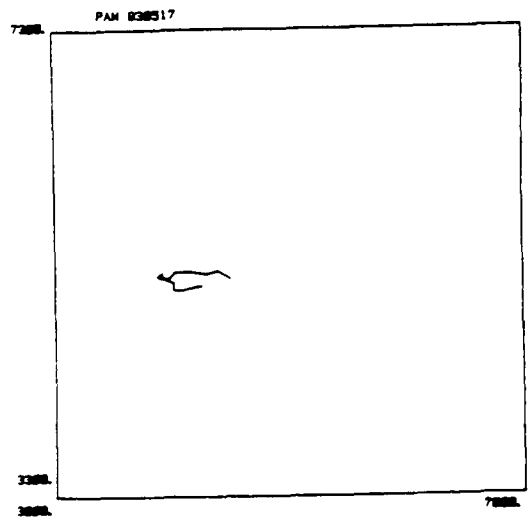
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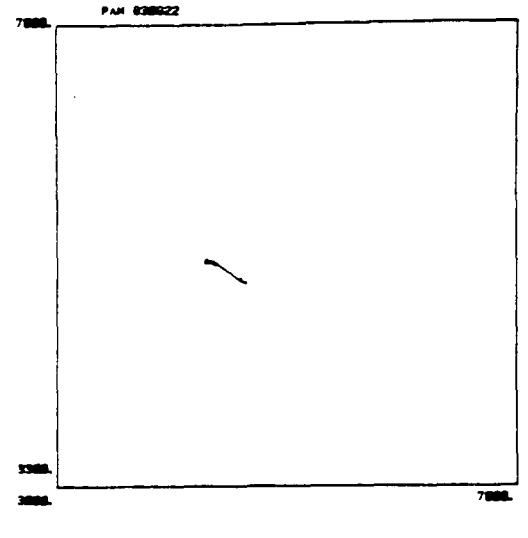
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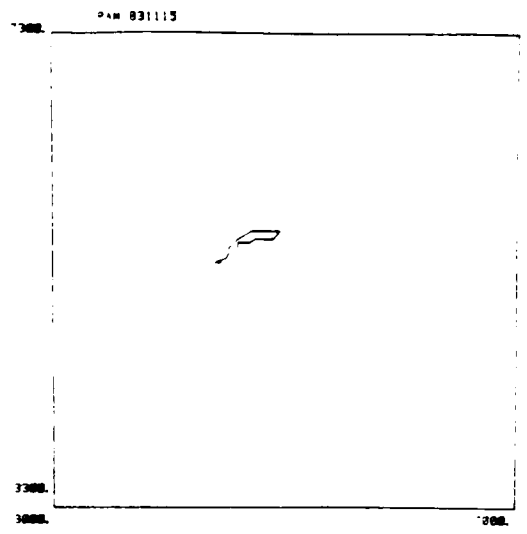
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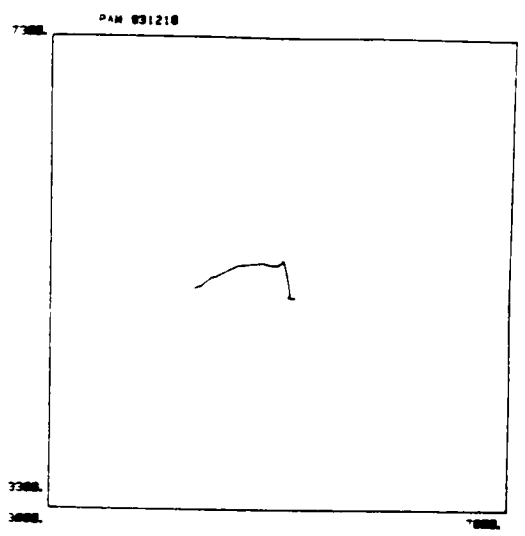
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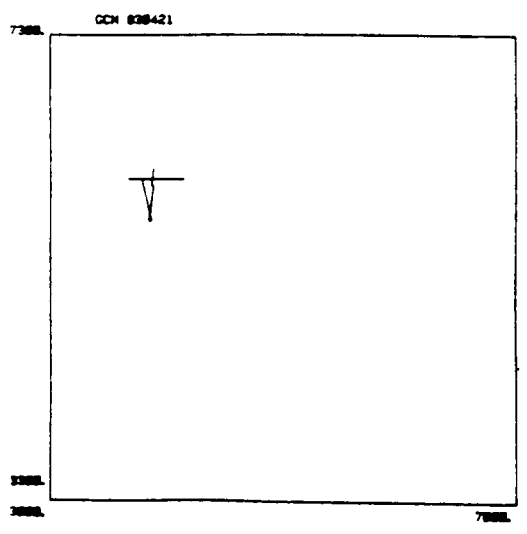
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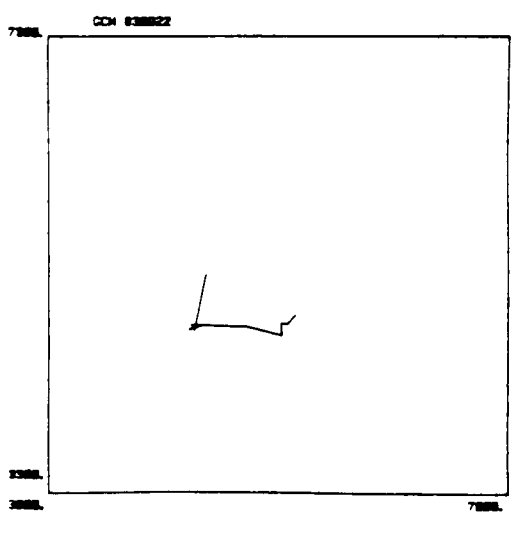
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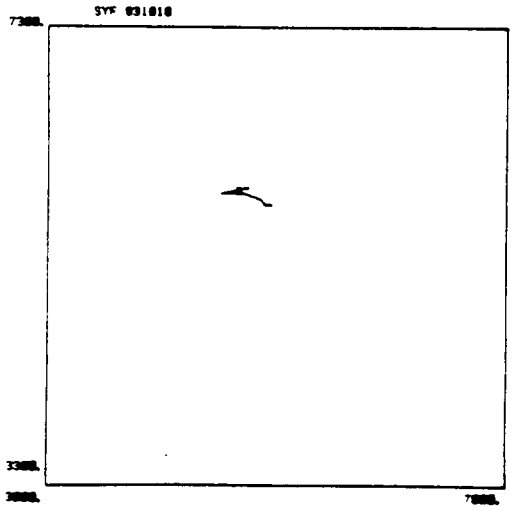
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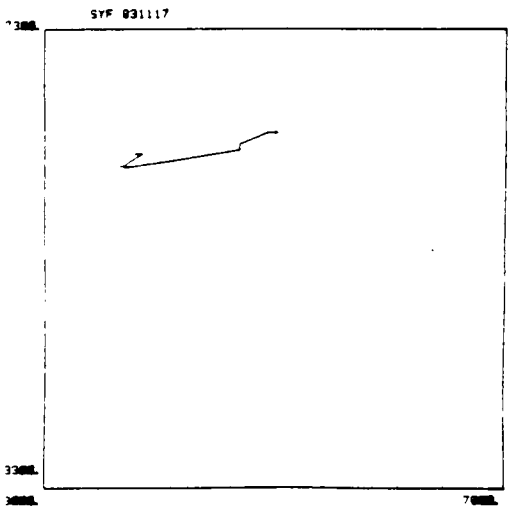
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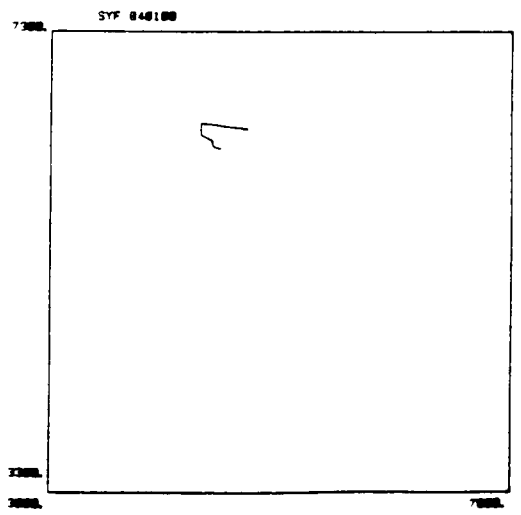
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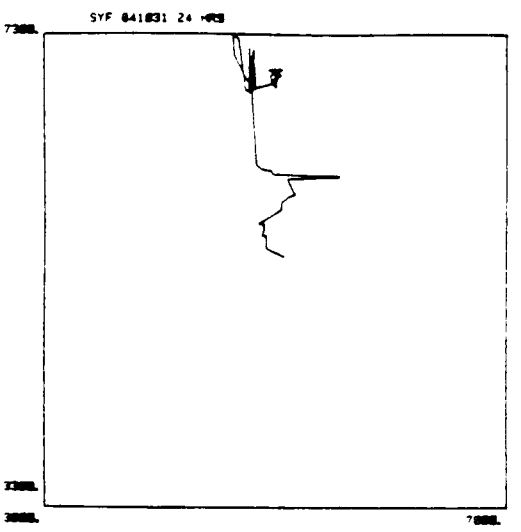

SYF 841831 24 HRS

Table 3.24.--The number and proportion of records of maras staying in 50 x 50 m grid cells at varying time intervals. Data comes from program LENSTAY run on all the radio collared animals. The criteria for using data sequences were that: (i) no more than 15 minute gaps existed in the record, (ii) the approximate time of arrival (to 15 minutes) at a grid cell was known, and (iii) the animal was subsequently recorded elsewhere within 15 minutes of its last sighting in a cell. Due to the 15 minute data interval, timings could be up to 30 minutes low since an animal could have arrived in a cell 14.99 minutes before being located there, and it could have stayed in that cell a further 14.99 minutes before being recorded elsewhere. All times are in minutes.

-Stay Time- (Minutes) Minimum	Maximum	Maximum Possible	Number Observations	Proportion Observations
0	10	40	396	0.67
10	20	50	81	0.14
20	40	70	35	0.06
40	60	90	22	0.04
60	90	120	29	0.05
90	120	150	11	0.02
120	180	210	12	0.02
180	240	270	4	0.01
> 240	-	-	3	0.01

seasonal ranges in one day, they rarely stay in one 50 x 50 m grid cell for more than 50 minutes, and their movement patterns suggest no regular daily routine. The results covering the mara's behavioural time budgets show that the animals spent close to half their time feeding every day. This result must be an underestimate of foraging time since it does not include time spent searching for food. In the next section I will be looking at mara habitat use patterns to see if the mara's movement and activity patterns can be tied to the distribution of food or other resources.

3.5 Mara Usage Of Habitat

In this section I will be looking at the following three aspects of mara habitat usage to see whether ranging patterns can be tied to specific habitat features.

1. The general pattern of habitat usage.
2. Seasonal fluctuations in 1 above.
3. Foraging behaviour and food habits.

3.5.1 General Patterns of Habitat Usage

Two independent sources will be used to explore mara habitat use (also see Section 3.2): (1) usage patterns as revealed through recording an animal's habitat while radio-tracking; and (2) vegetation cover preference patterns through comparing cover values, sampled on a 300 X 300 m grid system, with usage patterns revealed through radio-tracking.

Scan Defined Habitat Usage

The following habitat categories were used for this analysis: lagoon bed, open ground, scrub, and other. As described in Subsection 3.2.4, these data were obtained through recording the habitat and location every time a radio fix was recorded for an animal. These data were then used to create a distribution of habitat throughout the study site by totalling the number of unique 50 x 50 m cells visited by the radio-collared maras for each habitat type. The resulting distribution was 12% lagoon, 5% open, 81% scrub, and 2% other. To determine if maras were exercising any habitat preference the number of scans of animals in each habitat was compared with the distribution of habitats in the study area using the X^2 test (see Table 3.25). To insure independence between scans, and to limit the bias of not always being able to identify an animal's habitat while collecting radio fixes, data were selected at hour intervals. Of the 901 data points used from all 9 radio-collared animals, 6% (51) were in the unknown habitat category. The X^2 test results show that the maras' habitat use patterns varied significantly from the distribution of habitats at the La Blanca study area: the animals clearly spent most of their time (0.76) in scrub habitat (0.81 of the area), but they spent significantly more time in the open than expected. In fact, this underestimates this effect since the study area's habitat distribution was based only on the cells the radio-collared animals actually visited, and thus excludes the virtual 'sea' of scrub habitat which surrounds the La Blanca study area.

Table 3.25.--The number and proportion of fixes of radio-collared maras in different habitat types throughout the year, and in the four seasons, compared to the expected number if maras had been using the study area's habitat uniformly. The results of X^2 tests of the significance of these differences are shown below each table.

Habitat	Proportion	Observed	Expected	X^2
All Habitat Data				
Lagoon	0.11	91	104.15	1.66
Open	0.10	88	40.32	56.40
Scrub	0.76	647	692.09	2.94
Other	0.03	24	13.44	8.30
Total X^2 = 69.3, $P < 0.005$				
Winter Habitat Data				
Lagoon	0	0	16.66	16.66
Open	0.09	12	6.45	4.77
Scrub	0.90	123	110.74	1.36
Other	0.01	1	2.15	0.62
Total X^2 = 23.41, $P < 0.005$				
Spring Habitat Data				
Lagoon	0.16	58	45.09	3.70
Open	0.15	55	17.45	80.76
Scrub	0.66	244	299.64	10.33
Other	0.03	11	5.82	4.62
Total X^2 = 99.40, $P < 0.005$				
Summer Habitat Data				
Lagoon	0.16	20	15.81	1.11
Open	0.11	14	6.12	10.15
Scrub	0.66	85	105.04	3.82
Other	0.08	10	2.04	31.07
Total X^2 = 46.16, $P < 0.005$				
Fall Habitat Data				
Lagoon	0.10	13	26.59	6.94
Open	0.05	7	10.29	1.05
Scrub	1.51	195	176.69	1.90
Other	0.02	2	3.43	0.60
Total X^2 = 10.49, $P < 0.025$				

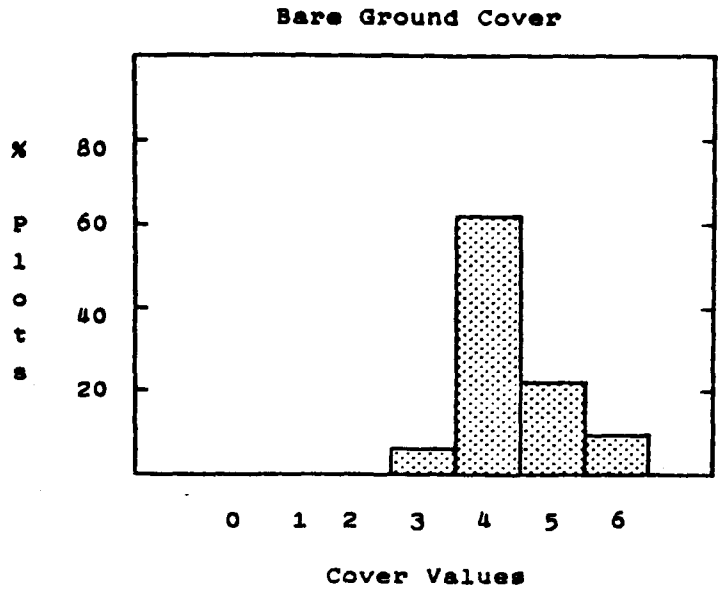
Cover Value Defined Habitat Usage

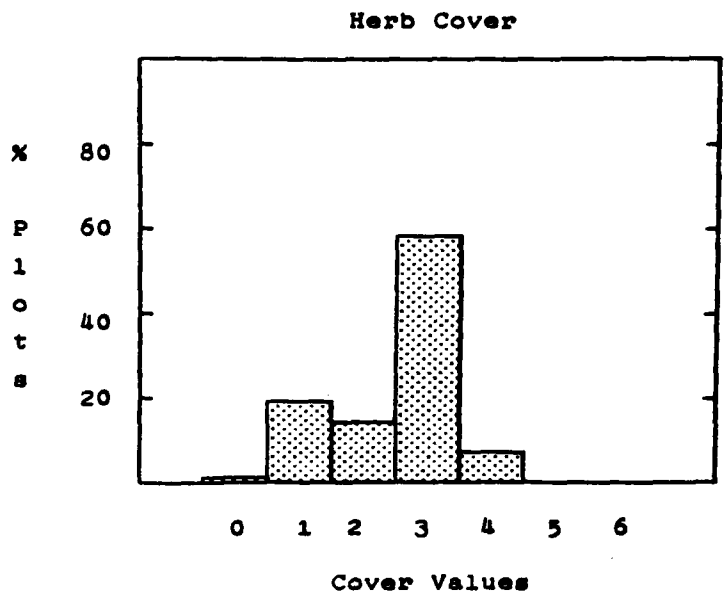
The goal of this analysis is to compare the radio-collared maras' vegetation cover range and usage with the overall pattern of vegetation cover in the study area. The vegetation cover range for a mara is defined as the subset of vegetation (300 x 300 m) cells which a mara had visited. The vegetation cover range usage incorporates the number of independent fixes of an animal in each vegetation cell so that it reflects time spent in different cells and thus actual usage patterns. From these data a distribution can be built up of the maras' range and range usage patterns for each vegetation cover category. Figure 3.20 shows the distribution of Braun-Blanquet cover values for each of the vegetation categories in the sampled area. Since these cover values are not normally distributed, the Mann-Whitney test was used to distinguish differences in vegetation cover.

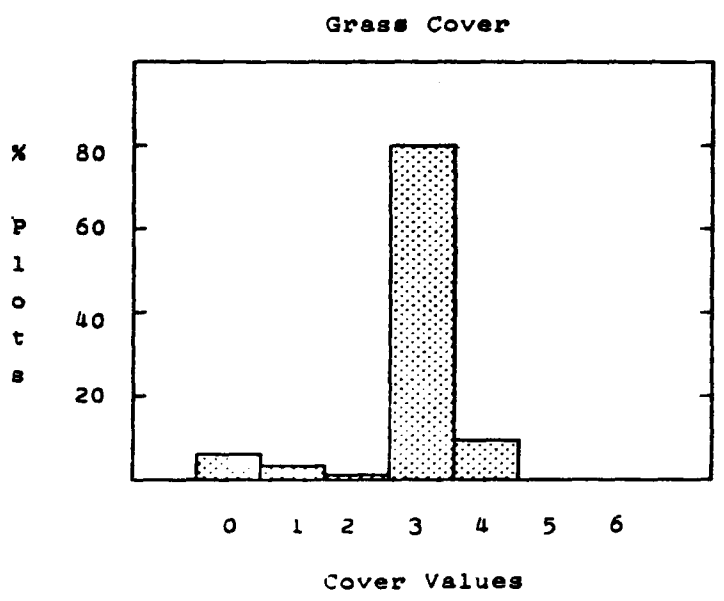
For the combined data on the movements of radio-collared maras three separate comparisons were made for each of the bare ground, herb, grass, and shrub vegetation categories. These were:

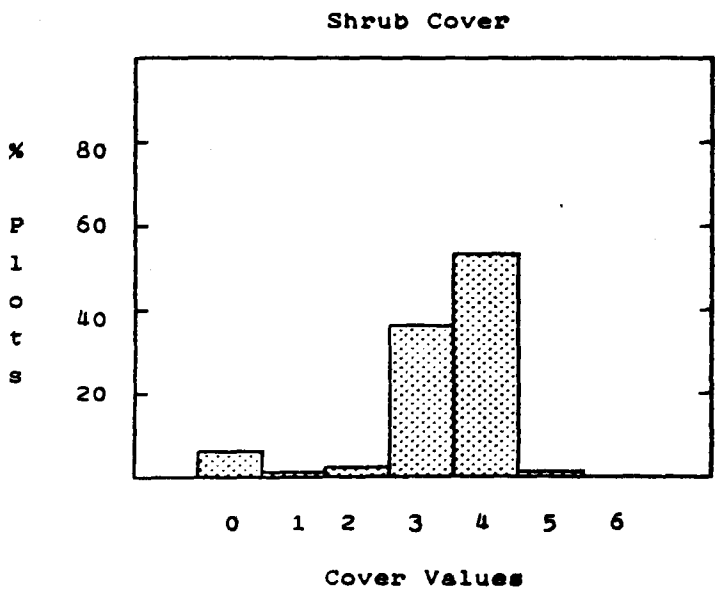
1. Between the study site vegetation cover and the vegetation cover of the maras' ranges. This comparison would show if maras were making any general selection in the areas they visited.
2. Between the study site's vegetation cover and the maras' vegetation usage. This comparison tests if maras were making any choices about which vegetation cover they preferred overall since it reflects how long they actually spent in cells with different cover values.
3. Between the maras' range vegetation cover and usage vegetation cover. This comparison tests what preferences maras have for specific vegetation cover

Figure 3.20.--Histograms of the percent of the plots sampled with each Braun-Blanquet cover value for the bare ground, herb, grass, and shrub cover types.









within the area available to them as defined by the range cover values.

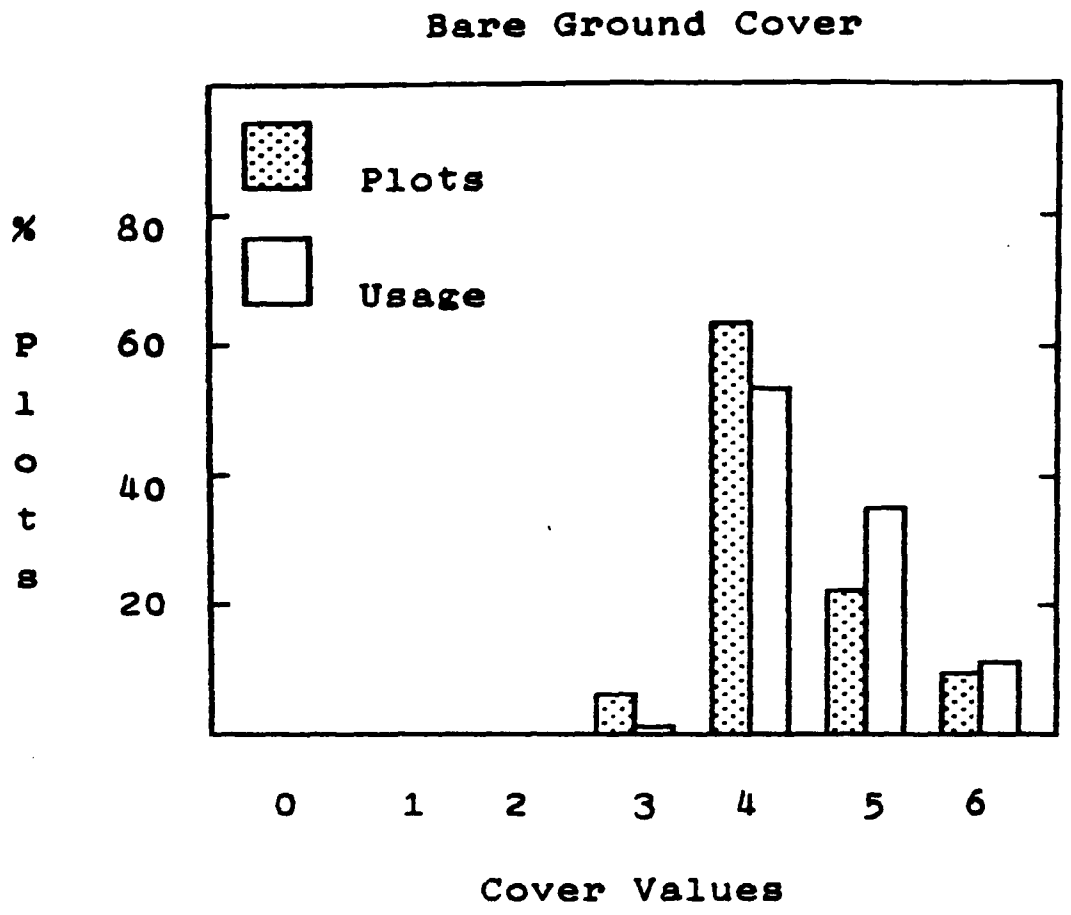
Results of these tests are shown in Table 3.26. The only significant differences found were that maras used vegetation cells with a higher percent bare ground cover and herb cover than expected if they had been using the study area uniformly (see Figure 3.21). The bare ground cover results tie in closely with the results presented on habitat usage, where I showed that maras spent more time in open habitat than expected. The result suggesting that maras were selecting areas with more herb cover may be misleading for the following reasons: (i) in Section 3.2 data analysis has shown that results pertaining to herb cover values may not be accurate, and (ii) in Subsection 3.5.3 evidence suggesting that grass plays a more important role in the maras diet than herbs (on the Peninsula Valdés) will be presented.

3.5.2 Seasonal Pattern of Habitat Usage

Pie charts are shown in Figure 3.22 of habitat use patterns in the four seasons of the year based on the number of times radio-collared maras were recorded in each habitat type. As these charts suggest, habitat use patterns were found to vary significantly between seasons (X^2 = 80.60, degrees of freedom = 9, $P < 0.001$; See Table 3.27). The most striking changes can be seen in the usage of the lagoons during the year: this fluctuates from nothing in the winter, to 15.8% of the observations in spring, 15.5% in summer, and 6% in the fall. These fluctuations fit in well with the water cycle on the Peninsula (see Chapter 2). In the drier seasons, spring and summer, the animals used the lagoons more. One reason for this may be that the water table on the lagoons would be closer to the surface than elsewhere. Thus forage on the lagoons could have a higher concentration

Table 3.26.--Mann-Whitney tests comparing the distributions of Braun-Blanquet cover values for the study site, range vegetation, and usage vegetation of the maras for each cover type (see text for sample definitions).

Type 1	Median	Type 2	Median	W	P Value
Bare Ground Cover					
Range	4	Usage	4	142749.5	0.0897
Range	4	Site	4	30798.5	0.2567
Usage	4	Site	4	954297.0	0.0095 **
Herb Cover					
Range	3	Usage	3	142468.5	0.0810
Range	3	Site	3	31104.0	0.1168
Usage	3	Site	3	956417.5	0.0017 **
Grass Cover					
Range	3	Usage	3	148480.5	0.4780
Range	3	Site	3	29537.0	0.5109
Usage	3	Site	3	943037.0	0.7951
Shrub Cover					
Range	4	Usage	3	159641.0	0.2252
Range	4	Site	4	29668.0	0.6375
Usage	3	Site	4	938134.0	0.1331



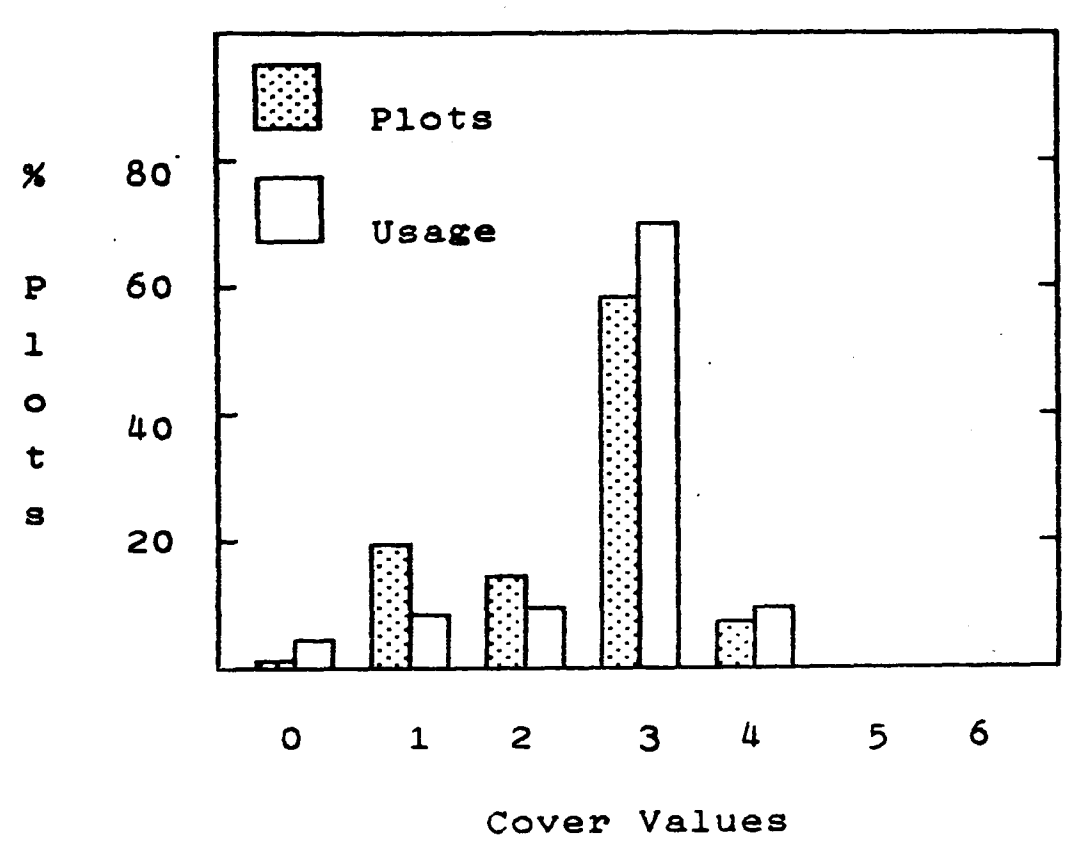
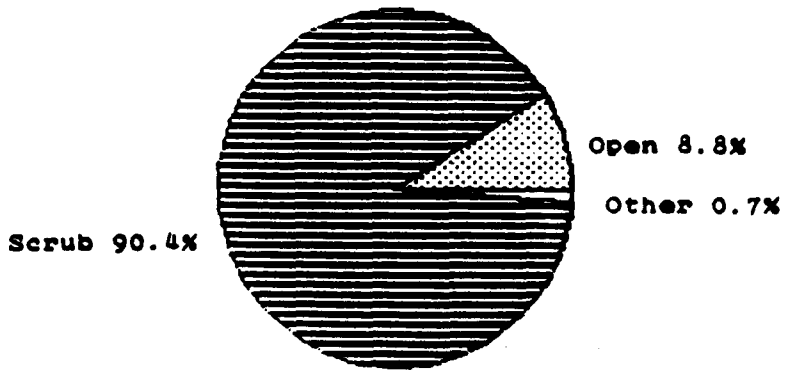
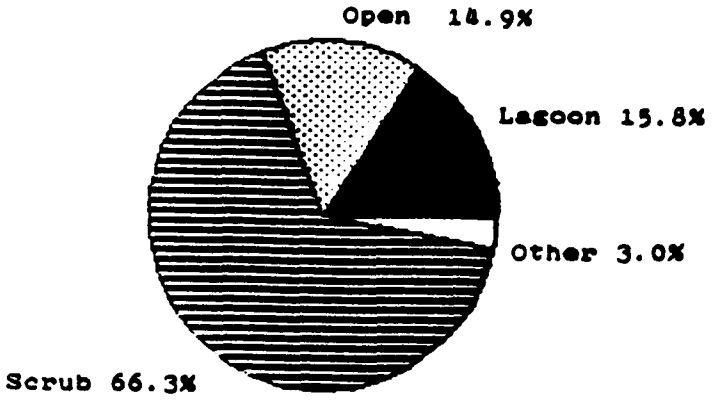


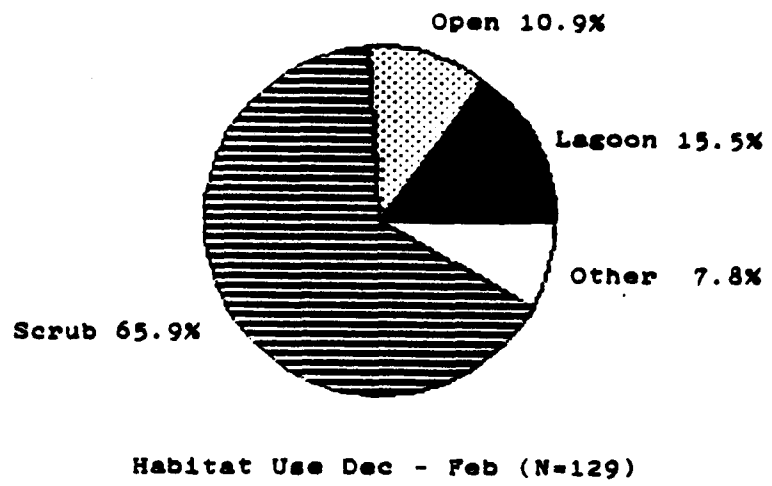
Figure 3.21.--Comparisons between the distribution of Braun-Blanquet cover values (see Section 3.2) in the study area and in the maras' vegetation cover usage. Histograms are shown for both the bare ground and herb cover types. The figures show the percent of each Braun-Blanquet cover value in each sample. The vegetation usage distribution is calculated by determining the percentage of independent fixes of the radio-collared maras (data selected at 1 hr intervals) with each cover value in each cover type.



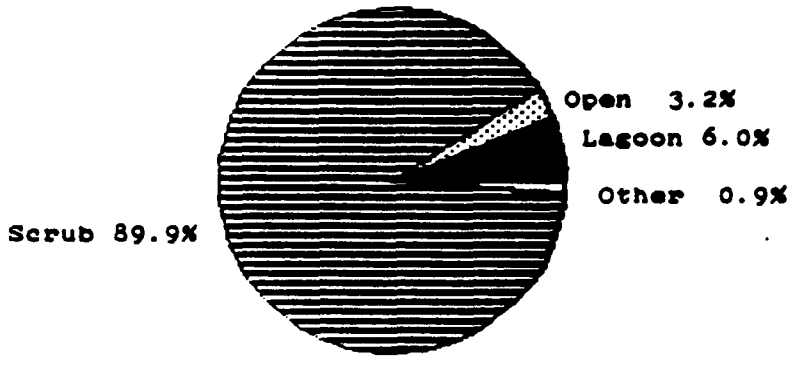
Habitat Use June - Aug (N=136)



Habitat Use Sep - Nov (N=368)



Habitat Use Dec - Feb (N=129)



Habitat Use Mar - May (N=217)

Figure 3.22.--Pie charts for each season of the percent of the fixes in which the radio tracked maras were recorded in the open, scrub, lagoon, and other habitat categories.

Table 3.27.--Seasonal differences in habitat use patterns. Observed counts, taken from radio-tracking data, and expected counts of maras in each habitat type. X^2 tests show a significant difference in the number of scans of maras in different habitats (X^2 = 80.60, df = 9, P < 0.001).

	-Winter-		-Spring-		-Summer-		-Fall-	
Habitat	Obs	Exp	Obs	Exp	Obs	Exp	Obs	Exp
Lagoon	0	15	58	39	20	14	13	23
Open	12	14	55	38	14	13	7	22
Scrub	123	104	244	280	85	98	195	165
Other	1	4	11	10	10	4	2	6
Total	136		368		129		217	

of water than in the surrounding areas in these months. I have only observed maras drinking water on one occasion. so the water content of the plants eaten must be important to the animals in maintaining water balance.

3.5.3 Foraging Behaviour and Food Habits

Although a detailed study was not made on mara foraging behaviour the following statements can be made: (i) maras are primarily grazers and not browsers--in 8463 scans of adult maras they were only observed browsing on 8 occasions compared to 4702 scans grazing; (2) maras have tiny mouths (see Figure 3.23) apparently adapted for selecting the most nutritious parts of the food plants.

An analysis was made on mara food habits as reflected in the presence of plant cuticles in faeces. Cuticle is the thin waxy, protective layer covering the surface of the leaves and stems of plants. The cuticle of each plant species has a characteristic pattern which can be used to identify it. Through inspecting (using a microscope) the cuticles in an herbivorous mammals' faeces, and comparing them with a reference collection of cuticles of known plants in the study area, the plant species consumed by the animal can be identified. By using a sampling system, this method can be used to calculate the proportion of cuticle of each plant species in the faeces to provide information on an herbivore's food habits. These proportions are, however, open to misinterpretation since they may not reflect the actual proportion of plant species consumed because of (i) differences in the surface area of epidermis per unit weight of a particular plant species, and (ii) differential digestion of the species consumed (Bhadresa, 1986). To be used effectively this technique must be coupled with feeding trials, which I was not able to do, on the herbivores concerned to ascertain the relationships between the amounts of food plants consumed to the

Figure 3.23 (Overleaf).

Photograph illustrating mara grazing behaviour. Note the small size of the mara's mouth, and the vegetation being fed on.

proportion of cuticles of these plants in the faeces.

Because of time constraints, and because of the lack of feeding trial data, I have chosen to identify cuticles in the maras' faeces only to monocot (grasses) and dicot (herbs) cuticles. A full study of mara food habits in the wild has been conducted elsewhere (see Kufner, 1983). It is an easy task to identify these two groups of plants by the different patterns of the cells outlined in the cuticles: monocotyledenous plant cells are long and narrow, and always aligned in parallel columns; dicotyledeneous plant cells, on the other hand, are arranged randomly.

To do this analysis I collected 10 piles of fresh faeces, located at least 200 m apart, in November 1981. In the laboratory, 1 faecal pellet was selected from each pile. These 10 faeces were gently crumbled together into a petri dish and mixed thoroughly. Domestic bleach (8% available chlorine content) was diluted in the proportion of 1:5, and this solution was poured onto the faeces. The solution was left to soak for about 1 hr, after which a pipette was used to deposit a drop of the solution onto each of 10 slides. Using a microscope with a 16 X objective, 5 transects were made across each slide, at 4 mm intervals counting the number of cuticle fragments which were identifiable as either dicot or monocot. A total of 476 cuticle fragments were identified as coming from grass plants, and only 36 as coming from herbs. This gives a grass to herb ration of 13:1. These results must be taken with caution for the following reasons: (i) only faeces from the month of November were analyzed, and (ii) the cuticle content of the faeces, as discussed above, may not reflect the proportion of plants eaten. However, the suggestion from these results is that grass plants play a more important role in the mara's diet than herbs in my study area.

I further analyzed faeces from pups from the entrance of three dens. Pup faeces are easily

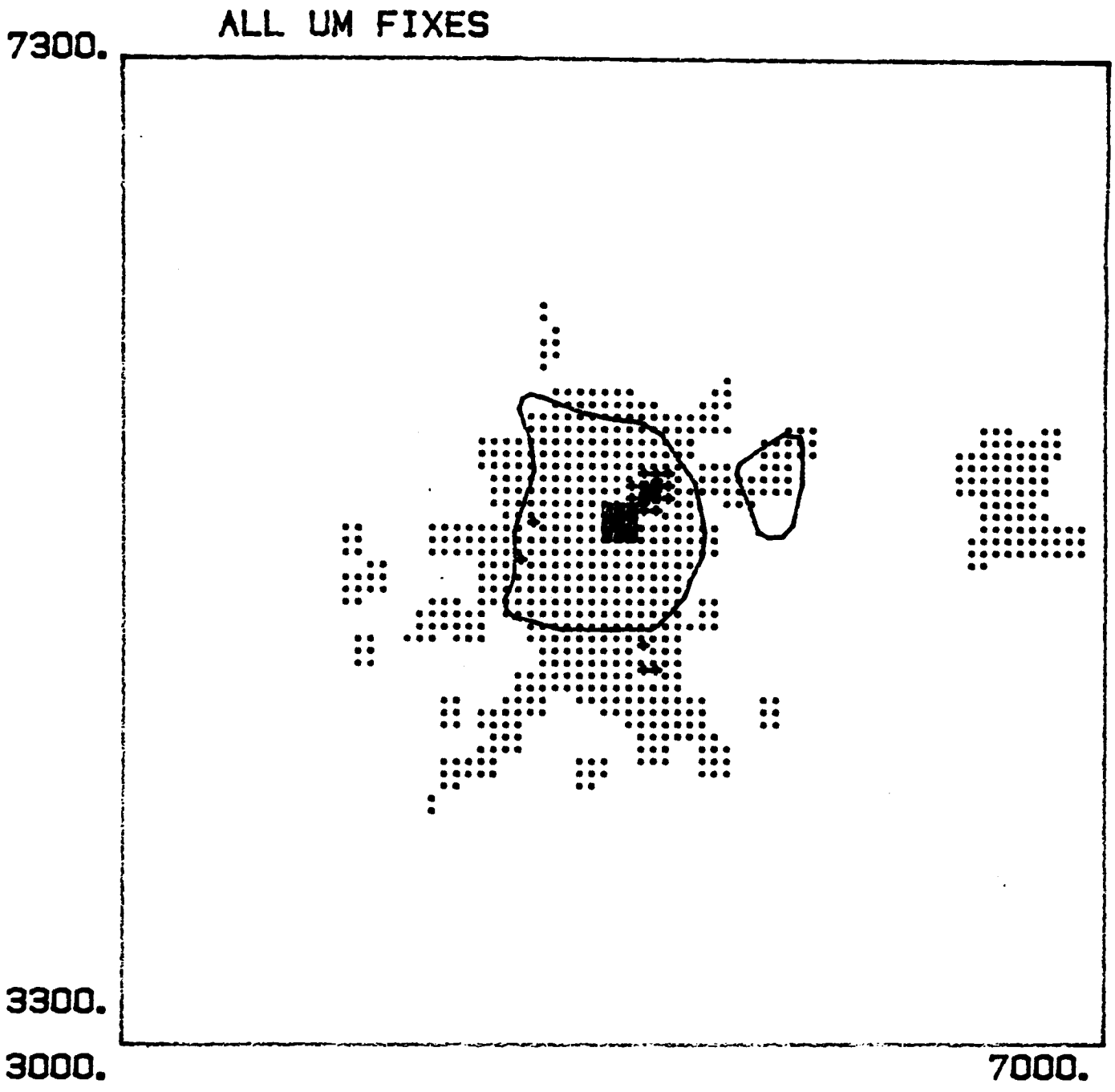
distinguishable since they measure only half the length or less of an adult faeces. Ten pup faeces were selected from the three dens and treated the same way as above. A total of 709 grass cuticle fragments were identified, compared to 14 herb cuticle fragments, giving a ratio of grass to herbs of 51:1. A X^2 test found this grass to herb ratio to be significantly different from that of the adults (X^2 = 20.03, df = 1, P < 0.005). Thus it appears that grasses may constitute a larger proportion of the pups' diet than the adult diet. It seems likely that this reflects the availability of herbs around the three dens where I collected faeces--an area where the adults did not spend much time feeding (see Chapter 5).

3.6 Spatial Relationships Between Pairs

It is the aim of this section to investigate the spatial relationship between pairs of maras. In particular, I will be looking at the spatial overlap and correlation between maras' ranges throughout the period during which pairs were tracked together, and within seasons.

Before going on to present the results the point must be made that there were many uncollared animals within the La Blanca study area. Up to 34 pairs used the La Blanca den sites in 1983 (see Chapter 4). Figure 3.24 shows an ICELL plot for all the unidentified maras sighted during the study period. The distribution of these fixes shows a convoluted pattern spreading out from the lagoon which reflects the pattern of dirt tracks (see Figure 3.2 above). These tracks were heavily patrolled while radio-tracking, and were also open, which meant that the opportunities for sighting non radio-collared maras on them was much higher than in the surrounding scrub. Even with this sampling bias, the fixes plotted cover much of the area occupied by

Figure 3.24.--ICELL plot of all the locations recorded for unmarked maras at the La Blanca study area during the entire period of field research.



the radio-collared animals. The radio-collared maras must, then, have been interacting spatially with many more animals than I was able to track.

3.6.1 Long Term Overlap Between Ranges

Three measures will be used to examine the spatial relationship between the animals being compared: (1) the area (composed of 50 x 50 m cells) which both animals being compared shared, (2) the proportion of each animal's total range included in the overlap zone (these data comes from the ICELL program), and (3) the spatial correlation between ranges (see Subsection 3.3.2 for a discussion of this method).

Figure 3.25 illustrates the variation in the proportion of ranges overlapping between all the maras tracked throughout the study period. The overlap of six paired ranges were compared for the 4 maras who were tracked for longer than one season. Results of these comparisons are shown in Table 3.28. In one comparison there was no overlap at all, in three of the comparisons there were less than 6 ha in the overlap zone, in the other two comparisons the ranges overlapped 26.25 ha and 48 ha. The proportion of ranges overlapping varied from 0.0 to 0.29. The correlation of ranges using the Spearman rank correlation for animals whose ranges overlapped at all varied from -0.46 to -0.84. Even -0.46 shows less concordance between ranges than for any of the between season correlations of ranges (-0.36 to -0.44) for a single mara with a one season lag (see Section 3.3.2, and Table 3.14).

3.6.2 Seasonal Overlap Between Ranges

Looking at the pattern within seasons for the 9 maras, Table 3.29 summarizes the number of hectares, and

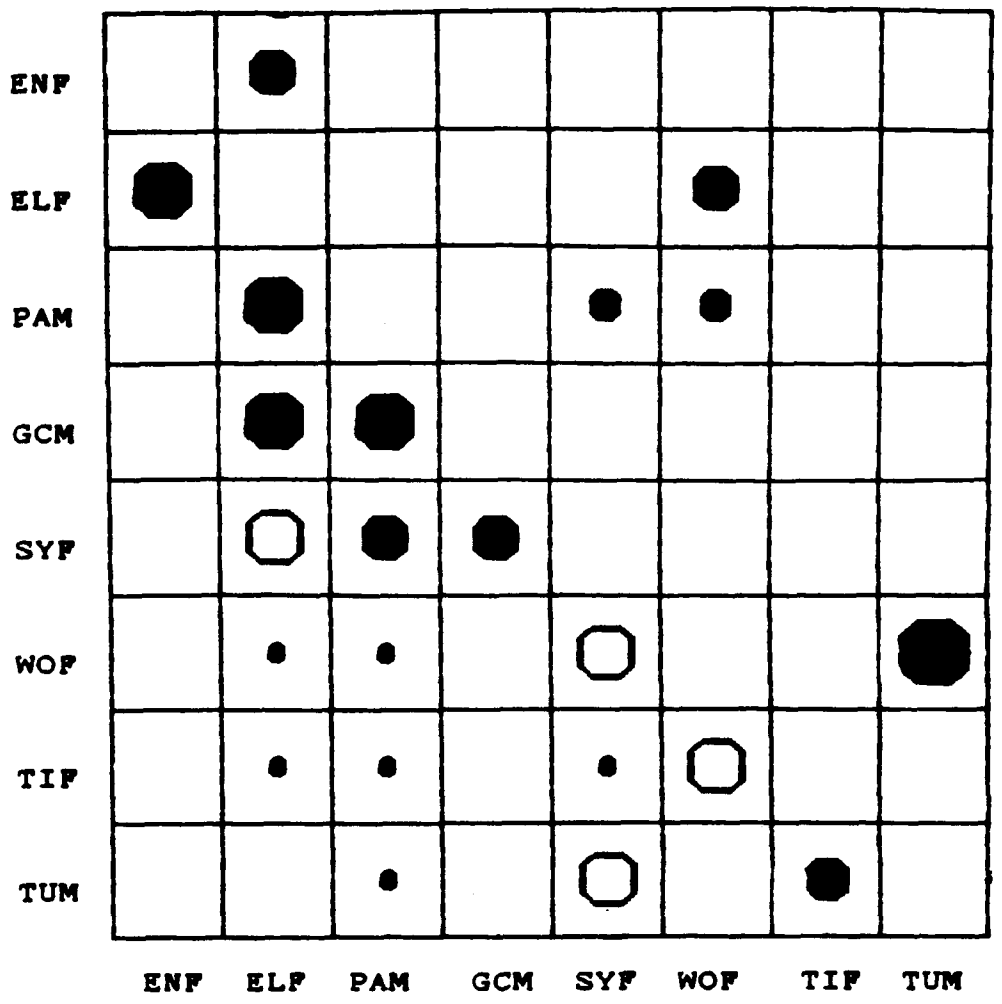


Figure 3.25.--Spatial overlap of maras' ranges. The symbol size shows the proportion of the animals' ranges being compared which overlap. Symbols are shown twice for those comparison where there were greater than a few points difference in the proportion of each range overlapping (due to the ranges being different sizes). No symbols are shown when animals were not tracked over the same time period.

Legend

Blank	Animals not intensively tracked at same time
•	0.01 - 0.05
●	0.06 - 0.10
●	0.11 - 0.20
●	0.21 - 0.30
●	0.31 - 0.40
○	No overlap

Table 3.28.--Overlap of ranges between animals throughout the period in which both maras (pairs) compared were followed. The number of hectares both animals' ranges shared, the proportion of each mara's range overlapping with the other, and the Spearman rank correlation coefficient of the two ranges are given.

Animals Compared	Dates Tracked Together	Overlap in ha	Proportion Range Mara 1	Mara 2	r_s
ELF - PAM	830413 - 840222	48.00	0.29	0.27	-0.46
ELF - SYF	831005 - 840222	0	0	0	-
ELF - TIF	831005 - 840222	1.25	0.01	0.01	-0.84
PAM - SYF	831005 - 841122	26.25	0.13	0.09	-0.68
PAM - TIF	831007 - 841122	5.50	0.03	0.02	-0.82
SYF - TIF	831007 - 841122	5.75	0.02	0.02	-0.83

Table 3.29.--Overlap of home ranges of individual maras in different seasons of the year. Numbers given for each comparison are: (i) number of ha both animals' ranges shared, and the proportion of the column (ii) and the row (iii) animals' ranges in the overlap zone. Measurements of overlap were obtained using ICELL.

Season		Comparisons Made		
Mar-May		ENF		
1983	ELF	21.75		
		(0.29,0.15)		
June-Aug		ELF		
1983	PAM	15.00		
		(0.20,0.17)		
Sep-Nov		ELF	PAM	GCM
1983	PAM	17.25		
		(0.17,0.15)		
	GCM	29.50	34.00	
		(0.29,0.24)	(0.29,0.28)	
	SYF	0	8.00	2.0
		-	(0.07,0.07)	(0.02,0.02)
Dec-Feb		ELF	PAM	SYF
1983-1984	PAM	0		
		-		
	SYF	0	0	
		-	-	
	WOF	3.50	2.00	0
		(0.04,0.11)	(0.04,0.06)	-
	TIF	0	1.50	0.50
		-	(0.03,0.02)	(0.01,0.01)
Sep-Nov		SYF	TIF	TUM
1984	TIF	1.75		
		(0.01,0.01)		
	TUM	0	33.00	
		-	(0.17,0.36)	
	PAM	0.25	1.50	0.50
		(0.0,0.0)	(0.01,0.02)	(0.01,0.01)

proportions of ranges, overlapping for five seasons from Fall 1983 to Spring 1984. The range overlap in the 21 comparisons made varied from none to a maximum of 33 ha. The maximum proportion of one animals' range contained in the overlap zone was 0.29. Correlations made between seasonal ranges for different animals varied considerably, but were always highly negative and never closer to 0 than -0.179 (maras TIF and TUM, see Table 3.30). Of the 21 comparisons made only three showed more concordance between ranges than the minimum degree of concordance (-0.44) for one animal's range with a one season lag (see above). All three of these cases were breeding season comparisons when the animals whose ranges were being compared probably shared the same den site (see Chapter 5).

Finally, I looked at the mean distance apart radio-collared animals were within seasons. For each range comparison I measured the distance between each fix for one animal with every other fix for the other animal (see Table 3.31). On average animals were widely spaced with the mean distance between maras varying from a minimum of 534 m to a maximum of 2232 m ($\bar{x}$ =1405 m, $\pm$ 448).

These results tie in well with the range correlation results suggesting that the radio-tracked maras were avoiding each other. This is well illustrated in Figure 3.26 which shows overlayed contour plots for two maras' ranges for the 6 animals (pairs) whose ranges overlapped more than 10 ha. The contour intervals in these plots show, for both animals, the relative intensity of usage of each part of the animals' ranges. From these figures one can see that the animals' ranges do overlap considerably; but that peak usage areas, as marked by close contour intervals, are always in different places--albeit often adjoining peak usage areas of the neighbouring mara pair.

Table 3.30.--Spearman rank correlations between different maras' ranges during entire period in which both animals were tracked, and within seasons. Correlations given only where ranges overlapped by at least one 50 x 50 m cell. Stars mark seasons in which both animals compared were tracked, but where their ranges did not overlap.

Maras Compared	Mar-May 1983	Jun-Aug 1983	Sep-Nov 1983	Dec-Feb 83-84	Sep-Nov 1984	All Data
ELF-ENF	-0.589	-	-	-	-	-
ELF-PAM	-	-0.556	-0.640	*	-	-0.462
ELF-GCM	-	-	-0.406	-	-	-
ELF-WOF	-	-	-	-0.638	-	-
ELF-TIF	-	-	-	*	-	-0.843
PAM-GCM	-	-	-0.274	-	-	-
PAM-SYF	-	-	-0.758	*	-0.761	-0.679
PAM-WOF	-	-	-	-0.779	-	-
PAM-TIF	-	-	-	-0.832	-0.781	-0.817
PAM-TUM	-	-	-	-	-0.830	-
SYF-GCM	-	-	-0.833	-	-	-
SYF-TIF	-	-	-	-0.844	-0.852	-0.834
TIF-TUM	-	-	-	-	-0.179	-

Table 3.31.--Monthly mean distances (in 100 m) between maras. Means are the average of the distances between the location of every fix of one animal and the location of every fix of the other animal being compared.

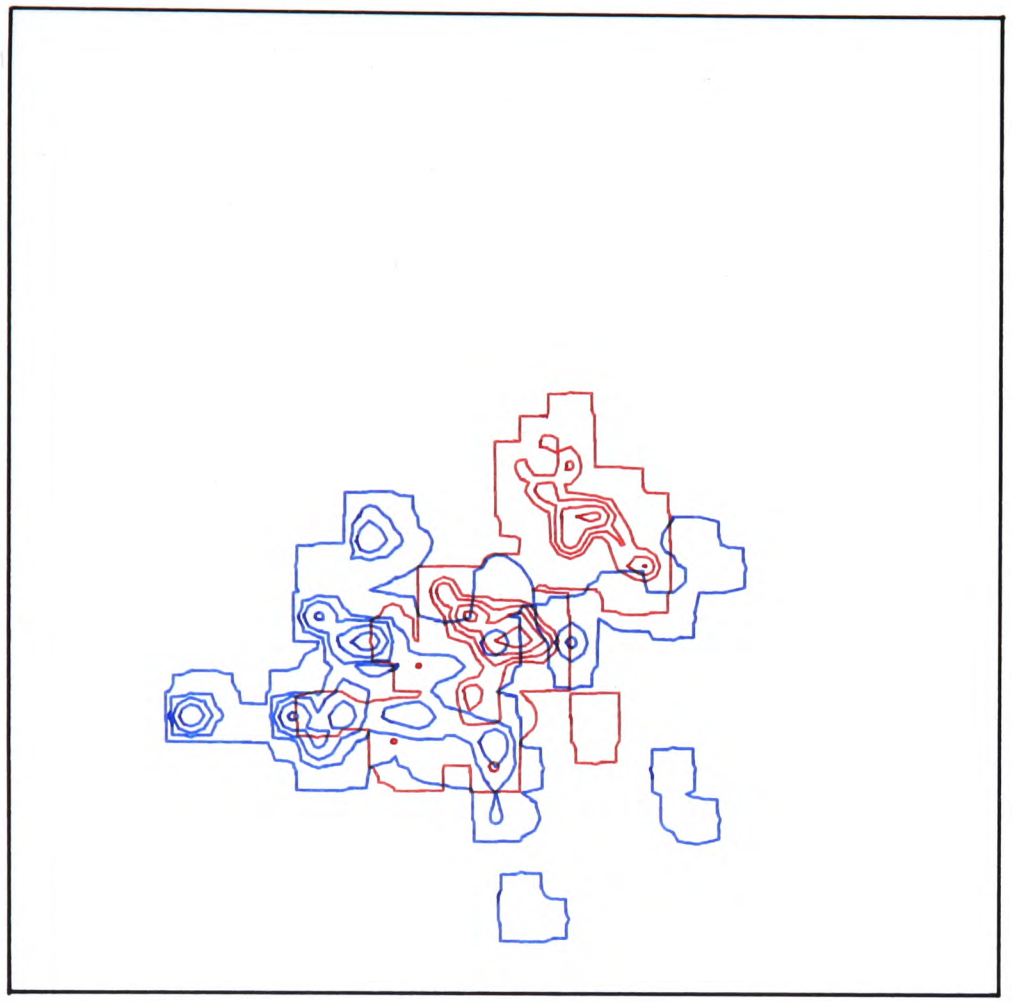
	-Comparisons Made-						
Month	ELF PAM	ELF SYF	ELF TIF	PAM SYF	PAM TIF	TIF SYF	Mean
Aug	7.67	-	-	11.20	18.28	14.92	13.02
Sept	5.34	-	-	11.17	18.26	16.22	12.75
Oct	7.45	13.02	11.34	12.56	13.32	16.24	12.32
Nov	11.11	18.94	12.01	11.50	13.83	18.19	14.26
Dec	9.40	14.95	18.18	8.33	19.54	22.32	15.45
Jan	16.13	19.57	6.64	12.56	19.74	19.77	15.74
Mean	9.52	16.62	12.04	11.22	17.16	17.94	

Figure 3.26 (3 pages).

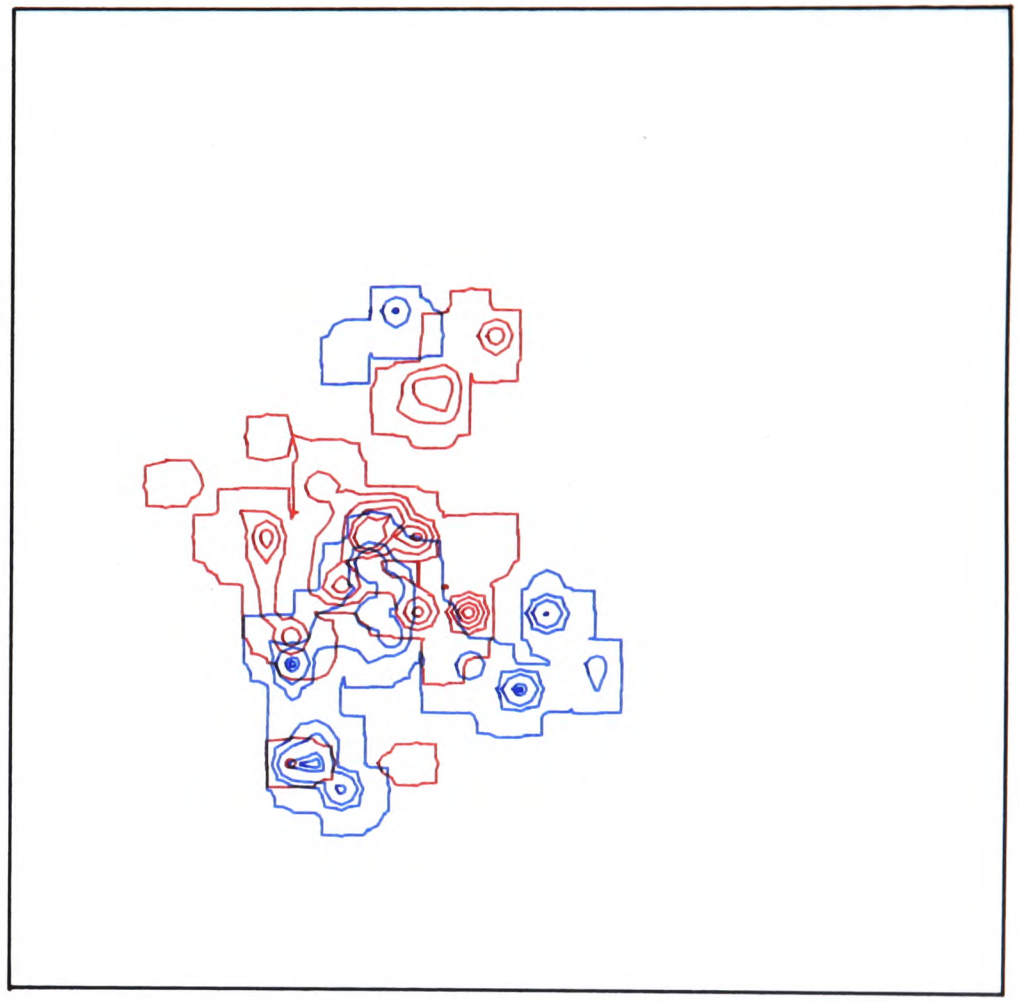
Contour plots showing the seasonal ranges for two maras overlayed on each other to illustrate the spatial relationship between the animals (pairs) being compared. The contour lines show the intensity of use (see text) of different parts of each animal's range. The contours are obtained by joining cells of equal intensity of use, with some 'smoothing' done by the contouring routine (CONTRA routine of the GHOST80 library). The contour intervals are spaced to encompass 0.90, 0.80, 0.60, 0.40, and 0.20 of the fixes in each animals range in increasing order of intensity of usage of each cell.

Colour codes for animals are:

Red	PAM
Blue	ELF
Green	GCM
Red	ENF
Blue	TIF
Red	TUM



ENF/ELF FALL 83



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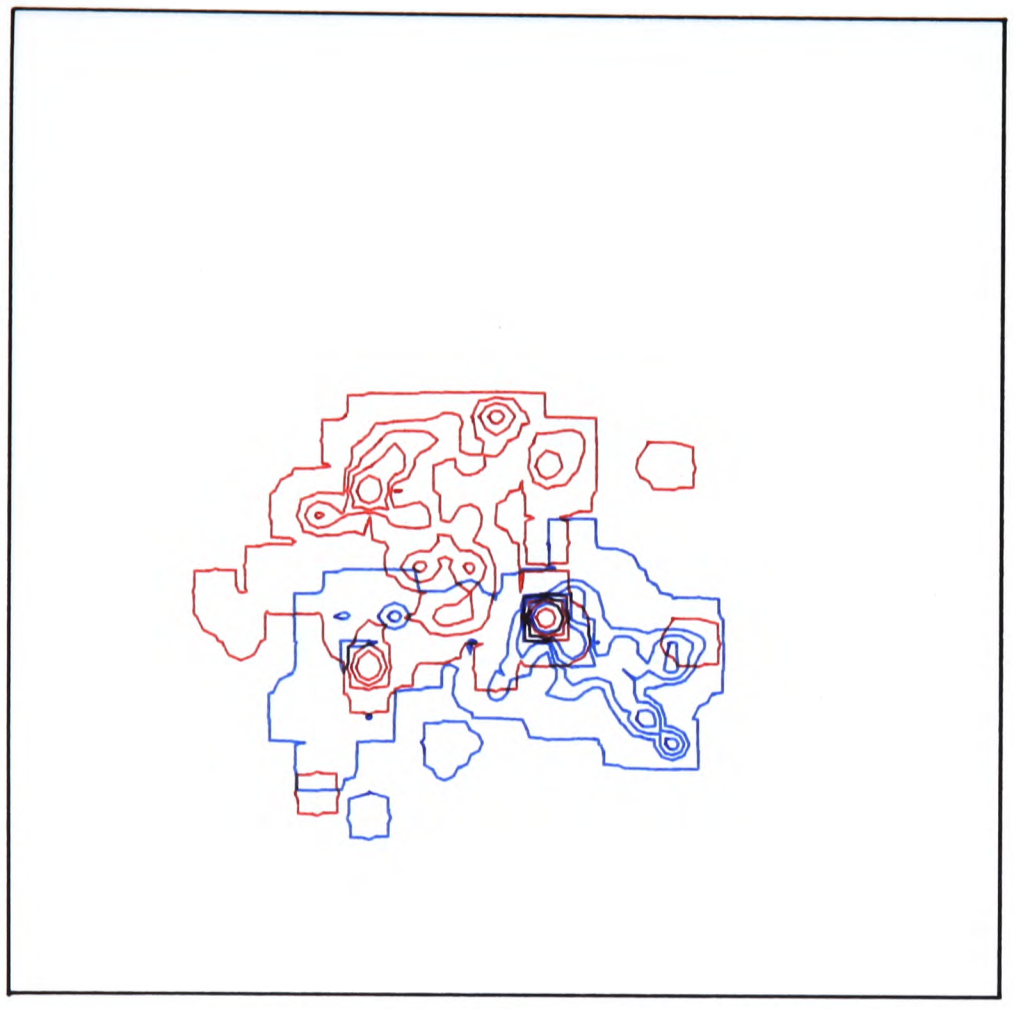

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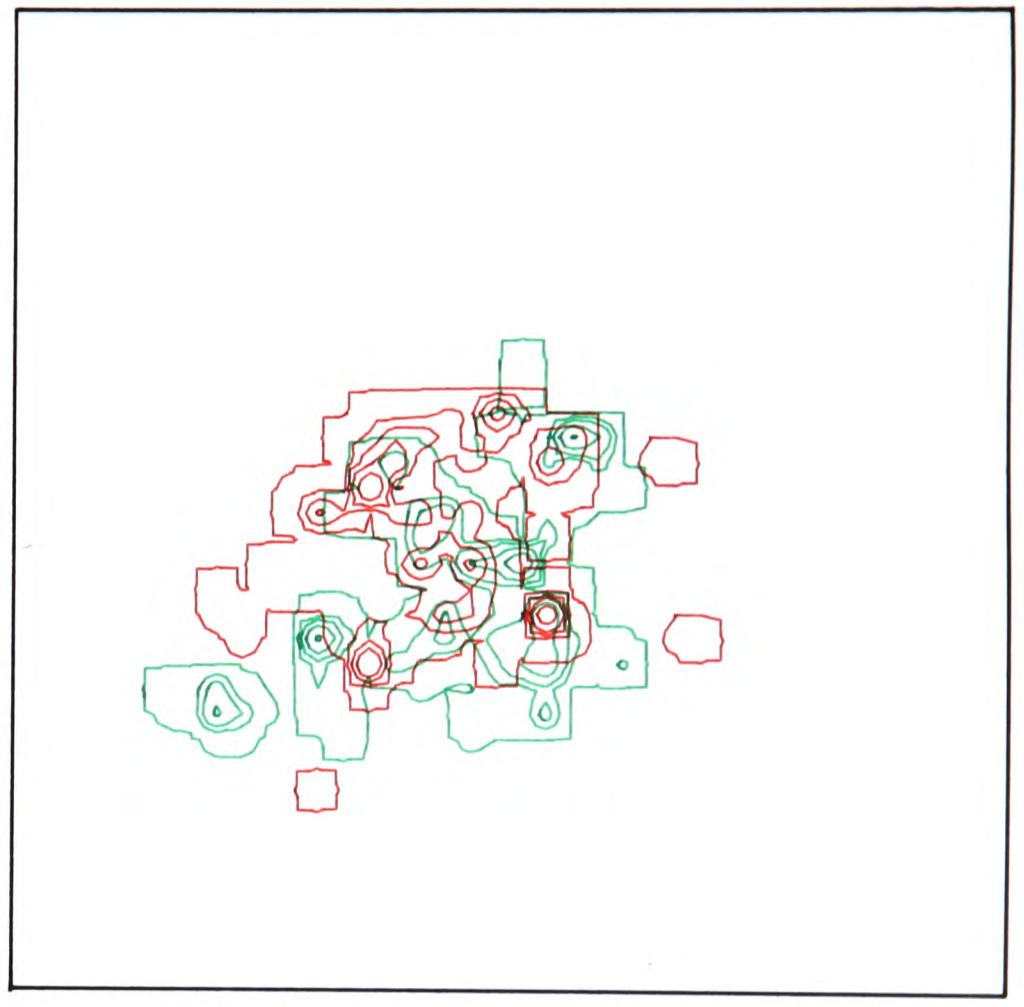

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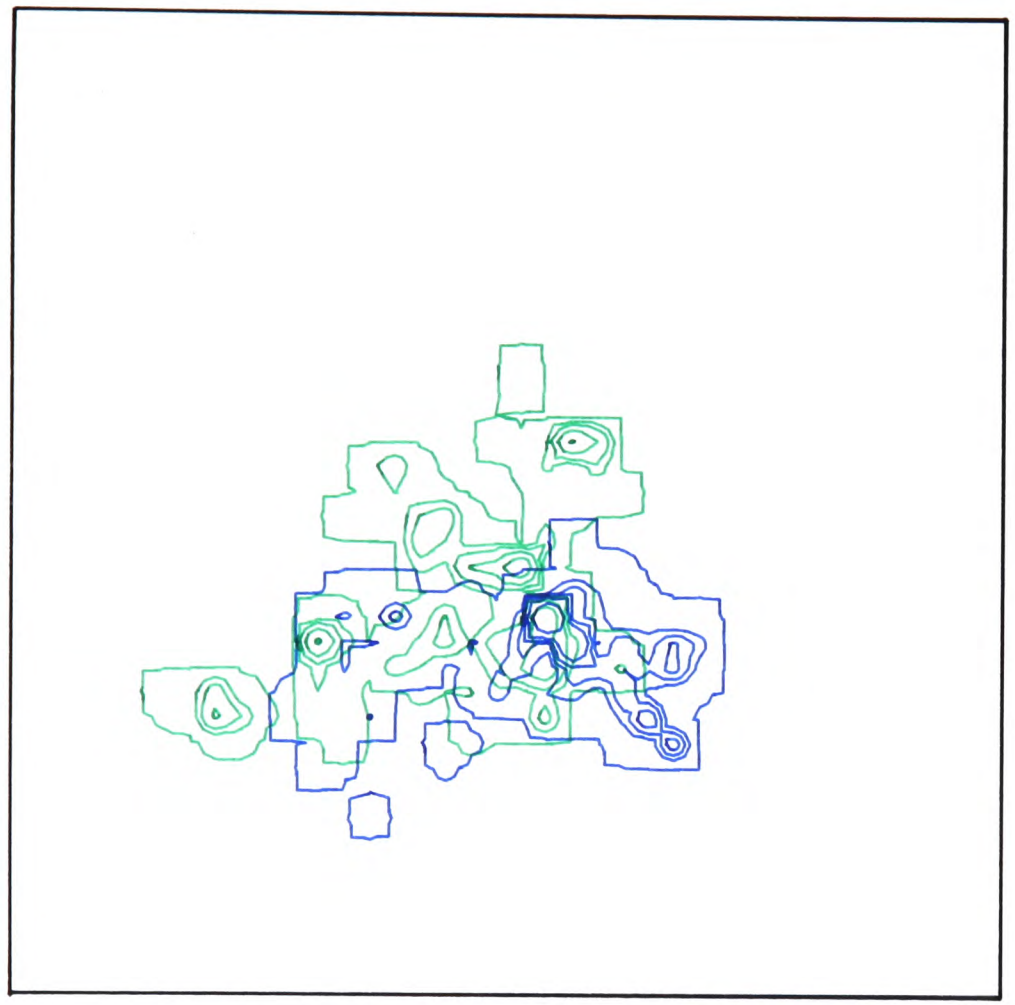

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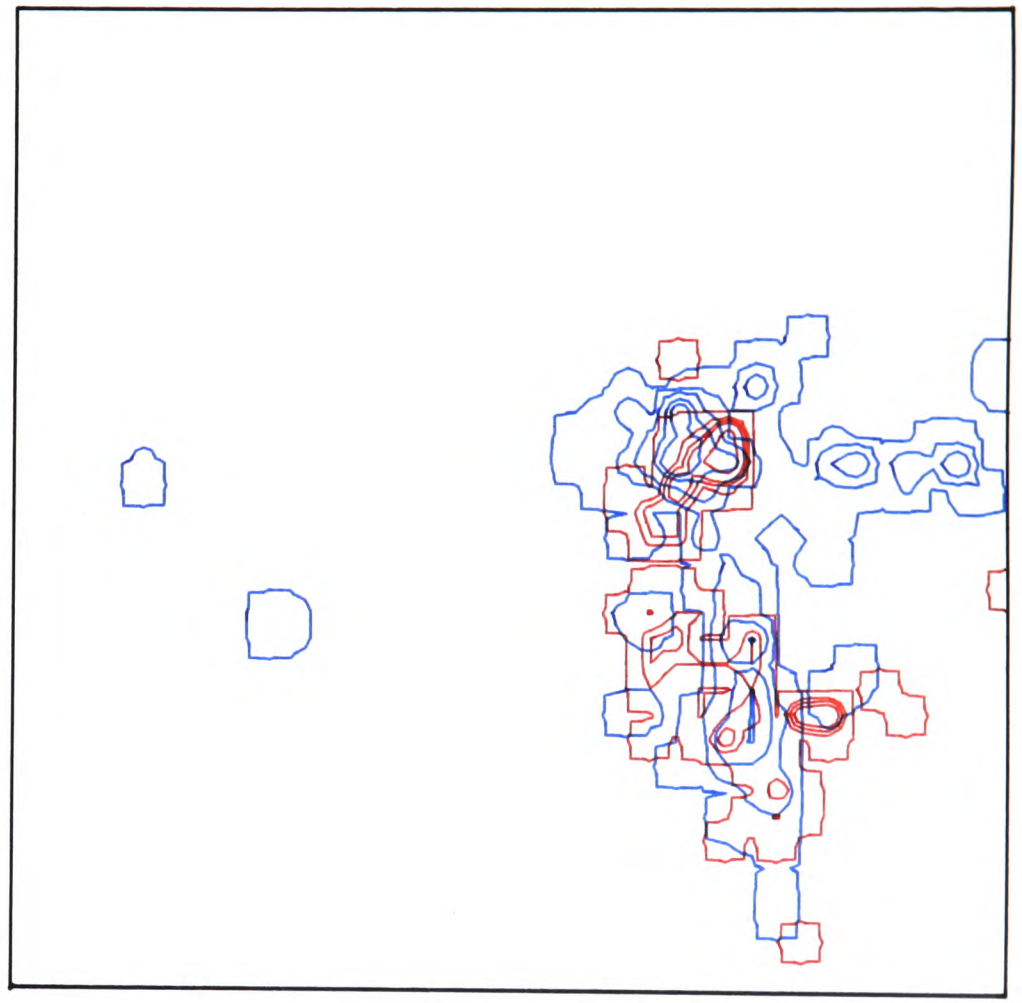


TIF/TUM SPRING 84

3.6.3 Mara Spatial Organization

Above, I have shown that mara home ranges are not static in location--mara pairs are continually moving into new areas. The animals are constrained in how far they can move since they tend to return to the same breeding sites each year (radio-collared maras were never found farther than 2 km from the La Blanca Lagoon). These breeding dens may be used by 20 or more pairs of maras (see Chapter 5). As a result, the areas near dens are heavily occupied by maras; while the surrounding scrub between denning areas appears to be relatively sparsely inhabited. All the radio-collared maras' seasonal ranges overlapped at least one grid cell with at least one other of the tracked mara pairs. Some animals' seasonal ranges overlapped up to 29% with another pair. However, the range correlations suggest strongly that, despite an appearance of considerable range overlap, mara pairs are avoiding each other. Overlapping ranges are tessalated, rather than overlayed, on top of each other.

Mara ranges are not used exclusively by one animal or a group of animals, thus their spacing patterns clearly do not fulfill the requirements of Wilson's (1975) definition of territoriality as described in Section 3.3 above. Davies (1978), however, defined a territory as whenever animals are spaced out more than expected from a random occupation of suitable habitat. Despite an apparent abundance of suitable habitat farther afield, the radio-tracked pairs' ranges were all within 2 km of the La Blanca den sites--the animals appear to be highly clumped. However, if one assumes, *post hoc*, that mara movements are constrained by a need to be near a communal denning site, and thus that the scrub farther off cannot be considered suitable habitat then different conclusions could be drawn. The tessalated nature of mara spacing patterns, the infrequency with which pairs are seen together, and the fact

that males may engage in fights when pairs meet, clearly suggest that maras are avoiding each other (see Chapter 4).

Doncaster (1985) has shown that, though the home ranges of red foxes in an urban and semi-urban environment may overlap considerably over time, they in fact are highly territorial with the ranges of different family groups continually floating around in unison. Frame (1984) has shown that a similar pattern may exist in cheetah females: their ranges may overlap completely, but they are never in the same place at the same time (as previously suggested by Eaton, 1974). Leyhausen (1965) has found that a similar pattern may exits in cats (see also Bick and Bick, 1965, for evidence of floating ranges in male damselflies). Future studies of mara ranging behaviour may very well show that the range in use on any given day (the prevailing range) is an exclusive use zone, and thus a sort of moving territory. Without more data, however, this is purely speculation.

3.7 Summary

The goal of this chapter has been to lay the ecological and behavioural framework upon which the complex analyses in the following chapters can be built. I have touched upon a wide range of disparate topics--on some of which I have little data. This was necessary so that the results in the following chapters could be seen within as thorough an ecological framework as possible. With results on so many topics presented I will not attempt to tie the chapter together in a conclusion--instead the most important results will be summarized.

1. Within the La Blanca study area, maras' home ranges were not stable in size or location. The animals were continually moving into new areas. Mara movements were

constrained by the need to return to breeding den sites each year (see Chapter 5), so all the ranges mapped were located within 2 km of the main La Blanca den sites. During the course of a year, radio-collared maras covered an area of something like 200 ha; however, the actual size of the range in use at any time was about 35 ha.

2. When looking at the configuration of ranges over periods of several months, the boundaries of the area covered are highly convoluted with lots of satellite cells. Within these ranges there are several areas of intensive use. These patterns are symptomatic of the dynamic nature of mara ranging behaviour. To look at the movement of maras over time, ranges were analyzed in seasonal blocks. Seasonal ranges for the nine radio collared maras had a mean size of 97.87 ha (± 13.59). No significant differences between range sizes in different seasons were found. There is considerable spatial overlap between maras' seasonal ranges, all of which seemed to maintain a central core area used throughout the period the animals were tracked. There was no consistent pattern in the changes in direction, orientation or location of ranges.
3. Daily range size, the number of hectares visited during daylight hours, varied from 2.25 to 23.25 ha with a mean of 10.25 ha (± 5.64). The animals may cover up to 60.25 ha in a 24 hr period. Although the mean distance travelled by maras during daylight hours was 1953 m (± 1697), the maximum distance travelled within a 24 hour period was 6326 m. The radio-collared maras stayed less than 50 minutes within 80% of the cells visited. I was unable to discern a pattern in their daily movements.
4. Maras are active throughout the day, with a tendency to be more active towards dawn and dusk. Analysis of the proportion of scans of maras engaging in different behaviours in different hours of the day revealed that,

in general, the animals spend more time resting at midday and more time feeding in the late afternoon.

5. Animals were feeding in a greater proportion of scans in the fall and summer than during the rest of the year. More time was spent resting in the summer months and less time in the spring than in the other seasons. Maras moved proportionally less in the summer. Overall they spent 46% of their time feeding, 18% sitting, 24% resting, 8% moving, and 4% engaging in other behaviours.
6. In roughly 76% of the fixes, the radio-collared maras were in scrub habitat. However, the animals spent significantly more time in the open than expected if they had been using the available area at random. This result is supported both, by analysis of habitat usage patterns, and vegetation cover value usage patterns. Usage of lagoons varies substantially in the different seasons: they were not used at all during the wet winter months; however, during the spring and summer the radio-collared maras were found on the lagoons in 15% of the fixes. Spring and summer are the driest seasons on the Peninsula Valdés, and it may be that more water is concentrated in the forage plants growing on the lagoons than in the surrounding scrub. The water content of plants must be important for maras since they almost never drink.
7. On the Peninsula Valdés maras are primarily grazing animals. They were only recorded browsing on shrubs in 8 scans compared to 4702 scans of maras grazing. They are probably selective feeders since they have tiny mouths which appear to be designed for choosing only the most nutritious food items. Analysis of mara faecal material revealed a dicot to monocot cuticle ratio of 13:1, suggesting that grasses play a more important role in their diet than herbs.
8. The amount of overlap between the seasonal ranges of the

different radio-tracked maras varied from none to a maximum of 33 ha. The maximum proportion of two ranges overlapping was 0.33. However, even in those cases where two maras (pairs of maras) ranges overlapped a lot (33 ha) the two ranges compared were highly negatively correlated. This shows that the utilization distributions of two pairs of maras whose ranges overlapped were actually very different--they were not using the same cells with the same intensity, and may have been actively avoiding each other.

9. The radio-collared maras must have interacted spatially with large numbers of other unmarked maras; so the full complexity of the maras' spatial organization at the La Blanca study area remains hidden. Furthermore, analysis of the spatial overlap between different radio-tracked maras was limited by not having enough data to look at overlap on a fine enough (daily) time scale. The evidence suggests that mara pairs living in the same area actively avoid each other. Too little evidence is available; but it may be that maras are territorial in the same sense that Doncaster (1985) has shown in red foxes: ranges overlap considerably when looked at over long periods of time, but the area in use at any moment by a given animal (or family) is an exclusive use zone into which other foxes seldom venture.

Chapter 4

THE ECOLOGY OF THE PAIR BOND

4.1 Introduction

The mara is one of the few species of mammals to have a monogamous breeding system. Monogamy is rare in mammals with some authors reporting that only 3% of the species studied have this social system (Kleiman, 1977). Circumstantial evidence long suggested that the pair-bond in maras is strong: the sheep herders of Patagonia hold the male mara up as an example of familial loyalty, and say that if one kills a female mara, one must also kill the male as it will never mate again. As in many legends there is some truth in this as the results presented below will show. The goals of this chapter are to describe how the pair-bond functions in maras, and to answer the question of why this species has adopted this social system.

The chapter will be divided into the following seven sections: (4.2) a review of the ecology of monogamy with reference to mammals, (4.3) a survey of the literature on maras, (4.4) a summary of analysis methods used, (4.5) a review of the evidence that maras are monogamous based on my field data and the literature, (4.6) an examination of the mara's pair-bond from both a behavioural and ecological perspective, (4.7) tests of the various hypotheses as to why maras have adopted this social system, and (4.8) a summary of the most important findings in this chapter.

4.2 Monogamy in Mammals

The Concise Oxford Dictionary (Oxford University Press, Oxford, 1976) defines monogamy as "the habit of having only one mate at a time". Monogamy has been used by mammalogists more broadly to refer to a social system where a mated pair remain together, normally reproducing sexually only with each other, through several breeding seasons. The pair often share the same home range, and remain apart from conspecifics. Occasional covert matings outside the pair do not negate the existence of monogamy. Monogamy does not necessarily imply a life-time relationship since, if one member of the pair dies the remaining mate may develop a bond with another individual of the opposite sex (Kleiman 1977; Wickler and Seibt, 1981; Wittenberger and Tilson, 1980).

Polygynous mammalian mating systems are comparatively well understood (see for example studies by Clutton-Brock et al, 1982, on red deer; and Le Boeuf, 1972 and 1974 on elephant seals). The theory of the evolution of monogamy in mammals, however, lags behind (Wittenberger and Tilson, 1980), and as the discussion below will show, a unified theory to explain monogamy in mammals does not exist. The trend among authors is to view mammalian monogamy as having arisen for a variety of reasons in different taxa (Kleiman, *Op. cit.* and 1981; Dunbar, 1984; Wittenberger and Tilson, *Op. cit.*).

Monogamy has been described as a rare mating system in mammals: Kleiman (*Op. cit.*) reports 3%, and Crook (1977) reports that 12.5% of the mammal species studied have this breeding system. However, Zeveloff and Boyce (1980) report that 52% of the mammal species in their sample (N=155), which they admitted to be biased, were monogamous. This suggests that these previous estimates of the proportion of

mammal species which are monogamous may be low. Trivers (1972), in his seminal paper on parental investment and sexual selection, raised the point that the kind and quantity of 'parental investment' in offspring by males versus females are very different in mammals. Parental investment is defined as any investment by parents in an individual offspring that increase the offspring's chances of surviving at the cost of the parent's ability to invest in other offspring (Trivers, *Op. cit.*). This point is pivotal in understanding why there appears to be a bias towards polygyny in mammals. The ways this difference affects the two sexes are outlined below:

- Because of the internal development of the young, female placental mammals have invested heavily in each offspring at birth. Also, eggs cannot be produced *ad libitum*, and gestation periods are long (up to 12 months or more); so, compared to males, females of many species are constrained to breeding at a slow rate. Due to these two factors, female mammals can be expected to continue to invest in their offspring post-partum to ensure that the energy they have invested does not go to waste through offspring mortality. Further, with their mammary glands (one of the distinguishing characteristics of mammals) females are able to supply all or most of the nutritional needs of the developing young post-partum. This males cannot do.

- The initial investment by males in their offspring consists of a small quantity of easily produced sperm. This, and the low likelihood of females abandoning young as shown above, means that males (other things being equal) may produce more offspring by mating with as many females as possible.

Kleiman (*Op. cit.*) describes the simplest mammalian social system as one of short stages of adult male and female

interactions that result in conception, short periods of maternal care of the young, probably exclusive but overlapping home-ranges, and polygyny. This system may have been the primal mammalian social system (Wilson, 1975), and it probably arises in mammals because of this differential parental investment in offspring prior to birth by male versus female parents.

This is very different from the situation in birds where the differences in parental investment between the sexes at hatching are smaller relative to the mammals. With a similar level of investment, females are almost as likely as males to abandon the young to their mates' care. The incentive for males to attempt to mate promiscuously may be small since they stand a high probability of losing their entire investment through offspring mortality if they desert the young. Males, thus, may best enhance their inclusive fitness (Hamilton, 1964) by staying with the female to help rear the young. The result is that roughly 90% of bird species are monogamous (Lack, 1968).

Why then does monogamy ever occur in mammals? Several hypotheses have been proposed--and most authors agree that no single one is adequate to explain monogamy in all cases. Below, I will first look at the preconditions which may be necessary for monogamy to arise, and then examine a range of hypotheses as to why monogamy has developed in different situations.

4.2.1 Preconditions for and Nature of Monogamy

These conditions do not necessarily always result in monogamy but they may be necessary for other factors to take effect.

Kleiman (*Op. cit.*) has suggested that monogamy may evolve when group living is favoured (see Chapter 5 for a detailed discussion of group living). Group living may be favoured for the following reasons: (i) a lower

susceptibility to predation through either group defense (see Kruuk, 1964) or cooperative vigilance (see Kenward, 1978), (ii) improved acquisition of food (see Kruuk, *Op. cit.*), and (iii) localization and limitation of some resource (see Cowan and Garson, 1985). However, the advantages to living in groups on their own would not necessarily lead to monogamy since groups could just as easily consist of, for example, two females as one male and one female.

Females must obtain benefits from monogamous pair-bonding that are not otherwise obtainable (Wittenberger and Tilson, *Op. cit.*). These might include: protection from predators or harassing males, avoidance of competition, or direct paternal investment in young which is not shareable with other females. Another precondition for monogamy, in some circumstances, is that females must be able to ascertain the true mated status of potential mates, and mates must not desert.

Kleiman (1977, 1981) differentiates two kinds of monogamy in mammals: 'facultative' and 'obligate' monogamy. She also states that the selective pressures leading to monogamy in both cases may be different. The two kinds of monogamy are characterized as follows:

Facultative Monogamy, which is typified by the following: a weak pair bond, polygyny occasionally occurs, mated pairs interact rarely and occasionally antagonistically, parental investment is indirect (often defense of territory only), development of the young is rapid, mature juveniles leave the parental territory and reach reproductive age early, males are more intra-sexually aggressive and territorial than females, and parent offspring conflict is responsible for juvenile dispersal.

Obligate Monogamy, which is typified by the following: sex role differences are slight and in some cases reversed (females may be more aggressive than males and more territorial), males exhibit paternal care

as do juveniles and siblings, young are dependent on their parents longer (sometimes even while sexually mature), the pair bond is strong, animals synchronize activities, allogrooming often occurs, sexual infidelity is prevented by intrasexual aggression and by the reproductive inhibition of siblings and offspring by the breeding pair, and the dispersal of young is forced by intrasexual aggression.

4.2.2 Hypotheses to Explain Monogamy

The following hypotheses have been proposed to explain why monogamy occurs in a variety of mammal species (see Kleiman, 1977 and 1981; Dunbar, 1984; Zeveloff and Boyce, 1980; and Wittenberger and Tilson, 1980):

1. The young need direct or indirect, nonshareable and indispensable, paternal care to survive (from Kleiman, 1977, and Trivers, 1972). Paternal care can take two forms: (i) direct care where males either carry the young (e.g. in *Callicebus moloch* a monogamous primate, Mendoza and Mason, 1986), bring food to the young (e.g. wolves, Mech, 1970), or both; and indirect care, either by males defending a territory guaranteeing the female and young access to the resources they need (e.g. elephant shrews, Rathbun, 1979), or guarding the young and females from predators (e.g. klipspringer, Dunbar, 1984). This is supported by Zeveloff and Boyce's findings (1980) that there is a strong correlation between monogamy and both altriciality and litter size, so that opportunities for males to invest in paternal care are greater. Also, high confidence of paternity (one of the preconditions for monogamy, see above) could be associated with short gestation periods typical of species producing altricial young.

2. The distribution of food or other resources may lead to monogamy under the following two circumstances: (i) In territorial species where the carrying capacity is not great enough to permit another female simultaneously raising a litter in the same range, and where males cannot monopolize sufficient resources to attract several females (from Kleiman, 1977; e.g. gibbons, Tenaza, 1975). (ii) In conditions of low population density, usually as a function of food resources being in rich but widely dispersed patches, where only a single female may be available to a male it may be uneconomic for the male to try to defend a territory large enough to encompass the ranges of several females (from Kleiman, 1977; e.g. dikdiks, Hendrichs and Hendrichs, 1971).

3. Monogamy should evolve in territorial sp : if pairing with an available unmated male is alwa better than pairing with an already mated male: i.e. there are no advantages to mating with a superior male, or a male holding a superior territory (from Wittenberger and Tilson, *Op. cit.*). Parental assistance by males may be important but not indispensable to females (e.g. reedbuck; Jungius, 1971).

4. Monogamy should evolve in non-territorial species when the majority of males can reproduce most successfully by defending exclusive access to a single female (from Wittenberger and Tilson, *Op. cit.*). This typically occurs where sex-ratios are male biased. Under these conditions females may or may not benefit, but the cost of preventing sequestering is too high to resist.

5. Monogamy should evolve even though the polygyny threshold is exceeded if aggression by females prevents males from acquiring additional mates (Wittenberger and

Tilson, *Op. cit.*). This would typically occur where a dominant female prevents breeding by a sexually mature subordinate female, or females prevent other females from entering the pair's territory (e.g. jackals; Moehlman, 1979).

4.2.3 Consequences of Monogamy

Once monogamy had formed various energy saving cooperative behaviours could develop. Amongst birds, mated males are typically larger than females and spend more time in territorial defense, while the smaller females spend more time foraging for the young (Martindale, 1982). A similar dimorphism in size and behaviour occurs in some mammals. However, in monogamous mammal species there is usually a minimum of sexual selection, and sexual dimorphism is typically reduced (Kleiman, 1977; Ralls, 1977). Kleiman (*Op. cit.*) described how none of the monogamous forms copulates outside the physiological oestrous period (in contrast with polygynous species) except the primates. The time spent in sexual and courtship behaviour could be reduced once a bond has been established. This would save energy for such behaviours as foraging and care of the young. In some species the period of actual sexual receptivity has been shortened to only a few hours a year. In addition to saving energy, this may also help the female ensure her mate's fidelity since he must stay near her to be certain of being present when she is receptive (M. Ridley, Pers. comm.; Dept. Zoology, Oxford).

One cooperative behaviour typical of monogamous species is territorial defense (Kleiman, 1977). Males often engage in territorial defense to prevent other males from approaching and mating with 'their' females. In polygynous species females are typically non-aggressive towards conspecifics. In contrast, in monogamous species females

often exhibit high levels of both inter- and intra-sexual aggression and dominance, thus defending resources for the mated pair and offspring (KLeiman, 1977). But, in these species pair-bonded animals still tend to be most aggressive towards same sex conspecifics. The importance of optimal behaviour (Krebs, 1978) thus has a further complexity in monogamous species since the optimal behaviour for a pair-bonded individual will then depend on what its mate is doing (Martindale, 1982).

Many factors influence the social organization of a species. Such parameters as differences in the dispersion of food or other resources, availability or selectivity of mates, predator pressures, and energy budgets may all affect what behaviours are most adaptive under certain environmental conditions. Since mating systems are strictly a behavioural attribute they may posses greater phenotypic plasticity than physiological or morphological adaptations. For these reasons the mating system of a species might be expected to stray from what is considered its norm in different habitat types. Thus, some species considered to be basically monogamous might under some circumstances exhibit polygyny or vice versa (Kleiman, 1977; Emlen and Oring, 1977; Zeveloff and Boyce, 1980). But, Clutton-Brock and Harvey (1977) report that in primates monogamous breeding seems to be an extremely stable characteristic, and that the switch from monogamy to polygyny is not easily achieved.

4.3 Captive Studies on Maras

In the most detailed captive study made to date, in a colony of about 70 maras in France, maras were found to have a monogamous pair-bond which lasted for at least the 2 years of the study (Dubost and Genest, 1974; Genest and

Dubost, 1974). Genest and Dubost (*Op. cit.*) further described the following characteristics of the mara's pair-bond:

1. The bond between mates is very strong, and if one of the partners dies there may be a considerable time lag before the survivor forms a bond with another animal. In one instance a male was still alone and exhibiting searching behaviour six weeks after its mate had died, despite the fact that there were several single females available.

2. The pair-bonded male and female usually remain within a few meters of each other. The female fills the role of leader and initiates activities (e.g. resting, walking, grazing, and movements towards the den). Females, however, are only 'passive' (*sic*) leaders since they do not make much effort (e.g. waiting for the male while moving) to maintain contact with their partners. Males, on the other hand, follow the female assiduously. Further, if a male becomes separated from his mate he searches for her and produces a high pitched whistle (presumably an attraction call). Two characteristics may assist the male in staying close to his partner: (i) The mara's highly visible white rump patch may serve as a flag to show that the female is active since it is only visible when a mara is standing or moving about, and is hidden when the mara is sitting (they usually graze in a sitting position) or lying. The other possible aid is (ii) a low 'grumble' vocalization which the two partners emit alternately while grazing and moving. These calls do not appear to carry more than a few meters, hence reducing the risk of detection by a predator, and thus appear to be adapted to maintaining close contact between mates.

3. Males defend a moving territory around their females. The male of a pair will not tolerate the approach of

another adult male (who may temporarily leave his mate) to within 10 m of his female. If such an approach occurs, he displays by circling in a tight figure of eight in front of the female, and marks the ground with his anal glands and faeces. If the intruder does not withdraw, the male of the pair advances and a violent attack and chase may ensue. Females on their own will tolerate a greater degree of proximity by another pair. It occasionally happens that the male of one pair is dominant and chases the other away. The victor will briefly stay by the other male's female and may sniff her genitals; but then returns to his own mate so that the losing pair is soon reunited. Females having a post-partum oestrus may be pursued aggressively by other males, and intense fights can develop between the oestrous female's male and other males. But, these fights usually occur after the female has already mated with her partner (presumably because he is aware of her reproductive state soonest), and males usually return to their own partners within an hour.

4. Strict fidelity of a male towards a female persisted even when there was a surplus of females in the population. Pair-bonded males would mate with spinster females, but would stay with these females only for the time necessary to mate. Lone females in the captive population, however, reproduced at the same rate as pair-bonded females.

5. The male does not take part in the rearing of the young. However, since he is virtually always close to the female, he ensures that other adults do not approach, thus allowing her undisturbed time with their own offspring. The male may also assist a female in difficulty. In one case a female with partially paralyzed hindquarters was able to support herself against the flank of her mate when fleeing. Another

male always placed himself between the blind side of his mate, who had lost an eye, and danger.

However, as Genest and Dubost (*Op. cit.*) have stated, "in the absence of information on the biology of this species under natural conditions, we cannot fully appreciate the role played by pair-living, nor can we judge whether it is a response to specific ecological conditions." In the results presented below I will try to place the mara's social system in perspective with its ecology in the wild.

4.4 Methods

The data sets used in this chapter were obtained from the QUERYMASTER data base, and then subsequently analyzed using the MINITAB and PSTAT statistical packages. Most of the data extraction and analyses methods used in this chapter have been presented in Chapter 2 (Methods and Study Site). Many of the analyses are based on comparing the frequencies of different behaviours between individuals, sexes, and the time of year. The data collection method used was to record the behaviour of every visible mara every 15 minutes (the general scan method--see Chapter 2). This can lead to a problem of data independence since a behaviour may last for longer than 15 minutes with the result that consecutive scans on the same animals may not be statistically independent. This problem was minimized by sampling, where necessary, from the scan data at a 1 hr interval to limit the effect of behavioural auto-correlation.

4.5 Are Wild Maras Monogamous?

The data on captive animals (see Section 4.3 above) shows conclusively that maras are monogamous under those conditions. In this section the evidence that maras are monogamous in the wild will be reviewed using my field observations. The evidence is of two types: (i) the distribution of observations of different group sizes which I observed in the wild, and (ii) case studies of intensively observed identifiable individuals. Each of these will be addressed in turn.

4.5.1 The Distribution of Group Sizes

Whenever maras were observed in the field I attempted to determine how many individuals there were in each group, and how many of these individuals were of each sex. A group was defined in the field as any maras located within 15 m of each other for all or most of the time they were observed. An observation of a group could vary from a brief sighting, lasting only a few seconds, of maras fleeing from a moving car in the scrub; or an extended observation session lasting several hours. These data were examined to look at the overall and seasonal patterns of mara group size and composition.

To prepare the data set for this analysis all observations of unique groups (not counting the same group more than once for a given day) were extracted from the QUERYMASTER data base (see Chapter 2). These data were then run through Program SELGROUP which determined the maximum number of animals seen in a group during the period it was observed. In total I was able to obtain estimates of the number of animals in 907 groups of maras.

However, many of these groups were observed only

fleetingly. To test the reliability of the size and composition estimates for groups viewed briefly, defined as those recorded in only one observation scan, the distribution of membership sizes was compared between groups recorded in one, and more than one scan. The median number of adults in the 439 groups which were recorded in single scans was 1 adult (54% of the total). For groups recorded in more than one scan the median number of adults was 2, with 57% of the groups containing 2 individuals (see Table 4.1). These distributions were found to be significantly different using the Mann-Whitney test ($W = 165668$, $P < 0.000$), with groups seen only once being significantly smaller than groups seen several times. As a result, only groups recorded in 2 or more observations scans during one observation session were used for the analyses done below.

Examining the group composition data (see Table 4.2) shows that of the groups for which I was able to identify the sexes of all the adults, 63% consisted of 1 adult male and 1 adult female, 17% consisted of lone females, 8% consisted of lone males, 6% consisted of 1 male with 2 females, and 6% consisted of groups with other compositions. A X^2 test on the number of groups containing 1, 2, and more than 2 adults in different bi-monthly blocks was made to investigate whether group composition changes during the year (see Table 4.3). The overall X^2 showed that there were no significant differences ($X^2 = 17.59$, df= 10, NS) in group size between bi-monthly blocks.

With these results it is clear that the majority of groups consist of one male and one female, and that this is

Table 4.1.--The distribution of numbers of maras counted when groups were viewed in only one scan and in more than one scan. Only data on adults are included in this table. Groups with 0 adults consisted of varying numbers of juveniles.

Number Adults in Group	Observed Once		Observed >= 2	
	Count	Prop	Count	Prop
0	4	0.01	5	0.01
1	240	0.54	105	0.23
2	166	0.38	266	0.57
3	22	0.05	70	0.15
4	7	0.02	16	0.03
5	0	0	3	0.01
6	2	0.00	1	0.00
Total	441		466	

Table 4.2.--The distribution of the number of adults of each sex in observed groups. Only groups used where the sexes of all adult members were know. A total of 288 males and 337 females were seen in groups where the sexes of all members were known.

Group Composition	Total Count	Prop Total
1 Male Only	27	0.08
1 Female Only	62	0.17
1 Male & 1 Female	223	0.63
1 Male & 2 Females	22	0.06
1 Female & 2 Males	8	0.02
Other	14	0.04
Total	356	1.00

Table 4.3.--The distribution of group sizes in different months of the year. Only groups used where the sexes of all adult members were known. Also, shows results of a X^2 test of whether there were significant differences in group size in different bi-monthly periods during the year.

	Number of Adults					
	1		2		>2	
Months	Obs	Exp	Obs	Exp	Obs	Exp
Jan-Feb	1	1.50	5	3.83	0	0.67
Mar-Apr	9	8.00	20	20.40	3	3.60
May-June	7	6.75	15	17.22	5	3.03
Jul-Aug	5	14.75	48	37.62	6	6.63
Sep-Oct	45	43.25	109	110.31	19	19.44
Nov-Dec	22	14.75	30	37.62	7	6.63
Total	89	89.00	227	227.00	40	40.00

X^2 Test Results

0.17	0.36	0.67
0.13	0.01	0.10
0.01	0.29	1.27
6.44	2.86	0.06
0.07	0.02	0.01
3.56	1.54	0.02

Total X^2 = 17.59, df = 10, Not Significant

the general pattern year round. However, it is noticeable that many of the groups seen did not consist of two individuals. In fact, 25% consisted of a single male or female. Several reasons might explain this: (i) there could be many non-pair bonded animals, (ii) pair-bonded maras might not spend all daylight hours together, or (iii) because of the short span of time most groups were watched there may be weaknesses in the data. How long the bonds between known individual maras lasted will be examined in the next subsection.

4.5.2 Individual Case Studies

A major problem in this study has been the sparsity of individually recognizable animals. A total of 22 maras were recognizable and followed for more than a few days (see Table 4.4, and Chapters 2 and 3). During 22 months of field work I only had three pairs where both partners were recognizable. On none of these pairs do I have more than a few months of data. The data on these three pairs are summarized below:

1. LRF and LRM were seen together at Estancia Larreburu from 17.9.81 to 12.11.81. Both animals were present every time this pair was observed.

2. GIF and TDM were captured at Puesto Centenario and were only seen on two occasions. They were first seen on 27.7.83 and last seen on 5.9.84, a span of 406 days.

3. TIF and LEM were observed together from 17.10.83 to 15.12.83. Both animals were radio-collared and I was able to follow them extensively. After 15.12.83 they were not found together again. LEM died shortly after being last tracked on 22 February 1984. TIF was tracked until 23.11.84, and was with a new mate in

Table 4.4.--The period over which individually identifiable maras were sighted, and the identity of accompanying animals. M = Male, F = Female, J = Juvenile, Ad = Adult of unknown sex.

Mara Name	First Sighted	Animals With	Last Sighted	Animals With	Span of Days
CAM	31.8.83		22.9.84	PJF	388
ELF	21.3.83	Alone	2.5.84	?	408
ENF	5.3.83	2 J,1 M	24.6.83	1 M	111
GCM	18.4.83		18.1.84	4 Ad	306
GIF	27.7.83	TDM	5.9.84	TDM	406
JAF	15.6.83		3.9.84	1 M	446
LEM	7.10.83	TIF	22.2.84	?	138
NAF	12.6.83	2 Ad	16.11.83	?	157
PAM	13.4.83		22.11.84	Alone	589
PJF	2.10.83	2P, 1Ad	22.9.84	CAM	356
PUF	15.10.83	1M, 1F	20.12.83	TIM, 3 J	66
SLF	7.10.83	2 Ad	21.11.84	1 M	411
SYF	5.10.83	Alone	23.11.84	?	415
TEF	17.10.83		1.12.84	1 M, 1 J	45
TIF	7.10.83	LEM	23.11.84	?	413
TIM	15.11.83		12.9.84	Alone	302
TUM	28.9.84		23.11.84	?	56
WAM	2.8.83		16.11.84	?	106
WOF	7.10.83		8.4.84	?	184
LRF	17.9.81	LRM	11.11.81	LRM	55

September 1984. It is probable that they split up because LEM was rapidly losing condition from an injury sustained when captured (also see Chapter 3).

For the nine most extensively observed animals, Table 4.5 shows the group composition for every half monthly block in which I was able to estimate group size. From this table it is clear that in the bulk of the bi-monthly periods (63%, or 82% for periods where the best estimates of group size were made) animals were sighted in pairs, but that pair-bonded animals sometimes seemed to be on their own. Also, some of the marked animals occasionally appeared in trios. These were of short duration for eight of the nine intensively observed animals. However, it seem likely that mara JAF was a member of a trio as she was seen with two other adult maras (1 male and 1 female) during 4 out of the 7 two week periods during which I was able to obtain a group size estimate for her.

Can we then clearly say that maras are monogamous? The data on captive animals seem conclusive, but those gathered in the wild are not so clear. This is a common problem in field studies; because of the difficulty of obtaining lifetime data on animals in the wild, the evidence that a species has a monogamous social system is often incomplete. Given this problem, Kleiman (1977) suggested that the following factors are evidence that a species is monogamous:

1. Pairs stay together both during and outside the period of reproduction.
2. Animals only copulate with their pair bonded mate.
3. No unrelated adults share a bonded pairs home-range.
4. Only one pair breeds at a time in family groups.

The field data strongly suggests that mara pairs stay together year round, both during and outside the period of

Table 4.5.--Changes in sizes of groups for known maras. Months are divided into bi-monthly periods. The best estimate of group size for each of the identified maras were used for each bi-monthly block. * mark entries were the estimates of group size were made based on only one or two sightings of the animal. In 63% (59:93) of the periods animals were sighted in pairs (82%, 59:72, if only the best data are used).

	-MARA NAMES-								
Months	CAM	ELF	GCM	JAF	PAM	PJF	SLF	SYF	TIF
-1983-									
Mar 2		2	2						
Apr 1		2			2				
2					1 *				
May 1									
2		1			2				
Jun 1		1 *			1 *				
2		2		3	1 *				
Jul 1									
2				1					
Aug 1				3	2				
2	3	3		3	2				
Sep 1				2	2				
2		2	2		2				
Oct 1	1 *	2	2		2	2	2	2	1 *
2	1 *	2	2		3	2	3	2	1
Nov1		2	2		2	2	1 *	2	1 *
2		2	2	2	2		2	2	1 *
Dec 1	2	1 *	2		2		2	1 *	1
2	1				2	1 *		2	2
-1984-									
Jan 1								1 *	1 *
2		1	2					2	
Aug 2	2							2	1 *
Sep 1	2			3	1 *			2	2
2	2				2			2	1 *
Oct 1					1 *		2	1 *	2
2								2	2
Nov 1							2	2	2
3							2		

reproduction. The data on the other three points are less clear. Without genetical data it was impossible to say whether maras only mated with one other individual. But, most matings leading to parturitions must occur (see Chapter 5) in June and July, a time when maras are spatially dispersed (see Chapter 3). This would, thus, limit a male's opportunities to encounter and mate with other females (this point is discussed in detail in Section 4.7). With regards to Point 3 above, although mara's home-ranges overlap considerably there is evidence that the radio-collared animals were avoiding each other in time and space (see Chapter 3). Kleiman's last point is not relevant since maras do not live in family groups. The overriding evidence that this species has a monogamous social system is the group size data--maras are seen in groups consisting of one male and one female 63% (or 82%, see above) of the time. However, a few animals may be in trios of one male and 2 females--although it is possible that third animals are a pair's offspring from the previous year. It is not unknown for trios to occasionally occur in other basically monogamous species (for example klipspringer, see Dunbar and Dunbar, 1974).

4.6 The Nature of the Pair Bond

In this section the behavioural relationship between paired males and females will be investigated. Much of this will be a rehash of Dubost and Genest's (1974; also see Genest and Dubost, 1974) work on captive maras. However, it is necessary to cover the same ground since data on wild maras have not been presented before. The topics which will be covered are: (i) spatial maintenance of the pair bond, (ii) behavioural coordination between mates, (iii) behavioural differences between the sexes, and (iv)

interactions between pairs. A number of other aspects of the pair bond will be discussed in detail at the end of the section.

4.6.1 Spatial Maintenance of the Pair Bond

I have already shown that the male-female pair is the commonest group size seen throughout the year (see Tables 4.2 and 4.3 above); and also have shown that at least some maras stay with the same mate for extended periods of time (maximum observed was 406 days, see Subsection 4.5.2). Here, data on the spatial maintenance of the bond will be presented.

While making observation scans on maras I recorded the distance to each mara's presumed mate every 5 minutes. These data were extracted at 1 hr independence intervals and are summarized in Table 4.6. Figure 4.1 shows a plot of the proportion of the observations of maras at varying distances from their mates (only one of the two records per observation pair were used here to avoid duplication). In 85% of the observations maras were within 10 mara lengths (each mara length measures about 77 cm, see Appendix A) of their mates. These data were then divided into bi-monthly blocks to examine if there were any seasonal trends using a X^2 test. But, no significant differences were found (X^2 = 11.89, df = 15, NS). Thus if the distance to mate data can be assumed to be a measure of the strength of the bond between two animals then, not only does the bond last, but it also seems to maintain the same intensity thoughout the year.

4.6.2 Behavioural Coordination Between Mates

Two topics relating to the maintenance of contact between paired animals are discussed below: (i) how the

Table 4.6.--The distribution of the number of times mates were observed at different distances apart. Distances are measured in mara lengths (approximately 77 cm.). Data taken from all 1983 and 1984 data selected at 1 hr intervals to ensure independence.

Distance to Mate in Mara Lengths	Number of Observations	Proportion of Observations
Touching	4	0.008
0 - 2	70	0.15
2 - 5	184	0.38
5 - 10	147	0.31
10 - 20	45	0.09
20 - 40	12	0.02
40 - 100	3	0.006
> 100	14	0.03
Total	479	1.00

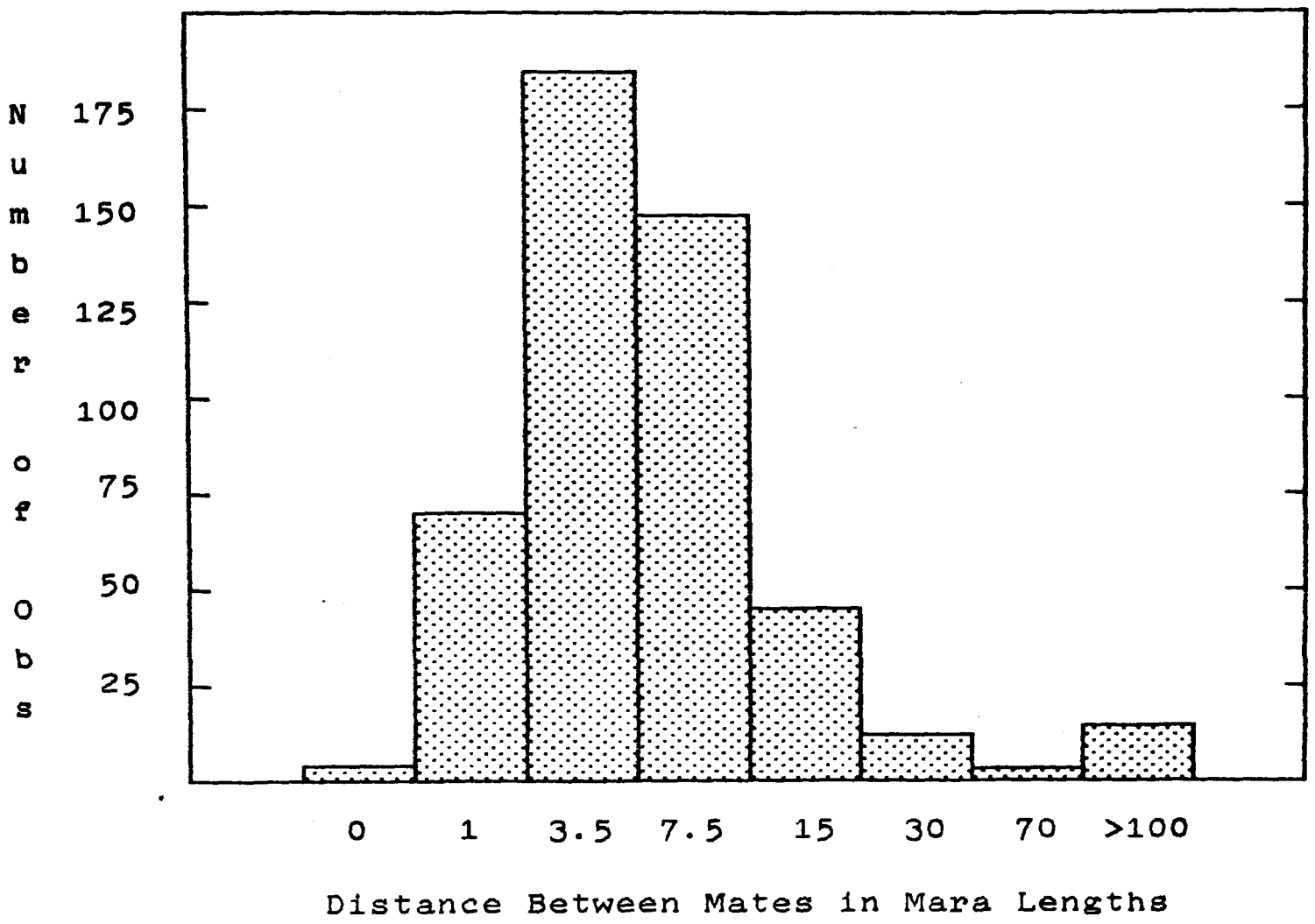


Figure 4.1.--The distribution of the distances between mates during general scans (N = 479). Distances measured in mara lengths (about 77 cm).

actual contact is maintained, and (ii) behavioural coordination between mates which may facilitate them staying together.

Maintenance of Contact

The scrub which the mara inhabits (see for example Figure 2.7 in Chapter 2) is slightly higher than the height of a sitting mara, as a result an animal need move only 5 or 10 m to be out of sight of its mate. Thus, the maintenance of contact between mates may be a problem for the mara. Investigating the way partners maintain contact may give us some insight into the nature of the pair bond. I have already mentioned the low pitched 'grumble' contact call (upon which detailed data were not collected) which may help the animals stay together (see Section 4.3). Genest and Dubost (1974) have shown that travelling pairs walk or trott in single file with the female usually leading the procession. They further suggest that females initiate most activities. Here two topics will be examined in turn below: (i) initiation of movement (reiterating material covered by Genest and Dubost, *Op. cit.*), but redone on my data to check behaviour of wild maras), and (ii) how each sex monitors their mates' movements.

While collecting behavioural scan data in 1981, every time a male or female moved between scans its movements, when a clear pattern existed, were recorded as being either towards or away from its mate. Scans were selected at an independence interval of 1 hr. The following results were obtained:

- Males were recorded moving towards their mates 130 (67%) times and away 64 (33%) times out of 1555 scans.

- Females were recorded moving towards their mates 35 (21%) times and away from their mates 129 (79%) times out of 1657 scans.

A X^2 test was used to compare the number of times males and females moved away and towards their mates between scans. The expected values were derived on the basis that both sexes move towards and away at the same frequency. Males were found to have moved towards their mates significantly more often than females, and females were found to have moved away from their mates significantly more often than males ($X^2 = 79.53$, $df = 4$, $P < 0.005$). These results clearly support Genest and Dubost's (*Op. cit.*) findings that females initiate most movements and that males follow the female.

To investigate the second topic: during the 1983 and 1984 field seasons data were collected to examine how mates might monitor each other's location as a means of maintaining contact. To do this, the orientation of the head (which delineates where an animal is looking, but see below) of each animal in a focal pair was recorded as being either: (i) oriented towards their mate (i.e. the mate was located within the quadrant centered on the direction in which the animal was looking), (ii) oriented parallel to their mate, or (iii) oriented away from their mate. The following results were obtained (summarized in Table 4.7):

- X^2 tests were used to examine whether both sexes oriented independently of their mate's position. The expected values for this test were made on the basis that if the sexes were orienting independently of their mates position they should have their heads oriented towards their mates in 25% of the scans, parallel to their mates in 50% of the scans, and oriented away from the mate in 25% of the scans. In both sexes the X^2 test gave significant results showing that head orientation was not independent of the mates position (males: $X^2 = 14.96$, $df = 2$, $P < 0.005$; females: $X^2 =$

Table 4.7.--X^2 tests of the orientation of mara males and females relative to their mates (see text for calculation of expected values). Data are from 1983 and 1984 only, and records are selected at 1 hour intervals. Two by Two X^2 tests further reveal that the only significant difference is in the orientation towards mate category with males oriented towards their mate significantly more than females ($X^2 = 6.05$, $df = 1$, $P < 0.025$).

Male Orientation with Female Orientation

Orientation	Males Observed	Males Expected	Females Observed	Females Expected	Total
Towards	29	21.99	14	21.01	43
Side	27	28.64	29	27.36	56
Away	34	39.38	43	37.63	77
Total	90	90.00	86	86.00	176

Total $X^2 = 6.27$, $df = 2$, $P < 0.05$

Observed Orientation of Sexes with Random Orientation

Orientation	Males Observed	Males Expected	Females Observed	Females Expected	Total
Towards	29	22.50	14	21.50	43
Side	27	45.00	29	43.00	56
Away	34	22.50	43	21.50	77
Total	90	90.00	86	86.00	176
Total X^2 (2 df)	14.96 $P < 0.005$		28.67 $P < 0.005$		

28.67, df = 2, P < 0.005). Males had their heads oriented towards and away from their mates more than expected; and females had their heads oriented away from their mates more than expected, and parallel to and towards their mates less than expected.

- To look at the differences between male and female orientation a X^2 test was made comparing the head orientation of the sexes. The results showed a significant difference between males and females (X^2 = 6.27, df = 2, P < 0.05). However, looking at each orientation category singly the only significant difference found was that males had their heads pointed towards their partner more than females (X^2 = 6.05, df = 1, P < 0.025).

For the females these results are similar to those on movement patterns, suggesting either that: (i) females both move and orient themselves away from their mates; or (ii) males choose to move behind the female and hence always stay to her rear. In practice, these two possibilities make little difference since they both suggest a pattern of females' controlling the movements of the pair. Interpreting orientation results for the male is more complicated, partly because I have no data on the mara's field of view. Small antelopes have a 270° field of view (Dunbar and Dunbar, 1980) and maras having a generally similar morphology, might be much the same. Thus, maras would not need to face their mate to keep them in sight. In fact, when maras are observing a source of potential danger (usually myself) they almost always look with their head oriented parallel to, and hence with only one eye towards, the potential danger. Because of this I suggest that if males were primarily concerned with monitoring the movements of their partner they would have their head oriented parallel to their mates most of the time. This, as the results above show, is not the case since they spend more

time than expected looking towards or away from their mate. This pattern might, however, be the optimal one for predator scanning which, as will be discussed in Section 4.7, has relevance for understanding why maras are monogamous.

Behavioural Coordination

While watching maras I was impressed by the degree of behavioural synchrony between partners: males and females usually seemed to be doing the same thing at the same time. This kind of behavioural synchrony, if it existed, could help keep the members of a pair in close proximity since it would prevent one animal being left behind resting when the other becomes active. Similar patterns have been reported for monogamous ungulates by Dunbar and Dunbar (*Op. cit.*), and Leuthold (1977).

To test for behavioural synchrony, scan data were extracted using a 1 hr independence interval from the QUERYMASTER data base. The behaviour codes were sorted into 6 general categories (see Chapter 3 for behavioural categorization); and the number of times each sex was observed behaving in each category was sorted against its mate's behaviour at the same time. Table 4.8 summarizes these observations, and also shows time budgets for the sexes (also see Figure 4.2). Looking at this table it is clear that the bulk (57%) of the observations fall along the middle line where both sexes were simultaneously engaging in the same general behaviour.

A X^2 test was used to check whether members of pairs were behaving independently of each other (see Table 4.9). For this purpose the males 'Other' behaviour category and 'Interacting with Pup' behaviour category had to be combined to ensure obtaining high enough expected values for the test. The X^2 test showed that the observed values were

Table 4.8.--Frequencies with which males and females were observed engaging in various combinations of activity during general scans. Samples selected at one hour intervals for the same mara pairs to insure independence of scans. Decimal values in the right-most column, and along the bottom of the table, show the proportion of observations of each sex engaging in each behaviour category. 57% of the observations occur on the centre line where both sexes were engaging in the same behaviours at the same time.

Female's Behaviour	Male's Behaviour: Feed	Sit	Lie	Move	Int W/P	Other	Total
Feed	118	38	12	14	0	6	188 0.392
Sit	13	56	4	8	0	3	84 0.175
Lie	8	7	38	1	0	2	56 0.117
Move	6	12	1	50	0	7	76 0.159
Inter w/P	4	41	7	2	4	2	60 0.125
Other	1	5	1	2	0	6	15 0.031
Total	150 0.313	159 0.332	63 0.132	77 0.161	4 0.008	26 0.054	479 1.000

Figure 4.2.--Graphical illustration of the coordination of behaviour between male and female mates. The size of the symbol represents the percentage of general scans observations of mates engaging in that combination of behaviours (N = 479).

Nothing	0 - 1 % of Observations
●	1.1 - 5 % of Observations
●	5.1 - 10 % of Observations
●	10.1 - 15 % of Observations
●	15.1 - 30 % of Observations

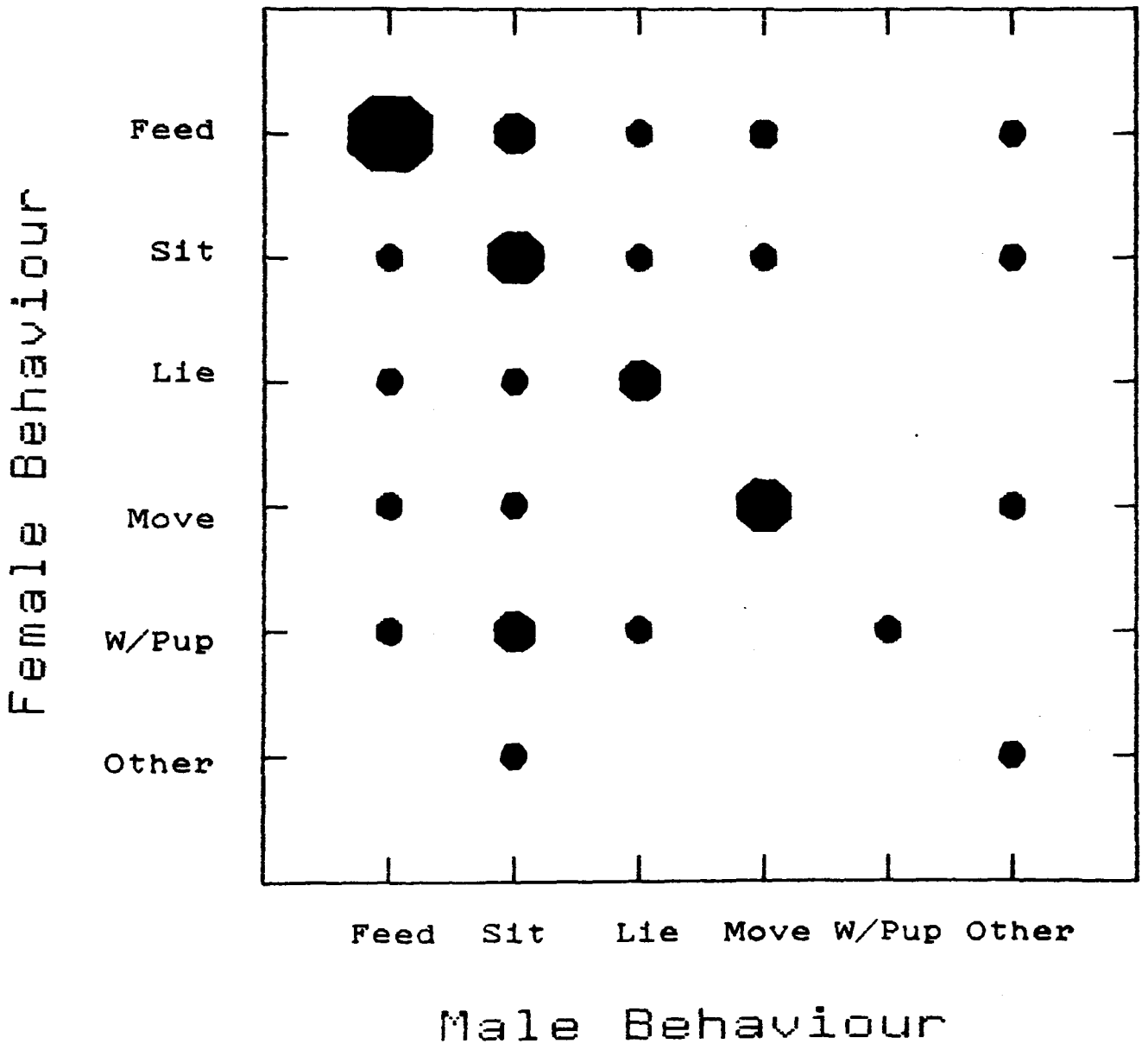


Table 4.9.--X^2 test of the assumption that mara males and females engage in different behaviours independently of their mate's behaviour. Data taken at 1 hr independence intervals. Expected values for each cell calculated on the basis of the conjoint probability of both sexes engaging in each behaviour combination if they were behaving at random and independently of their mate's activities.

	-Male Behaviour-										
Female Behav	Feed Obs	Feed Exp	Sit Obs	Sit Exp	Lie Obs	Lie Exp	Move Obs	Move Exp	Mscl Obs	Mscl Exp	Total
Feed	118	58.9	38	62.4	12	24.7	14	30.2	6	11.8	188
Sit	13	26.3	56	27.9	4	11.0	8	13.5	3	5.3	84
Lie	8	17.5	7	18.6	38	7.4	1	9.0	2	3.5	56
Move	6	23.8	12	25.2	1	10.0	50	12.2	7	4.8	76
IntW/P	4	18.8	41	19.9	7	7.9	2	9.6	6	3.8	60
Other	1	4.7	5	5.0	1	2.0	2	2.4	6	0.9	15
Total	150		159		63		77		30		479

X^2 Test Results

59.4	9.5	6.6	8.7	2.8
6.7	28.4	4.5	2.2	1.0
5.2	7.2	127.4	7.1	0.6
13.3	6.9	8.1	116.8	1.1
11.6	22.3	0.1	6.1	1.3
2.9	0.0	0.5	0.1	27.3

Total X^2 = 173.5, df = 20, $P < 0.005$

significantly different from those expected (X^2 = 173.5, df = 20, P < 0.005) if animals had been engaging in different behaviours independently of their mate's behaviour.

To further test the significance of this result, 2 by 2 X^2 tables were constructed for each cell comparing the observed frequency of that behaviour combination against the derived likelihood of obtaining that behaviour combination (see Table 4.10). Only those cells where expected values were 5 or greater were used. The observed number of observations of behaviour combinations are only significantly greater than the expected values in five cases: in the four cases where both sexes were engaging in the same behaviour (both feeding, both sitting, both lying, and both moving); and when the female was caring for the pups and the male sitting.

Thus, the data show that there is a high degree of behavioural synchrony between mates. If the behaviour combination where the female was caring for the pups and the male sitting (since males do not otherwise care for the young) is included, 65% of the time both members of the pair were engaging in equivalent behaviours.

4.6.3 Behavioural Differences Between the Sexes

In this subsection the differences between male and female behavioural time budgets will be examined (summarized in Table 4.11 and Figure 4.3; also see Chapter 5). As above, behavioural scan data were selected for each sex at 1 hr intervals. The number of times each sex was observed engaging in each behaviour category were tabulated. Tables 4.12 to 4.20 show time budgets for the two sexes under varying conditions (they also show results of X^2 tests comparing the time budgets). Overall the time budgets of males and females were found to be significantly different (X^2 = 119.05, df = 7, P < 0.005). The main differences were that: males sit and interact with other adults more than

Table 4.10.--The results of 2 by 2 X^2 tests of the likelihood of the co-occurrence of behaviours for mara pairs. '+' and '-' in the 4 th column refer to whether the observed value was greater or less than the derived expected value.

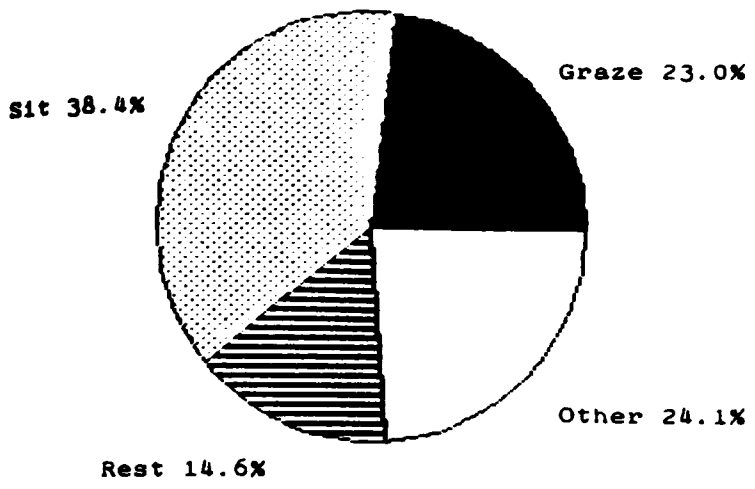
-Behaviour- Male	Female	Number Observed		Number Expected	X^2 Value	P <
Feed	Feed	118	+	58.9	142.3	0.005
	Sit	13	-	26.3	11.9	0.005
	Lie	8	-	17.5	8.6	0.005
	Move	6	-	23.8	23.0	0.005
	Int W/Pup	4	-	18.8	19.4	0.005
Sit	Feed	38	-	62.4	23.5	0.005
	Sit	56	+	27.9	51.5	0.005
	Lie	7	-	18.6	12.3	0.005
	Move	12	-	25.2	12.3	0.005
	Int W/pup	41	+	19.9	38.2	0.005
Lie	Feed	12	-	24.7	12.4	0.005
	Sit	4	-	11.0	6.3	0.025
	Lie	38	+	7.4	166.1	0.005
	Move	1	-	10.0	11.1	0.005
	Int W/Pup	7		7.9	0.1	N.S.
Move	Feed	14	-	30.2	17.1	0.005
	Sit	8		13.5	3.2	N.S.
	Lie	1	-	9.0	9.6	0.005
	Move	50	+	12.2	165.5	0.005
	Int W/Pup	2	-	9.6	8.3	0.005

Table 4.11.--Summary of inter-sexual and inter-seasonal differences in behaviour. All data obtained at 1 hr independence intervals to minimize auto-correlation of the data. Results and X^2 statistics for each comparisons made are shown in Tables 4.12 to 4.20.

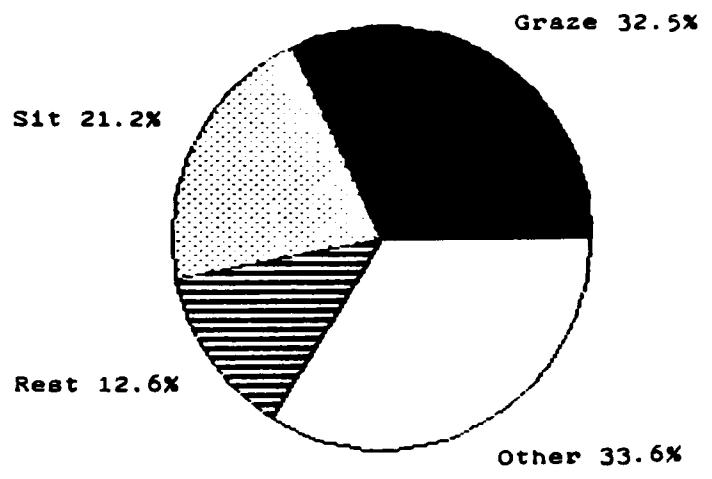
Comparison Made	Result
OVERALL	
Male vs Females	Significantly different. Males (i) sit more, (ii) interact with other adults more, and (iii) interact with pups less than females.
OUTSIDE BREEDING SEASON	
Male vs Female	No significant differences.
IN VS OUT OF BREEDING SEASON	
Females	Significantly different. During breeding season females (i) feed less, (ii) sit more, (iii) lie less, and (iv) engage in miscellaneous behaviours more (includes parenting) than outside breeding season.
Males	Significantly different. During the breeding season males (i) feed less, (ii) sit more, and (iii) engage in miscellaneous behaviours (primarily interact with other adults) more.
DURING BREEDING SEASON	
Male vs Female	Significantly different. Males sit more than females.
Male vs Female at dens	Significantly different. Females (i) sit less and (ii) interact with pups more than males.
Females, at vs away from dens	Significantly different. At den females (i) feed less and (ii) engage in miscellaneous behaviour (mostly parenting) more than away from the den.
Males, at vs away from dens	Significantly different. Males at den (i) feed less and (ii) sit more than away from den.
Male vs Female, away from dens	Significantly different. Males (i) feed less and (ii) sit more than females while away from the den.

Figure 4.3 (2 Pages).

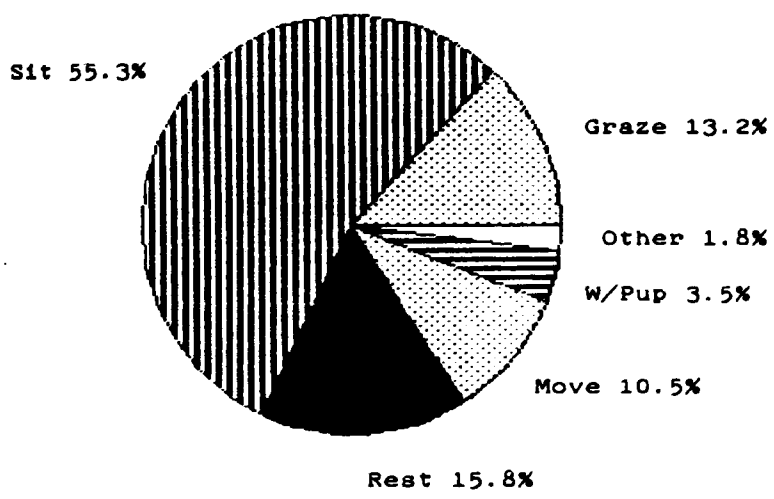
Pie charts illustrating the proportion of observations, or time budgets, of mara males and females engaging in different general behaviour categories at different times of the year, and at and away from the den.



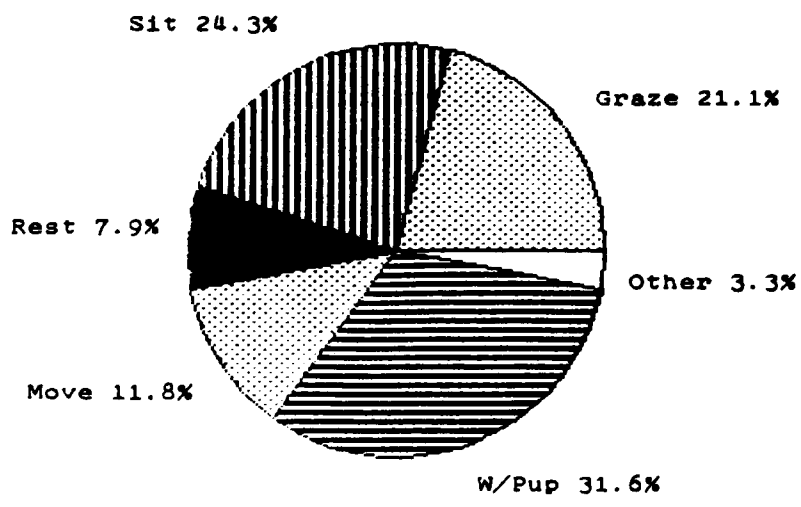
Male Behaviour During Breeding Season



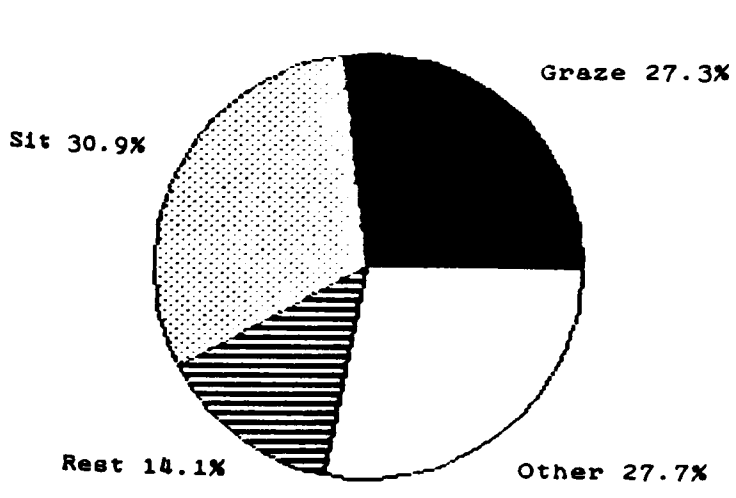
Female Behaviour During Breeding Season



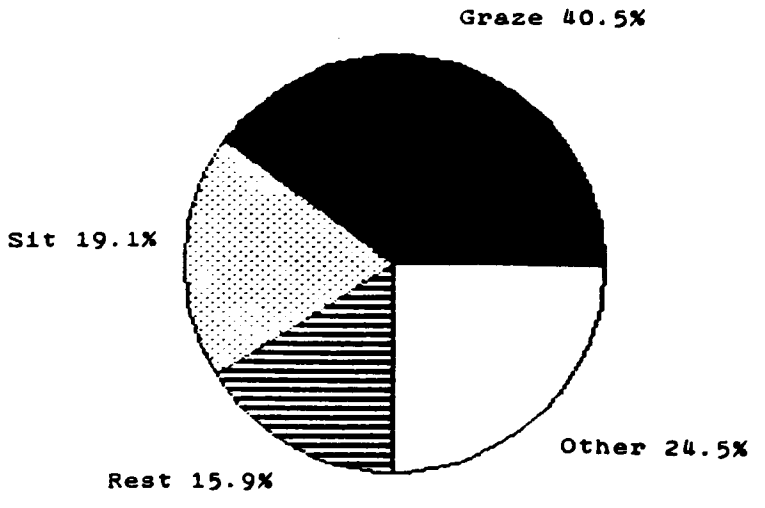
Breeding Season: Male Behaviour At Den



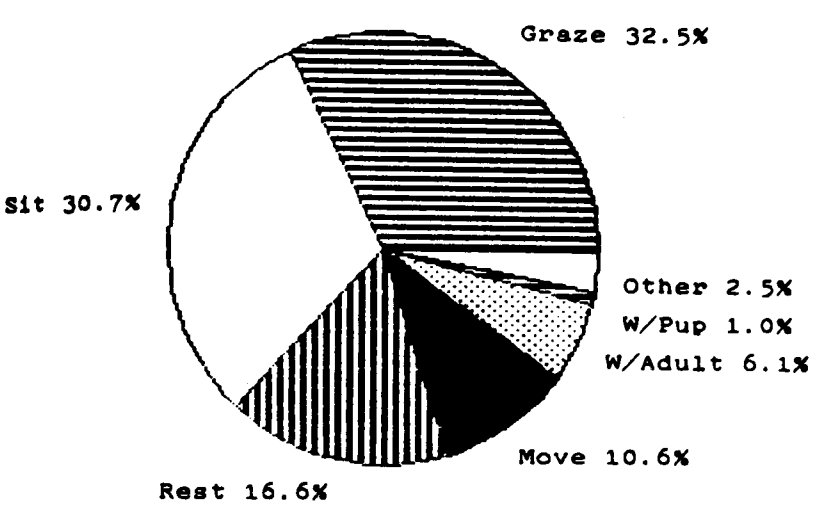
Breeding Season: Female Behaviour At Den



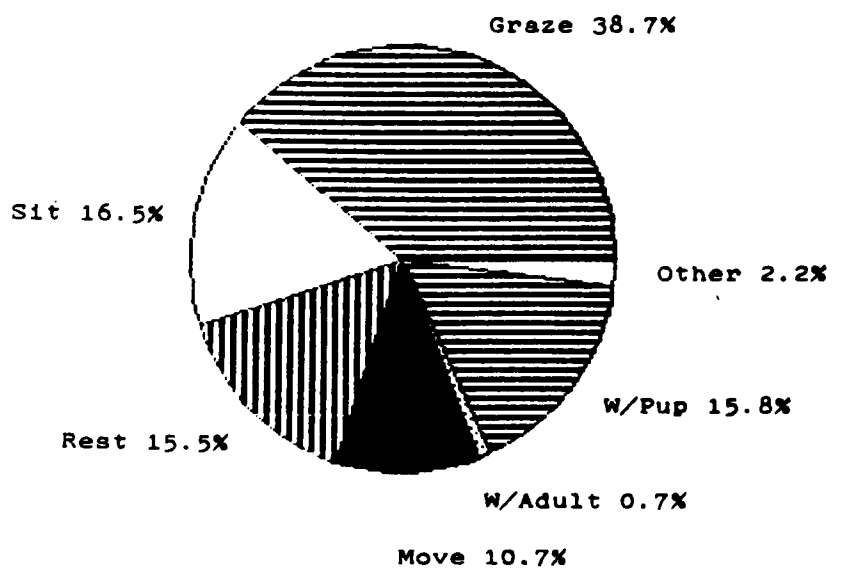
Breeding Season
Male Behaviour Away From Den



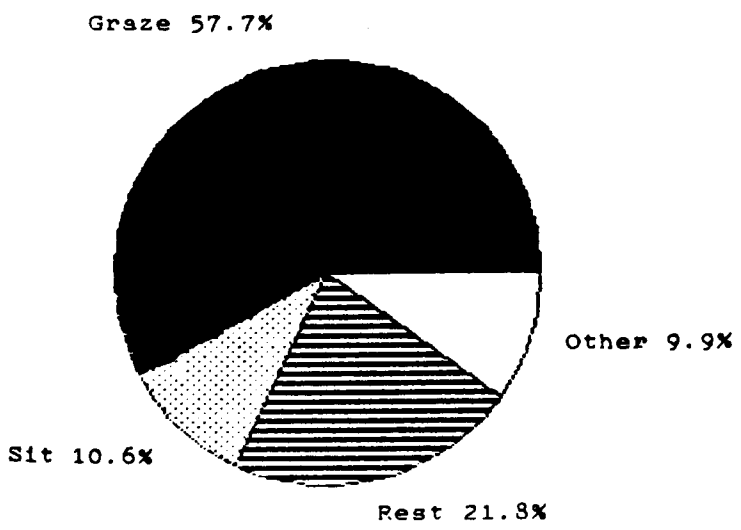
Breeding Season
Female Behaviour Away From Den



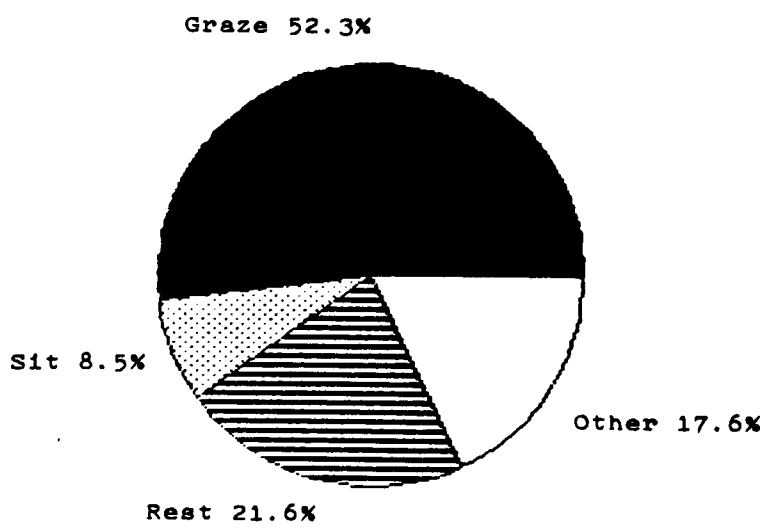
Male Behaviour Overall



Female Behaviour Overall



Male Behaviour Outside Breeding Season



Female Behaviour Outside Breeding Season

Table 4.12.--The number of independent scan observations of mara males and females behaving in each of 7 behaviour categories. Data taken from all observations of adult maras selected at 1 hr intervals.

Behaviour	-Male Totals- Observed	Expected	-Female Totals- Observed	Expected
Graze	166	182.80	225	208.20
Sit	157	118.28	96	134.72
Rest	85	81.82	90	93.18
Move	54	54.23	62	61.77
Interact W/Adults	31	16.36	4	18.64
Interact W/Pups	5	45.35	92	51.65
Other	13	12.16	13	13.84
Total	511	511.00	582	582.00
X^2 Test Results		1.54		1.36
		12.67		11.13
		0.12		0.11
		0.00		0.00
		13.09		11.50
		35.90		31.52
		0.06		0.05

Total X^2 = 119.05, df = 7, P < 0.005

Table 4.13.--Comparison of male and female behaviour outside the breeding season.

Behaviour	-Males- Observed	Expected	-Females- Observed	Expected	Total
Graze	82	77.45	104	108.55	186
Sit	15	13.33	17	18.67	32
Rest	31	30.82	43	43.18	74
Other	14	20.40	35	28.60	49
Total	142	142.00	199	199.00	341
X^2 Test Results		0.27		0.19	
		0.21		0.15	
		0.00		0.00	
		2.01		1.43	

Total X^2 = 4.26, df = 3, Not significant

Table 4.14.--Comparison of female mara behaviour during and outside the breeding season.

Behaviour	-Non-Breeding- Observed	Expected	-Breeding- Observed	Expected	Total
Graze	104	78.42	121	146.58	225
Sit	17	33.46	79	62.54	96
Rest	43	31.37	47	58.63	90
Other	35	55.76	125	104.24	160
Total	199	199.00	372	372.00	571
X^2 Test Results		8.35		4.47	
		8.10		4.33	
		4.32		2.31	
		7.73		4.14	

Total $X^2 = 43.73$, df = 3, $P < 0.005$

Table 4.15.--Comparison of male behaviour during and outside the breeding season.

Behaviour	-Non-Breeding- Observed	Expected	-Breeding- Observed	Expected	Total
Graze	82	46.32	85	120.68	167
Sit	15	43.54	142	113.46	157
Rest	31	23.57	54	61.43	85
Other	14	28.57	89	74.43	103
Total	142	142.00	370	370.00	512
X^2 Test Results		27.49		10.55	
		18.71		7.18	
		2.34		0.90	
		7.43		2.85	

Total $X^2 = 77.45$, df = 3, $P < 0.005$

Table 4.16.--Comparison between male and female behaviour during the breeding season.

	-Males-		-Females-		
Behaviour	Observed	Expected	Observed	Expected	Total
Graze	85	102.72	121	103.28	206
Sit	142	110.20	79	110.80	221
Rest	54	50.36	47	50.64	101
Other	89	106.71	125	107.29	214
Total	370	370.00	372	372.00	742
X^2 Test Results		3.06		3.04	
		9.17		9.13	
		0.26		0.26	
		2.94		2.92	

Total X^2 = 30.79, df = 3, P < 0.005

Table 4.17.--Comparison between male and female behaviour at breeding den sites.

Behaviour	-Male Totals- Observed	Expected	-Female Totals- Observed	Expected	Total
Graze	15	20.14	32	26.86	47
Sit	63	42.86	37	57.14	100
Rest	18	12.86	12	17.14	30
Move	12	12.86	18	17.14	30
Inter W/Pups	4	22.29	48	29.71	52
Other	2	3.00	5	4.00	7
Total	114	114.00	152	152.00	266
X^2 Test Results		1.31		0.98	
		9.47		7.10	
		2.06		1.54	
		0.06		0.04	
		15.00		11.25	
		0.33		0.25	

Total X^2 = 49.39, df = 6, P < 0.005

Table 4.18.--Comparison of male and female behaviour away from den sites during the breeding season.

Behaviour	-Males- Observed	Expected	-Females- Observed	Expected	Total
Graze	70	85.51	89	73.49	159
Sit	79	65.08	42	55.92	121
Rest	36	38.18	35	32.82	71
Other	71	67.23	54	57.77	125
Total	256	256.00	220	220.00	476
X^2 Test Results		2.81		3.27	
		2.98		3.47	
		0.13		0.15	
		0.21		0.25	

Total X^2 = 13.26, df = 3, P < 0.005

Table 4.19.--Comparison of female behaviour at the den versus away from den during the breeding season.

Behaviour	-Behav at den- Observed	Expected	-Behav Away From Den- Observed	Expected	Total
Graze	32	49.44	89	71.56	121
Sit	37	32.28	42	46.72	79
Rest	12	19.20	35	27.80	47
Other	71	51.08	54	73.92	125
Total	152	152.00	220	220.00	372
X^2 Test Results		6.15		4.25	
		0.69		0.48	
		2.70		1.87	
		7.77		5.37	

Total X^2 = 29.28, df = 3, P < 0.005

Table 4.20.--Comparison of male behaviour at the den versus away from the den during the breeding season.

Behaviour	-Behav at Den- Observed	Expected	-Behav Away From Den- Observed	Expected	Total
Graze	15	26.19	70	58.81	85
Sit	63	43.75	79	98.25	142
Rest	18	16.64	36	37.36	54
Other	18	27.42	71	61.58	89
Total	114	114.00	256	256.00	370
X^2 Test Results		4.78		2.13	
		8.47		3.77	
		0.11		0.05	
		3.24		1.44	

Total X^2 = 23.99, df = 3, P < 0.005

females, and females interact with pups more than males. The overall pattern of the differences in behaviour between males and females is as follows:

1. Outside the breeding season there are no differences between the behavioural time budgets of males and females.

2. During the breeding season both sexes feed less, sit more, and engage in a variety of miscellaneous behaviours (including the interact with adult and the with-pup behaviour categories) more than outside the breeding season.

3. The sexes have different time budgets during the breeding season: at the den females interact more with pups than males, and feed more than males while away from the den; while males spend more time sitting than females both at and away from the den.

The significance of these differences will be discussed in more detail in the next section (4.7).

4.6.4 Relations Between Pairs

Here I will be examining both the nature of the behavioural interactions and the spatial relationships between pairs (covered in detail in Chapter 3).

Genest and Dubost (*Op. cit.*; and Dubost and Genest, *Op. cit.*) have already described (also see Section 4.3) the nature of mara behavioural interactions. The main points they make are that: (i) females were never observed to behave aggressively towards other adults, (ii) males defend an area with a radius of about 15 m around their female, and will fight with any other male which attempts to approach their mate; and (iii) when fights occur they are short lived and appear to have no long term consequences for either pair involved. In the rare cases where one male chased off the

other, the winner will approach and stay by the loser's female for a few minutes. However, winners were never seen to take over the other female with the result that losing pairs were always quickly reunited. My observations support these findings. The frequency of aggressive behavioural interactions during the year are discussed in Chapter 5 where I show that 95% of the 252 aggressive interactions between pairs observed occurred during the pupping season (roughly 15 August to 30 November), and that 94% of these took place at breeding den sites. The other 13 interactions observed were scattered through the other months of the year. These results show clearly that virtually all aggressive interactions take place at dens during the peak of the pupping season. Aggression at the den is probably associated with the presence (or potential presence) of females in oestrus. The function of aggression away from dens, and outside the periods when females come into oestrus, is not known; but it may be associated with maintenance of spacing between pairs so that maras can minimize competition for food in any given patch (see Chapter 3 and below).

In Chapter 3 I describe the maras ranging patterns and spatial organization. Here I will summarize the main points relevant to understanding pair-bonding in maras.

- Mara ranging behaviour is extremely dynamic with pairs continually moving into new areas--within a year the animals cover an area of about 200 ha, while at any given moment the prevailing range measures about 35 ha. On a given day animals covered a mean of 10.25 ha, but may cover as much as 60.25 ha within a 24 hr period. Animals usually stayed less than 50 mins in any 50 x 50 m cell. Maras are primarily grazing animals. They are probably highly selective feeders since they have tiny mouths apparently adapted for choosing only the most nutritious food items. They spend on average 46% of the day feeding. The pattern

of feeding, moving over a large proportion of their range in a day and staying only a short time in any given cell, suggests that their food sources are widely dispersed and that the resources in any given patch are quickly used.

Some radio-collared animal's ranges overlapped substantially. However, even in those cases where two pairs' ranges overlapped a lot (e.g. 33 ha) the two ranges were highly negatively correlated showing that the two pairs' utilization distributions were very different. Pairs living adjacently were not using the same cells with the same intensity, and may have been actively avoiding each other.

4.7 Tests of Hypotheses

With the fundamentals of the mara's pair bond and spatial organization (see above and Chapter 3) described, I will now tackle the question of why mara's have adopted a monogamous social system. In the light of the hypotheses reported in the literature (see Section 4.2) as to why mammals are monogamous, and the above results, I propose the following not necessarily exclusive hypotheses (see Dunbar, 1984; Kleiman, 1977; Kleiman, 1981; and Wittenberger and Tilson, 1980):

1. Maras are monogamous because the pattern of resource dispersal in their habitat militates against the formation of large groups; thus, either:

    1.1. Animals are spatially dispersed in such a way that a viable home range is normally only adequate to maintain two individuals.

1.2. Due to the pattern of resource distribution, a maximum of 2 (sometimes 3) individuals can graze in a given patch at a given instant, although the ranges of two pairs living adjacently may overlap considerably.

2. Maras are monogamous because males reproduce most successfully by staying with a single female either because:

   2.1. **There** is a male bias in the population and males do better by sequestering a single female than by trying to mate promiscuously.

   2.2. Females are widely dispersed, and the oestrous period is short (they are only receptive for about an hour, see Chapter 5), so that males do better by staying and mating with a single female than by trying to find several females with which to mate.

3. Maras are monogamous because female aggression keeps males from acquiring additional females.

4. Maras are monogamous because of the need for direct paternal care of the young.

5. Maras are monogamous because females spend most of the time feeding to meet their high energetic needs due to the demands of lactation and gestation, and spend little time predator scanning, and hence need a male to guard them from predators.

Each of these possibilities will be addressed in turn below.

Effects of Resource Distribution

Since detailed data were not collected on mara food habits or food availability it is difficult to test this

hypothesis directly. Instead I have had to rely on inference from the maras' ranging patterns and spatial organization.

It is straightforward to assess the first sub-hypotheses: that the animals are spatially dispersed in such a way that a viable home range is normally only adequate to maintain two individuals. This would require different pairs to be occupying non-overlapping home-ranges. Clearly this is not the case as different pairs' ranges overlapped up to 33% or more of their total area (see Chapter 3). Further, individual maras are capable of covering a lot of ground (up to 60.25 ha) in a day, and it seems likely that one male could cover an area incorporating the ranges of two females.

A number of factors must be investigated to assess the second sub-hypothesis that: due to the pattern of resource dispersion a maximum of 2 (or occasionally 3) individuals can graze in a given patch simultaneously. Below I present a list of relevant factors:

1. The general pattern of mara spatial organization is of pairs inhabiting largely overlapping territories; but with the utilization distribution (see Chapter 3, Section 3.6) of maras using overlapping ranges being negatively correlated, showing that the pairs were actively avoiding each other.
2. Large grazing groups do, albeit rarely, form: up to 70 animals have been seen grazing together on an open lagoon measuring about 8 ha. These large grazing groups were only sighted in January and February. This is the driest time of year, and it seems likely that the vegetation on the lagoons at this time of year is more nutritious than that available in the surrounding scrub (see Chapters 2 and 3).
3. The mara's ranging behaviour of continually moving into new patches (50 X 50 m cells) and staying in each patch for less than an hour suggests that (i) the food

resources in any given patch are quickly exhausted, and (ii) that resources are dispersed in an unpredictable and irregular pattern (see Subsection 4.6.4 and Chapter 3).

The second point, above, shows that given certain environmental conditions maras will graze near each other, and hence suggests that the more 'normal' dispersed ranging pattern of pairs avoiding each other is probably due to the distribution of food resources, and not social factors. Furthermore, the mara's ranging behaviour of pairs staying in each patch (50 X 50 m cells) for less than an hour (see Chapter 3), and of individual pairs avoiding each other, suggests that the dispersion of resources forces the animals to space out to avoid competing for the rapidly depleted resources in any one location. Under these circumstances, foraging conditions alone might favour maras being solitary. On the other hand, with maras spending on average 46% of their time feeding (see Chapter 3), during which time their heads are lowered, and thus their ability to detect predators severly impaired, it seems likely that they could be more vigilant, and hence safer, foraging in groups. A group of 2 or 3 maras might be the optimal compromise. Thus, this argument may explain why maras live in groups of 2 or 3 animals, but it does not explain why mara groups usually consist of one male and one female.

Males Sequester Females

Regarding the first sub-hypotheses that males reproduce most successfully by defending access to a single female: sequestering individual females would be especially advantageous for males where sex ratios are male-biased because the majority of males would then achieve higher success by claiming sole possession of one female rather

than by taking their chances in a promiscuous lottery system. Females may or may not benefit from being sequestered, but the costs of resisting the male's continual presence must exceed the costs of accepting his presence. The following factors suggest that this hypothesis does not apply to maras:

- Males stay with the females throughout the year even though mating only occurs between June and October (most matings resulting in parturitions occur in June and July, see Chapter 5). This would not be necessary if sequestration of females for mating purposes was all there was to the monogamous bond.
- Although the difference is not significant, the data in Table 4.2 (see above) suggests that there may be a slight female bias in my study area with slightly more females than males in the population **(337 females, 288 males, Z=1.93, NS)**. The presence of at least one trio consisting of one male and two females (see Subsection 4.5.2) also supports this. It seems highly unlikely that there were more males than females in the population.

The following factors are relevant to assessing the second sub-hypothesis: that males do better by staying with a single female.

The ranging behaviour of maras suggest that their movements in pursuit of food are relatively unpredictable: the radio-collared animals were constantly moving into new areas throughout the period they were tracked, and their ranging patterns seemed adapted to using unpredictable and irregularly distributed patches which were quickly exhausted (see above and Chapter 3). Thus female maras must be, likewise, widely and unpredictably dispersed.

- Most matings leading to successful parturitions must occur in June and July (see Chapter 5), a time of year when maras are highly dispersed (see Chapter 3). Furthermore, the female's oestrous period only lasts for a few hours at the most (see Chapter 5).

Thus, during the time of year when most matings occur females would be highly dispersed and difficult to find. Finding a female in oestrus would be doubly difficult. The energetic costs for males would be very high; and, in addition, males would be forced into time consuming and energetically costly fights with other males over oestrous females. Under these circumstances the risk for a male of being at the wrong place at the right time would be high. Female spacing patterns would make it economically difficult for a male, no matter how powerful, to monopolize several females: the would be polygamist would simply exhaust himself searching for females in oestrus, and fighting over the few he found. Hence it seems likely that males might best ensure that they have an opportunity to reproduce by staying with a single female throughout the period in which she is receptive. This hypothesis appears to have considerable relevance as to monogamy in maras, but it would not account for the pair staying together year round.

Females Chase off Other Females

This is typically seen in territorial species where only one male and one female in a territory breed. Females might either, prevent other females from entering the territory, or keep other females in the territory from breeding through aggression. Because female maras were never observed acting aggressively towards each other there is no evidence that the monogamous bond is maintained by females.

THE ECOLOGY OF THE PAIR BOND

The Need for Direct or Indirect Paternal Care

The kind and quantity of paternal care of the young by maras is discussed in Chapter 5, and the relevant points are summarized here. There is little direct evidence of paternal care by male maras. They neither carry nor bring food back to the young. However, males spend over half their time (57% see Chapter 5) sitting while at the den, and 68% (41:60) of the time sitting while females are nursing the pups. Also, males occasionally were seen sitting for several hours by breeding dens in the absence of females. Sitting is the behaviour category associated with highest vigilance; and, as I will show in the next chapter, increased vigilance at the den is probably the main reason why maras den communally. Thus, although mara males do not directly care for the young they do appear to invest in a substantial amount of indirect paternal care: i.e. pup guarding. However, it seems unlikely that guarding the young is the main reason why maras have opted for monogamy since several females could, and do (as shown in Chapter 5), cooperate in pup guarding.

A Response to Energetic Constraints

Throughout this chapter I have presented considerable evidence that maras pairs coordinate their activities closely:

- Males maintain contact with their mates, while females move independently.

- Males spend more time sitting (the behaviour associated with highest vigilance) than females during the breeding season.
- Females spend more time feeding than males, at least during the breeding seasons, almost certainly in response to the high energetic demands of gestation and lactation.
- Only females engage in direct care of the young.

Thus there seems to be a clear division of labour between the male and females in a pair: males invest in guarding and maintaining contact with their mates; and females invest in taking care of the young, and feeding to supply the nutritional demands of lactation and gestation. Further, because females initiate most movements, and probably decide where the pair goes, they may be acting so as to meet their energetic requirements most efficiently. It seems unlikely, however, that the advantages of this coordination **are** the reason monogamy has arisen in maras since a male could fill these roles for several females, as the presence of a few trios of one male and two females suggests. Also, groups of females moving together without males might be able to benefit from most of the advantages of predator defense available to the monogamous pair.

The answer to why maras are monogamous is complex, as the evaluations of the hypotheses presented above show. Looking at these various hypotheses in detail, however, I suggest the following:

1. The distribution and nature of food resources (Hypothesis 1) has led to maras feeding in small widely dispersed groups.
2. Given the mara's ranging patterns, and the short period in which females are sexually receptive, males reproduce most successfully by staying with one female to insure having at least one mating since the energetic cost of trying to mate with several widely dispersed females is

so high (Hypothesis 2). This raises the question of whether females are not helping to force monogamy on the males through having such a short period of sexual receptivity. However, due to the lack of data on the female's oestrus cycle in the wild this is so far only speculation.

3. Since the males opportunities for mating promiscuously are low, they may improve on their investment by continuing to guard the same female (and to a lesser extent their young) from predators throughout the year (Hypothesis 4). This has led to the development of the extreme degree of coordination between mates discussed above.

With these results it is clear that the path that has led to monogamy in maras is not a simple one. A variety of factors have worked together to favour the development of this social system.

A striking aspect of the pair-bond is the high degree of coordination which has developed between mated males and females. Also, it is interesting that Dubost and Genest's (1974) study reports that an equally strong pair-bond exists in captive maras. This is surprising for the following reasons: (i) in captivity there were 70 or more maras in the population all living within a 10.3 ha enclosure, and (ii) females were breeding year round (unlike in the wild). Thus, there would appear to have been ample opportunities for a polygynous social system to develop, as is the mammalian norm (Wilson, 1975). Mating systems are often thought to have a great degree of plasticity (see Crook and Gartlan, 1966), so it is surprising that the monogamous bond in the captive maras had not broken down despite the apparent opportunities for males to increase their reproductive success by monopolizing several females. It would appear that maras are like the monogamous primates for which monogamy has been reported to be an extremely stable characteristic (Clutton-Brock and Harvey, 1977).

4.8 Summary

In this chapter I have attempted to do two things: describe the nature of the pair-bond in maras, and evaluate different hypotheses as to why maras have adopted this social system. Here, the main findings presented will be summarized:

1. Out of 441 groups seen, 63% consisted of 1 adult male and 1 adult female. This pattern was maintained throughout the year. In 62% (82% when only the best data are used) of the bi-monthly periods in which 22 individually identifiable maras were seen, they were in groups consisting of two animals--one male and one female. Some animals, however, were sighted on their own (25% of groups seen). In addition a few trios were seen: 73% (22:30) consisted of one male and **two females**, with the other 26% consisting of one female and two males. The small size of third animals in some of the trios suggests they may be young, however it is certain that some males accompanied two females at least temporarily. Thus, the available evidence clearly shows that, as in captivity, maras in the wild form monogamous pair-bonds which last throughout the year.

2. In 85% of the observations paired maras, identified within observation periods by their behavioural synchrony and proximity to each other, were within 10 mara lengths (77 cm) of their mates (N = 479). The maintenance of contact between paired maras may be difficult, both because the scrub vegetation is higher than a mara, and because animals move far during a day (up to 6 km or more). Data on maras in captivity show that contact between mates is maintained mainly by the

male. Female's initiate movement and serve as the 'passive' leader of the pair (Dubost and Genest, 1974). The same seems to be true in the wild: females move away from their mates more than males, while the reverse holds true in males; also females tended to be oriented with their mates to the rear. The males' orientation tended to be either towards or away from their mates, and may be geared towards efficient predator scanning.

3. The degree of behavioural synchrony between paired males and females is striking: 57% of the time both animals in a pair were observed they were doing the same thing. There were, however, behavioural differences between the time budgets of the sexes, summarized as follows: (i) outside the breeding season there were no significant differences; while (ii) during the breeding season both sexes feed less, sit, engage in interactions with other adults, and interact with pups more. Further, females interact more with pups (males hardly interact with pups at all) and spend more time grazing than males, while males sit (the behaviour associated with vigilance) and interact with other males (usually agonistically) more. While females were with the pups (usually nursing), males were sitting 68% of the time.

4. Fights between males were observed almost exclusively during the pupping season. This is the only time of year in which males have ready contact with several females which may be sexually receptive.

5. The suggestion from the behavioural and orientational differences between the sexes is that females are geared towards finding food to fulfill the high energetic requirements of lactation and gestation, and towards directly caring for the pups. Males, on the other hand, are geared more towards maintaining contact with their mate, defending her from the approaches of other males, and scanning for predators which could serve to protect

both their mates and offspring.

Several hypotheses were evaluated to explain why maras are monogamous. Three hypotheses, each building on the other, are suggested to trace the evolutionary pathway leading to monogamy in maras: (i) The distribution of food resources has meant that maras feed in small groups in widely dispersed and unpredictable patches. (ii) Because of the wide dispersion of maras due to the pattern of food distribution, and because of the shortness of the female's oestrous period, it is energetically costly for males to find sexually receptive females. Thus, the opportunities for males to mate with several females are low, so males may best maximize their inclusive fitness by staying with one female rather than by trying to mate polygynously. (iii) Once monogamy has been favoured a variety of pressures have led to maras adopting the extreme degree of coordination between pair-bonded males and females we see today. Now that the social system has developed it has proven particularly resilient to environmental pressures, with mara males maintaining the system even when opportunities (in captivity) to mate polygynously present themselves.

Chapter 5

COMMUNAL DENNING

5.1 Introduction

In this chapter I discuss the workings of the mara's communal denning system. As discussed in Chapter 4, maras are monogamous with mated males and females remaining together throughout the year. Despite their monogamous breeding system maras give birth to, and rear their pups at communal dens; where up to 20 or more pairs crêche their young together in one burrow. This system is partly analogous to those found among certain birds (see for example Vehrencamp, 1978, and Crook, 1964), but appears to be unique amongst mammals. The aims of this chapter are to describe the mara's communal denning system, and then to examine this system from an evolutionary perspective to determine what advantages it confers on individual maras.

In Section 5.2 the literature on why animals live in groups will be reviewed to provide a theoretical background to the chapter. Section 5.3 will be devoted to a description of the breeding biology of the mara based on my observations and results from other studies. The following sections will be devoted to describing: the patterns of den usage by maras (Section 5.4); how adults care for their offspring (Section 5.5); the behaviour of mara pups (Section 5.6); and the nature of interactions between adults at the den (Section 5.7). Three hypotheses as to why maras den communally will be examined in Section 5.8. Finally, in Section 5.9 the main findings presented will be summarized.

5.2 Theoretical Basis: Why Animals Live in Groups

Alexander (1974), amongst others, has argued that there are no automatic or universal benefits from group living. There are, however, a number of automatic and universal disadvantages such as increased likelihood of disease and parasite transmission, and increased intensity of competition for resources, including mates. Other potential costs of group living include greater conspicuousness, which may render an animal less effective as a predator or more vulnerable as prey; increased probability of misdirected parental care, and a heightened risk of incest (Hoogland and Sherman, 1976; and Hoogland, 1979). Groups, then, must form and persist only if the individuals involved gain in inclusive fitness (Williams, 1966; and others). Below, I will be examining those factors which may favour the formation of groups, despite their inherent disadvantages, which are relevant to understanding the mara's communal denning system.

For the purposes of this discussion a group can be considered as a collection of 2 or more individuals. For maras a group, as distinguished from a pair, will be considered as between 3 and 20 or more adults within 30 m of each other. Maras are herbivores, so I will be discussing mainly those aspects of 'group-living theory' relevant to non-carnivorous animals. The kinds of factors favouring the formation of groups can be divided into four main categories:

1. The following factors may favour group living, either together or independently, as a means of avoiding predators:

    1.1. Animals living in a group may collectively be more vigilant and hence safer from predators, than they would be if alone (see for example Kenward, 1978). Further, as group size increases the benefits of

more animals watching may level off so that individuals could spend more time doing other things, such as feeding or resting (see Bertram, 1980).

1.2. Animals in a group could act together to chase off predators from which a single individual would be unable to protect itself (see Kruuk, 1964).

1.3. Many prey moving together could confuse a charging predator making it difficult to focus on one particular individual (see Neile and Cullen, 1974; and Jarman, 1974).

1.4. Concentrations of animals may provide safety for their members since the chance of a predator taking any given individual decreases as group size increases (Hamilton, 1971). In particular, weak animals could benefit since it might be difficult for a predator to detect their poor condition amongst the other individuals (Kruuk, 1972; and Estes, 1976).

1.5. Although groups may be more conspicuous than single animals, "it is unlikely that the number of attacks on a group is proportional to its size; a herd of say a hundred animals does not have to withstand one hundred times as many attacks as a lone animal" (Bertram, 1974).

1.6. Groups could form for the simple reason that scarce, albeit large, aggregations of animals might be difficult for a predator to encounter (Vine, 1973; and Treisman, 1975).

2. The nature of food resources may necessitate animals banding together to find, catch and/or retain prey which individual animals would be unable to take (see Kruuk, *Op. cit.*; and Schaller, 1972). These reasons are typically given to explain why some predatory species live in groups; but they may also apply to herbivorous animals--e.g. quelea's (a species of weaver birds)

follow each other to food (de Groot, 1980).

3. The quality and distribution of some critical resource such as food or a breeding site may force the formation of groups (see Alexander, 1974; and especially Cowan and Garson, 1985). Jarman (*Op. cit.*) for antelopes, and Crook and Gartlan (1966) for primates have found the following general effects: (i) when resources are of low quality and highly patchy in distribution they favour the formation of small groups; (ii) when resources are of low quality and homogeneously distributed they favour the formation of large groups; (iii) when resources are of high quality and patchy they favour the formation of large groups; and (iv) when of high quality and homogeneously distributed they favour the formation of small groups which often are territorial.
4. Finally, certain patterns of "resource dispersion" may create conditions where the smallest maintainable territory can support a group larger than the minimum breeding unit. In this case, irrespective of advantages to sociality, the cost to a dominant of evicting individuals may be greater than the cost of allowing them to remain (Macdonald, 1983; Kruuk and Macdonald, 1985; and Carr and Macdonald, 1986).

According to Alexander (1974) groups form as a result of combinations of the above selective pressures and, thereafter social behaviour may evolve. Alexander gives three reasons why social behaviour could arise in group-living animals: (i) it could enhance the original advantage of group living, (ii) it could reduce the likelihood of disease and parasite transmission, or (iii) reproductive competition amongst group members could lead to the development of, for example, polygyny or dominance hierarchies.

Group Living Monogamous Species

Communally denning mammal species are common: family groups of wolves share a single den site (Mech, 1970), warthogs form family groups which move around during the day and return to large burrows to sleep at night (Cumming, 1975), groups of mole rats live together in communal burrows with only one 'queen' female producing young (Jarvis, 1973), prairie dogs live in large colonies (Hoogland, 1979); of the mara's relatives the plains viscacha (*Lagostomus maximus*), and the cavies (such as *Cavia aperea*, *Galea musteloides*, and *Microcavia australis*) all live in groups around burrows (Weir, 1974; and Rood, 1972). In all of these species there are either dominance hierarchies, or only one female and one male in the group usually produce young. In the mammal literature I have been unable to find any monogamous species which, like the mara, practices communal denning with all pairs producing young. To find a vertebrate with a similar social system I have had to turn to birds.

Many monogamous bird species nest in colonies with each pair using its own nest (e.g. herring gulls; Tinbergen, 1953). However, few birds seem to have adopted a system similar to the mara. In some species several females lay their eggs in one nest to be incubated by a single male: e.g. rheas and tinamous (Bruning, 1974; and Lancaster, 1964). A few species build communal nests in which each pair occupies a private chamber and rears it own brood: e.g. the African weaverlike bird, *Bubalornis albirostris*; and the wattled starling, *Creatophora cinerea* (Crook, 1964; and Lack, 1968). In these last species, the advantage of collaborating to this extent appears to be the improvement in defense against predators (Lack, *Op. cit.*).

One avian species which both maintains monogamous pairs and nests communally is the groove-billed ani (*Crotophaga sulcirostris*). In groove-billed anis, groups are composed of monogamously mated pairs which defend a

common feeding and nesting territory, construct a single nest, and share the raising of the joint brood (Vehrencamp, 1977 and 1978). The typical group consists of two or three pairs, but solitary pairs are not uncommon. All pairs lay in the nest, but incubation effort varies with only the group's alpha male covering the eggs and nestlings at night. The alpha pair has higher reproductive success. Predation, however, is highest on the adults while incubating. Vehrencamp suggests that the advantage of communal nesting to anis is the reduction of parental care costs, particularly the risk of mortality during incubation.

5.3 The Mara's Breeding Biology

In this section the mara's breeding biology will be described. The following topics will be covered: gestation period, lactation period, birth of the pups, growth of the pups, and breeding seasonality.

5.3.1 Pregnancy and Gestation

In captivity in France, Dubost and Genest (1974) report the mara's gestation period as ranging from 3.0 to 3.65 months (91 to 111 days, N = 58). They further suggest that this variation could be due to (i) seasonal variation, (ii) missed observations of later copulations, or (iii) delayed implantation of the foetus. Litter sizes vary from 1 to 3; and Dubost and Genest (*Op. cit.*) reported that of 63 pregnancies recorded to term 70% produced twins, 25% produced single pups, and 5% produced triplets. Because of difficulties in marking pups I was unable to accurately determine litter sizes in the wild. Of 9 lactating identifiable females during one pupping season, 7 (78%) were

recorded as having 2 pups, with the other 2 (22%) having a single pup each. These results suggest a similar pattern in wild mara litter sizes to those reported by Dubost and Genest (*Op. cit.*).

5.3.2 Parturition

Maras were observed giving birth on three occasions (see descriptions in Appendix C). One unmarked female was observed giving birth to two pups on 14 August 1983 at Chicken Den, Puesto El Salitral. The radio-collared females ELF and SYF were seen to give birth to pups on, respectively, 15 September 1983 and 15 September 1984. Both SYF (2 pups) and ELF (1 pup?) gave birth at Ash Den, Puesto La Blanca.

In the days prior to parturition females engage in a lot of exploratory activity. Heavily pregnant females were observed intensely investigating the area around the dens at each study site. An example of this is that on 3 October 1981, at Estancia Larreburu, I saw a heavily pregnant female visit three different dens. She spent at least an hour in the vicinity of each den and entered and explored each one in detail.

The three females who were observed giving birth showed the same pattern of behaviour. On the day of the birth the females arrived at the den 1 to 2 hrs before parturition. During this pre-parturition period the females were particularly alert: all three walked around the den and investigated surrounding armadillo and owl burrows, and other features. All three females then sat in, and dug at, the entrance to the dens. After this period of intense activity the females gave birth to the first pup. The pups are born in a membraneous sack which the females licked off immediately post-partum. SYF gave birth to her second pup 17 min after the first; and she passed, and ate, the afterbirth 14 min later. I once found a placenta in the

entrance to a den, but assume they are usually eaten. Pups are able to walk almost immediately post-partum.

The unmarked female produced her pups within the den mouth; and ELF produced her pups about 1 m away. SYF, however, gave birth 10 m away in the open because she had been chased from the den by the male of another pair. In the 10 min following parturition, SYF slowly led the tottering and extremely vulnerable pup to the den. Since I saw so few births, despite the numerous hours spent observing at dens during periods when births must have been occurring, most probably take place deep in the den's mouth where females seemed to spend a lot of time. It is unlikely that births occurred at night since I never observed adults visiting the den after dusk.

After parturition the females stayed within a few metres of the den for a further 2 to 3 hrs. During this time all three females groomed and nursed their pups. SYF and ELF had considerable difficulties with pups of other pairs trying to gain access to their teats, and chased these other young off many times. The unmarked female's pups were grazing within 1.5 hrs of birth, although only in the mouth of the den. Two to three hours after birth the females left the den area.

The role of the male during these three births appeared to be important. EL1 and SY1, in particular, repeatedly chased other pairs away from the den. EL1 chased other maras 27 times in 5.5 hrs, SY1 chased 16 times in 3 hrs, and the unmarked male chased twice in 4 hrs at the den. Both the unmarked male and SY1 showed great interest in the newborn pups--sniffing them carefully. EL1 showed no interest, but he was almost continually occupied chasing off other males. In all three cases the pairs left the area chin-rump-following, suggesting that the females were coming into a post-partum oestrus. The closeness of the post-partum oestrus may, in part, explain the large number of chases observed. However, providing space around the

female, so that she can give birth free of distractions from other investigating maras, may also be an important function of the males' vigorous defense of the area around their mates.

These observations follow closely those reported by Dubost and Genest (*Op. cit.*). In addition, A Kacelnik (Pers. comm., Dept. Zool. Ox. Univ.) reported seeing maras in the Buenos Aires zoo partially filling in the mouth of the den after the new born pups had entered; perhaps as a means of inhibiting the entrance of predators.

5.3.3 Lactation and Growth of the Pups

The two longest periods over which identifiable females were seen suckling pups were 68 and 71 days (see Table 5.1). However, these pups when first seen being nursed were already well coordinated, and hence were probably at least a week old. This suggests that pups are nursed for at least 75 to 78 days. Dubost and Genest (*Op. cit.*) report a lactation period of 77 days (11 weeks) which ties in well with these results.

Pups born in September and October are nearly adult size by January or February. They are, however, still distinguishable as juveniles until well into the Austral autumn (April-May). In March 1984 three juvenile males were caught. They weighed respectively 6.8 kg, 5.8 kg, and 2.3 kg; or 83, 71, and 28% of the mean adult weight of 8.12 kg (see Appendix A). The smaller of these must have been a late born pup (see below)--perhaps a December or January birth. The other two appeared to be average size young of the year when compared visually to other young, who were all about five to six months old.

Table 5.1.--Duration of time over which marked females were observed nursing pups within one breeding season. Data taken from all years and all dens. Dens: [A] Ash, [H] Horse Bones, [C] Chicken, [O] Owl, [E] Estancia, [F] Airport, and [M] Molino. Pups are size/age categorized into 4 groups (see details in Table 5.2) with size 1 being the smallest and size 4 pups the largest.

Mara Name	-First Sighting- Date	Pup Size	Number Pups	-Last Sighting- Date	Pup Size	Number Pups	Span Days Observed Nursing
ELF[A]	15.9.83	Born	1	8.10.83	3	1	24
GC2[A]	19.9.83	2	1	28.11.83	Juv	2	71 *
NL2[H]	16.9.83	2	2	3.10.83	3	1	18
OC2[C]	14.8.83	Born	2	28.8.83	2	2	15
PA2[A]	7.9.83	?	2	29.9.83	?	1	23
PJF[A]	28.9.83	2	2	10.11.83	4	1	44
PUF[O]	3.10.83	2	2	9.12.83	Juv	2	68 *
SLF[O]	15.10.83	4	1	9.12.83	Juv	1	56
SYF[A]	15.9.84	Born	2	17.9.84	1	2	3
TEF[A]	4.10.84	?	-	17.10.84	2	-	18
WB2[E]	1.10.81	-	-	26.10.81	-	-	26
TE2[E]	6.10.81	-	-	2.11.81	-	-	28
SC2[F]	14.10.81	-	-	30.10.81	-	-	17
NE2[F]	4.10.81	-	-	2.11.81	-	-	30
LRF[F]	21.9.81	-	-	2.11.81	-	-	43
DN2[M]	8.9.81	-	-	20.9.81	-	-	13

* Longest lactation periods observed. In both cases pups must have been at least a week old when first seen being nursed since they were already well coordinated and partly grown.

5.3.4 Breeding Seasonality

Dubost and Genest (1974) reported captive maras breeding throughout the year with a slight drop in the birth rate between June and August (winter in the Southern Hemisphere). However, at my Patagonian study site the occurrence of births was highly seasonal. During three years of field work pups were only observed between August and March (see Figure 5.1); and size 1 pups, probably less than two weeks old (see classification protocol in Table 5.2), were only seen between 14 August and 2 November. All the pups seen in February and March, because of their large size, must have been 2 to 3 months old. A shepherd (Sr. Laquirique, Pto Madryn, Argentina) reported seeing new born pups on one occasion at the beginning of February at the El Salitral study area, and I have seen some pups which were probably less than a month old at the end of January. Thus, the pupping season on the Valdés Peninsula can be considered to run from mid-August to mid-January.

Figure 5.2 shows histograms of the total number of unique size 1 pups seen at the intensively observed den sites per 15 day period during the 1983 and 1984 breeding seasons. This figure also shows the proportion of the total maximum number of pups which were size 1 per 15 day period. In 1983 there appeared to be a peak of births between the 1st and 15th of October as shown by the large number of size 1 pups seen then. In 1984 the peak appeared earlier, during the last two weeks of September. These histograms show that a large proportion of the pups seen were newly born in late August and early September; and, that this proportion drops off rapidly as relatively fewer pups are born compared to the number of pups which have already matured beyond size (category) 1. By the middle of November no new size 1 pups were seen at any of the intensively studied dens.

The monomodal nature of the histograms in Figure 5.3, showing the maximum number of pups of all sizes seen on

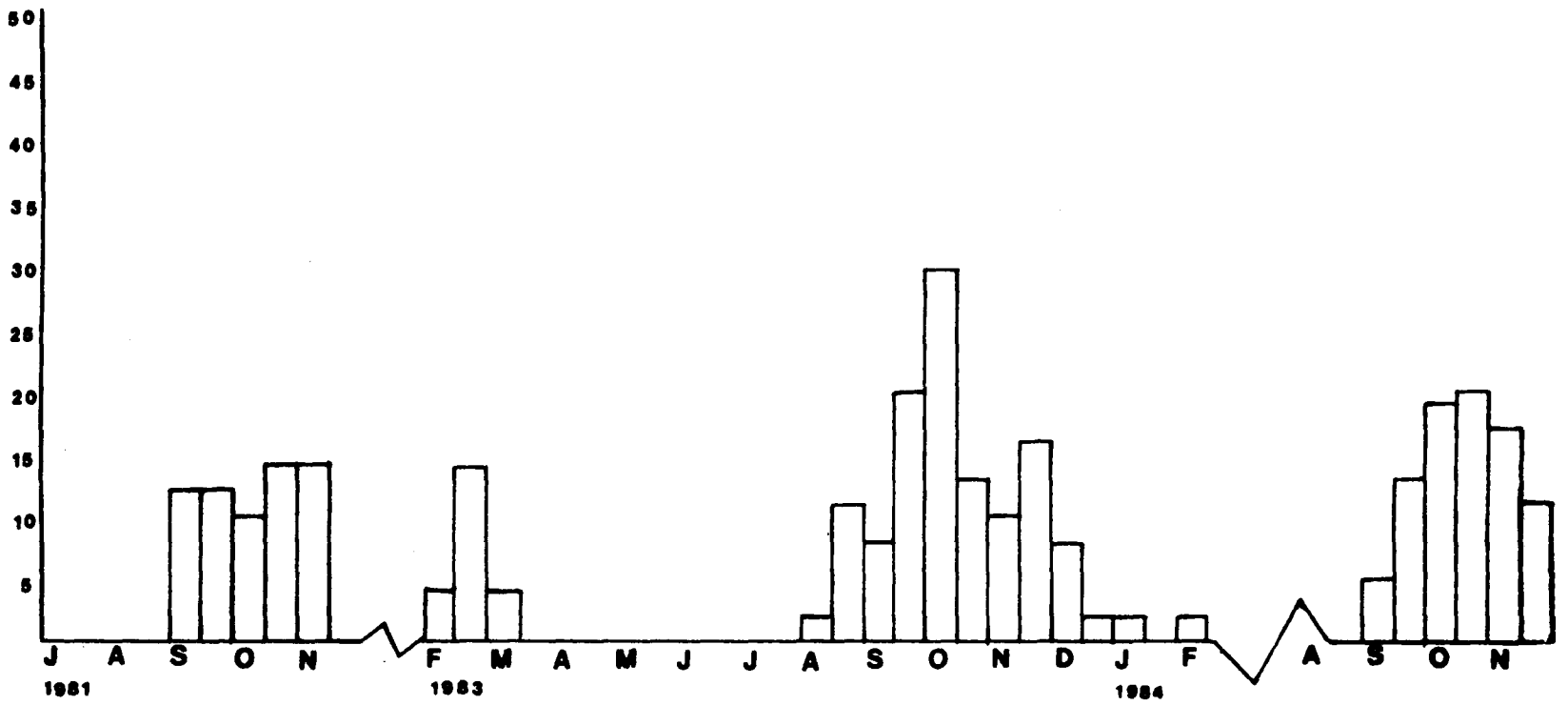


Figure 5.1.--Histogram of the maximum number of pups sighted on a given day during each two week period over 22 months of field work.

Table 5.2.--Criteria for classifying pups into 4 size categories.

Size 1	Tiniest pups, do not walk well and their legs are enormous relative to body size. Some pups still have a visible umbillicus.
Size 2	Larger than size 1, but still small; while being suckled their heads are raised to the teat, and their bodies are generally below the upper teat of a sitting mara.
Size 3	Large pups, but still not as coordinated as size 4 pups. While being suckled their heads go down to the teat, and their back is at least at the level of the upper teat on a sitting female.
Size 4	Large (± 3/4 adult size) and well coordinated, run easily. They look like small adults.

Figure 5.2 (2 Pages).

Histograms of the number of unique size one pups, and the proportion of all pups which were size 1, seen during two week periods at the intensively observed den sites during the 1983 and 1984 pupping seasons.

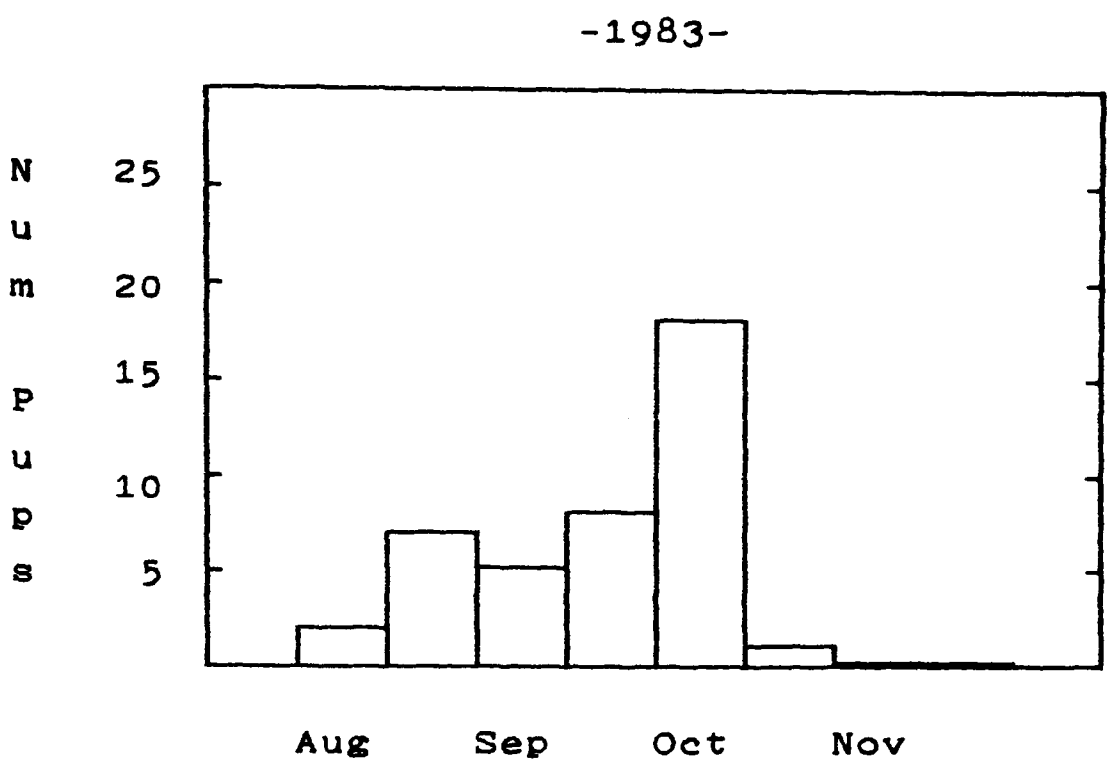
A. Number of size 1 pups in 1983.

B. Number of size 1 pups in 1984.

C. Proportion of pups which were size 1 in 1983.

D. Proportion of pups which were size 1 in 1984.

A.


-1983-
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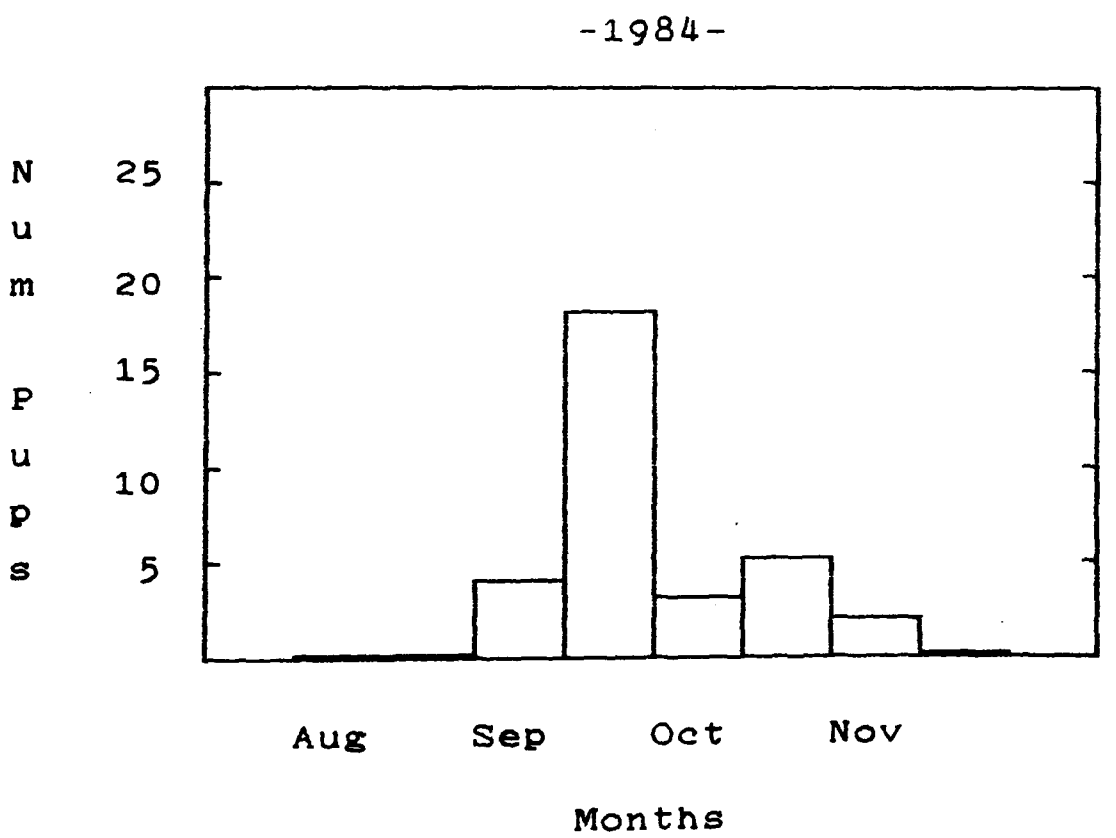
B.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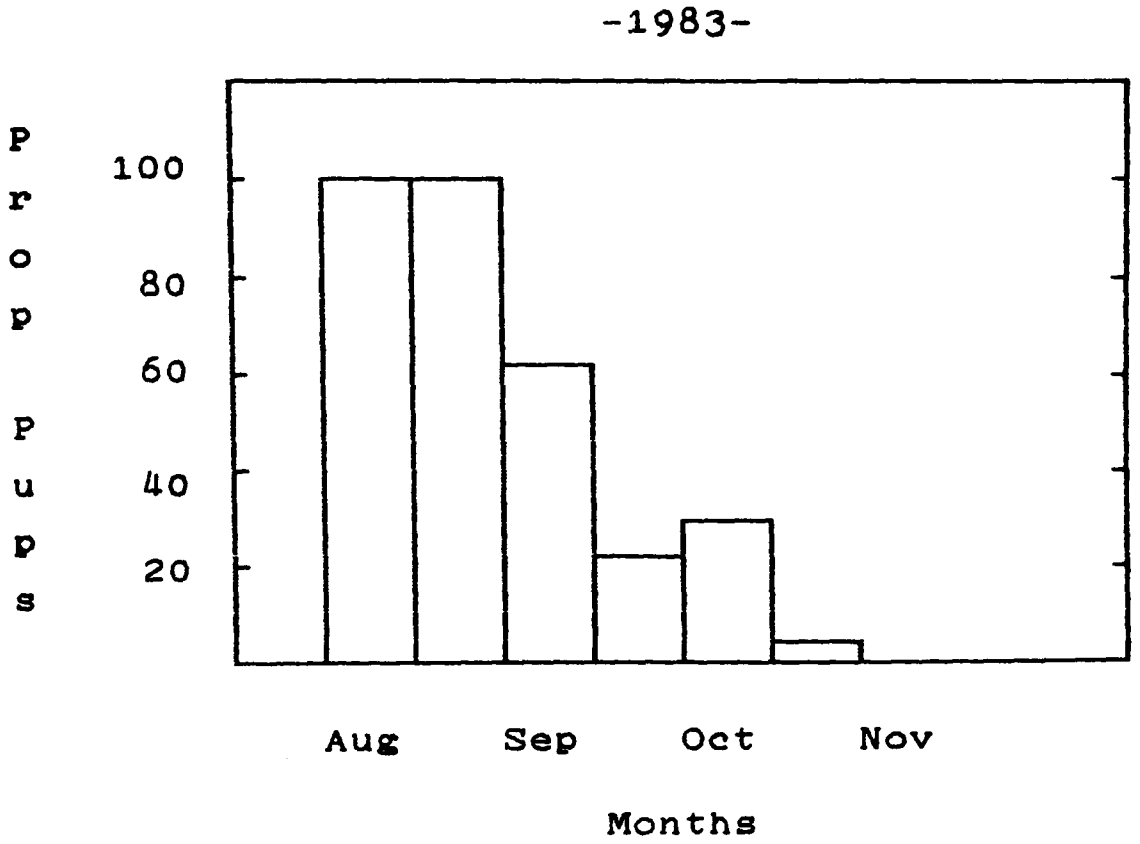
C.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Prop pups
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80
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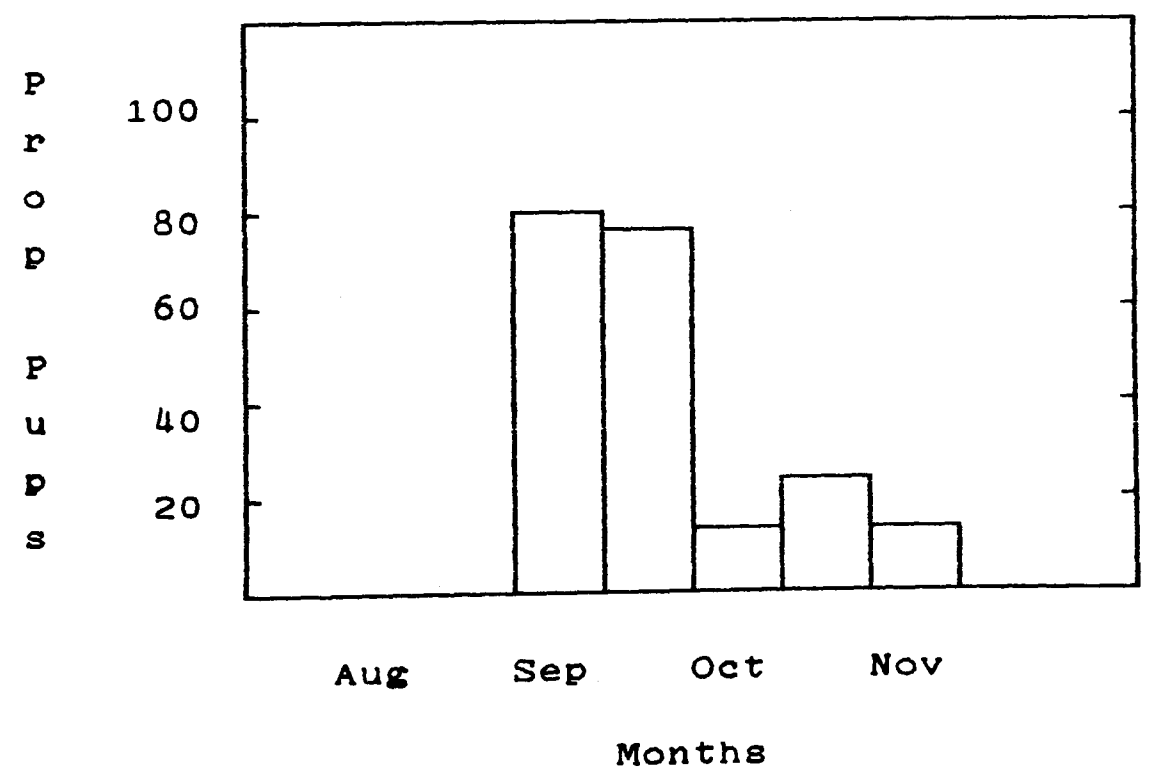
Months

D.


-1984-
Prop pups
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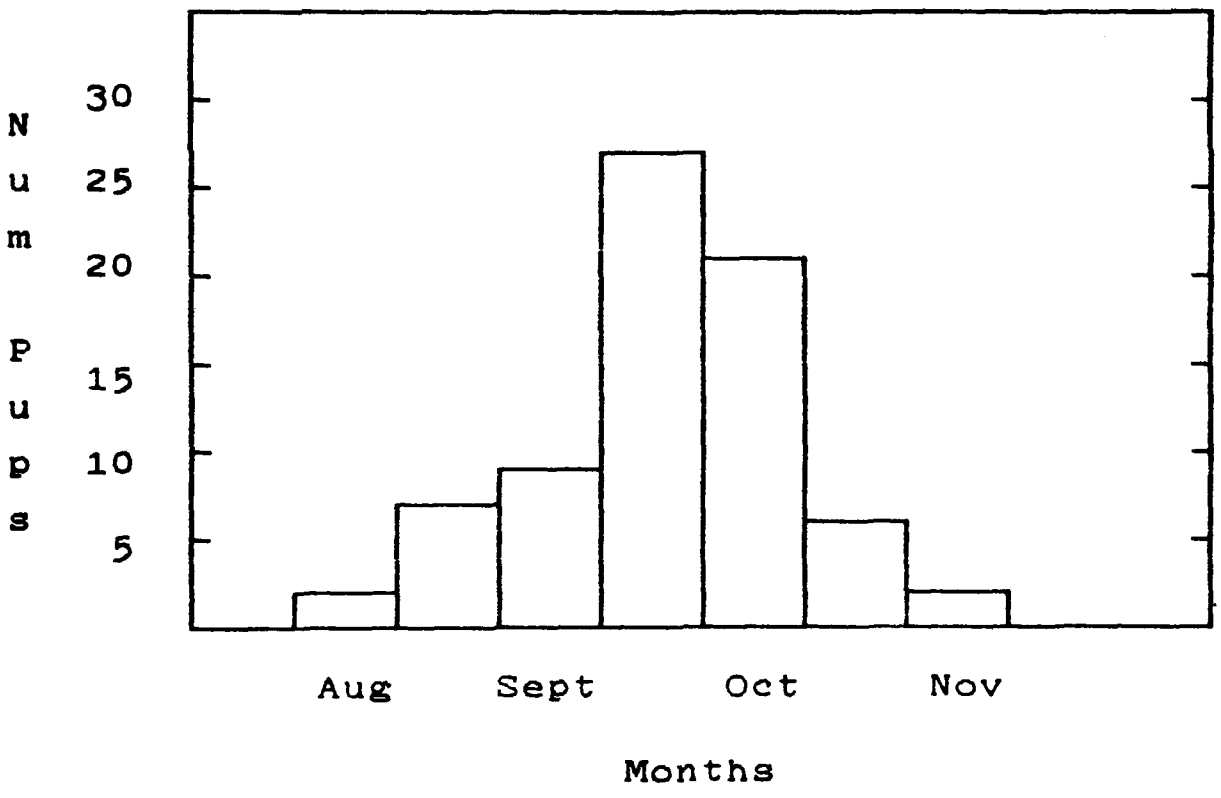


Figure 5.3.--Histogram of the maximum number of pups of all sizes seen on a given day within two week periods during the combined 1983 and 1984 pupping seasons.

a given day during each two week period, strongly suggest that females are only producing one litter annually. Further, the number of size 1 pups seen (see Figure 5.2) drops off sharply by the end of October, with no climb later on to suggest that females were producing a second litter. There is no evidence that wild females have the three to four pregnancies a year Dubost and Genest (*Op. cit.*) have described as the norm in captive animals. It seems likely that environmental conditions in the wild, at least on the Valdés Peninsula, do not allow reproduction at such a high level.

What then of the post-partum oestrus described above? With a gestation period of approximately 100 days one would expect females producing pups in late August to give birth to another litter at the end of November or early December, a time when new born pups were never seen. Nevertheless, one female which was killed by a shepherd on 26 October 1981 was both lactating and carrying 2 tiny foetuses. Also, the few births reported in late January suggest a late October mating, which could have resulted from a post-partum oestrus. Thus, at least some females must become pregnant soon after giving birth. One possible explanation is that females mate post-partum, but reabsorb the foetuses if their offspring survive. I will be showing later that there is considerable pup mortality (see Section 5.4), and carrying a foetus while lactating may be a good insurance policy against offspring loss. A similar phenomenon occurs in the mara's relative the coypu, *Myocastor coypus*, where females reabsorb litters depending on the male to female ratio of the foetuses and environmental conditions (Gosling and Petrie, 1981; see also data on wallabies in Kaufmann, 1974).

5.4 The Ecology of Denning

The pattern of den usage by breeding maras will be described in this section. At my three main study sites (Estancia Larreburu, Puesto La Blanca, and Puesto El Salitral) a total of 29 mara dens were found, of which 15 were occupied by pups. Eight dens were observed intensively; and by counting different years as independent, detailed denning records were obtained on 11 dens over three breeding seasons. A further 20 dens, 16 of which were known to be used, were found away from these three sites on the Valdés Peninsula. In total 710.42 hrs were spent intensively observing den sites, and numerous hours were spent wandering over the countryside collecting data on dens opportunistically. These data will be used to illustrate the following aspects of the mara's denning ecology: (i) the general pattern of den usage, (ii) seasonal and annual patterns, (iii) the distribution of den membership sizes, (iv) breeding success and mortality, and (v) the degree of association between maras using different dens.

5.4.1 Methods

Three main methodologies, apart from those already mentioned in Chapter 2, were used to collect and analyze data. These were: (i) finding and assessing the status of dens, (ii) estimating den membership size, and (iii) estimating pup mortality.

Finding and Assessing Den Status

Data on dens other than those in my three study sites were collected opportunistically. Once every two weeks during the breeding season I drove or walked around the Peninsula looking for maras and signs of dens. When dens were found their locations were mapped and they were judged to be active or inactive. Dens were judged to be active, that is used by adults for the purpose of rearing pups, if I saw mara adults or pups at them, or earth had been moved in their mouths recently and there were lots of fresh tracks and faeces present. Estimates of dens' ages were made by asking the local shepherds. The term 'den site' is used to refer to dens where more than one burrow was used; while 'den' was used to refer to breeding sites where only one burrow, perhaps with various entrances, was used.

Estimating Daily Den Membership

Estimating the number of mara adults and pups using a den on any given day was complicated by the lack of identifiable adults: at my most intensively studied den in 1983, Ash Den Site, of the 15 or so adult pairs using the den only four maras were individually identifiable. With few recognizable individuals, and the confusion of mara pairs continually moving in and out of the area around a den (see Section 5.5), it was difficult to estimate the number of animals using a den. It was, however, feasible to count the number of pups (but see following paragraph). Since there is small variation in litter sizes in maras (see

Section 5.3) pup counts could be used to obtain a daily estimate of adult membership size for a den. Based on the findings of Dubost and Genest (*Op cit*) that 70 % of litters were twins, 25 % were singletons, and 5 % were triplets, the following formula was used to estimate the number of females using a den on a given day.

Formula 5.1

NF = Number of Females at Den

NP = Number of Pups at Den

$$NF = \frac{(NP * 0.7)}{2} + (NP * 0.25) + \frac{(NP * 0.05)}{3}$$

For all practical purposes (but see Chapter 4), the number of females with pups at a den is synonymous with the number of monogamous pairs using a den.

Although more practical than counting adults, obtaining a daily estimate of den membership size through direct pup counts was not always straightforward. While recording den scans, made every 10 to 15 minutes, all visible pups were counted (see Chapter 2 for methods of data collection). The maximum number of pups counted in a single scan during the day was used to estimate the minimum daily den membership size using Formula 5.1. However, using the maximum pup count could lead to underestimating den membership because pups in different size categories were not visible to the same extent--older (size four) pups tended to leave the den early in the morning and stay away most of the day; while smaller, younger pups might come out only when their own parents were at the den. Thus, the maximum number of pups recorded during scans would not account for those which had left the area for the day before observations began, or which were inside the den.

More accurate estimates of daily den membership size were obtained while collecting pup scan data. At each pup scan (made every 10 mins) the number of each size category of pup was recorded. So the daily estimate of the number of pups at a den was obtained by adding up the maximum count

for each pup size category, regardless of when recorded during the day. This method consistently gave higher estimates of the number of pups at a den: of 42 days where both den scan and pup scan data were collected, den scans averaged 0.84 (± 0.14) of the pup scan derived estimates of the number of pups at a den. Even using this method, the numbers obtained should be treated as an index of den membership size since accurate counts could not be obtained without more identifiable pups and adults.

Estimating Seasonal Den Membership

The best estimates of the total number of pups or adults which used a den during a breeding season, were for dens where pup scans were made regularly (approximately once a week). To obtain an estimate, a chart was prepared with the days of the year down one side and with a column for each pup which used the den across the top (see for example Table 5.3). Then, for each day the den was watched the age category (1 to 4) for each pup observed was entered across the page horizontally from the oldest pup to the youngest. The next day observations were made at the den, the age category of each pup seen was again marked on the chart; but this time matching them with pups from the previous session, so that the presence of a given pup through the breeding season can be followed down a column. The following rules were used to match pups in successive observation days: (i) pups can not go down in age as the season progresses; and (ii) if for a given pup, more than 3 weeks have passed since an unmatched pup of the same age was recorded, and no older pups were available to match with it, same age category pups were considered new animals. This last rule only applies to size one, two, and three pups since size four pups were sighted at dens inconsistently. These charts were used to

Table 5.3.--Sample chart of growth of pups at Owl Den during the 1983 and 1984 denning seasons. M's mark where pups may have died according to the criteria in the text.

	-Number of Pups at Den-														
Date	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1983															
26.8.83		*	*	*	*										
8.9.83				1	1										
14.9.83			2	1	1										
20.9.83			*	*	*										
30.9.83	4	4	4	*	*										
3.10.83		4	4	3	3	3	2	2	2	2	2	1			
7.10.83							3	3	2	2	2	1	1	1	
15.10.83		4	4	4	3	3	3	3	2	2	2	1	1	1	1
24.10.83					M	M	4	4	M	3	3	2	2	2	2
1.11.83										4	4	3	3	3	3
1984															
9.10.84	2														
14.10.84	3	2	2	2											
15.10.84	M	M	M	M	1										
16.10.84					M										

estimate how many adults and pups used a given den during a breeding season and to illustrate how the number of pups using a den changes as the season progresses. There are two problems with this technique: (i) it could underestimate den membership size since pups could have left the area before observations began, or come after observations ended; and (ii) matching pups observed between different observation sessions could underestimate the number of pups born at a den since a new pup might be confused with an animal which had died.

Estimating Mortality

Rough estimates of mortality at the den were based on the disappearances of pups from a chart (see Table 5.3) prior to reaching the critical size 4 age category when pups became fairly independent from the den. Only in a few cases could I be certain that pups had died: either I found a dead body, or the pups disappeared suddenly from a den site and I was sure they had not been moved elsewhere.

5.4.2 General Patterns of Den Usage

Table 5.4 shows the number of pups observed at each den in each year they were studied at my three main study areas. In Table 5.5 the location and habitat around each den studied is described (for more details of the study areas see Chapter 2). Data on the respective membership sizes, numbers, and locations of dens at each of the three study areas, as well as those dens which were observed opportunistically elsewhere, are summarized below.

Table 5.4.--The number of hours and days over which intensive observations were made at different den sites. Also shows the estimated number of pups, adult pairs, and number of pups which died prior to reaching size category 4 at each of the intensively studied den sites.

Den Site	Year	Obs Hours	Days Watched	Number Pairs	Number Pups	Pup Mortality
----------Estancia Larreburu----------						
Molino	1981	36.9	6	9	14	?
"	1983	-	-	?	?	?
Airport	1981	150.76	23	9	14	?
"	1983	-	-	3	6	?
"	1984	-	-	3	6	?
Estancia	1981	95.25	20	5	8	?
"	1983	-	-	?	?	?
"	1984	-	-	?	?	?
Corral	1981	-	-	1	2	2
Fence	1981	-	-	1	2	?
La Anita	1981	-	-	2	4	?
----------Puesto La Blanca----------						
Ash	1983	109.00	13	22	33	14
"	1984	38.79	6	9	14	12
Owl	1983	59.39	7	9	15	3
"	1984	26.43	3	3	5	5
Goose I	1983	-	-	1	1	1
Goose II	1983	-	-	2	4	4
High Lag.	1984	-	-	1	1	1
----------Puesto El Salitral----------						
Chicken	1983	32.24	5	5	8	?
"	1984	98.68	15	19	31	7
Corral	1983	27.27	4	7	12	?
"	1984	5.0	1	1	2	2
Horse Bone	1983	32.41	5	8	14	?
----------Grassy Valley----------						
Boliche	1984	-	-	2	3	?
Valley	1983	-	-	1	2	?
"	1984	-	-	2	3	?
----------Puesto Centenario----------						
Main	1983	-	-	1	1	?
"	1983	-	-	1	1	?
Valley	1983	-	-	?	A	?
"	1983	-	-	2	3	?
----------Other Areas----------						
Martillo	1983	-	-	1	2	?
Cliff	1984	-	-	1	2	2

Table 5.5.--Descriptions of the main dens observed during the 1981, 1983, and 1984 breeding seasons.

Den Site	-Number- Dens	Hole	Closest Human Site	Closest Active Den	Habitat
Estancia Larreburu					
Molino	2	2	2000 m	2000 m	Open, near corral
Airport	2	6	250 m	250 m	Airstrip on scrub edge
Estancia	1	3	60 m	70 m	On scrub edge
Corral	1	1	60 m	70 m	In sheep corral
Fence	1	1	300 m	150 m	In scrub near house
La Anita	1	1	100 m	500 m	In scrub, edge of lagoon
Puesto La Blanca					
Ash	2	3	60 m	200 m	Open ground near house
Owl	1	4	100 m	200 m	Scrub, near house
Goose I	1	1	400 m	50 m	Lagoon edge in open
Goose II	1	1	450 m	50 m	On lagoon
High Lag.	1	1	2000 m	1800 m	Small lagoon in scrub
Puesto El Salitral					
Chicken	1	1	60 m	180 m	Open ground near house
Corral	2	3	150 m	180 m	Scrub edge in open
Horse Bone	2	4	150 m	180 m	Scrub edge in open
Grassy Valley					
Boliche	1	1	2000 m	500 m	Open Valley, scrub edge
Valley	1	1	2000 m	500 m	Open Valley, scrub edge
Puesto Centenario					
Main	1	1	4000 m	400 m	Open valley, corral 300m
Valley	1	1	4000 m	400 m	Open valley, corral 500m
Other Areas					
Martillo	1	1	8000 m	4000 m	Open patch in scrub
Cliff	1	1	2000 m	?	Scrub, edge of sea cliff

Estancia Larreburu and Environs

In 1981 intensive observations were made here at three different dens: Molino Den Site, Estancia Den and Airport Den Site. An additional three dens, Corral Den, Fence Den and La Anita Den, were observed opportunistically. All these dens except the Molino and La Anita Dens were located within 300 m of a human occupied house. Molino Den Site was located at an outlying corral about 2 km away; and La Anita Den was located next to another Estancia about 1 km away. A total of 7 active and 6 inactive or unknown status dens were found in the study area (see Figure 5.4). Since pup scan data were not collected here, estimates of den membership (see Table 5.4) are based solely on the maximum number of pups, regardless of size, seen at the den each day observations were made. A minimum of 39 pups were born at this study site in 1981: 14 pups at Molino Den Site, 8 at Estancia Den, 14 at Airport Den Site, 2 at Fence Den, 2 at Corral Den, and 4 at La Anita Den (see Tables 5.6, 5.7, and 5.8 for daily pup counts at three of these dens). Using Formula 5.1, an estimated 24 pairs produced pups at these dens in 1981. In 1983 and 1984 these dens were observed sporadically, and all but the La Anita and Fence dens were still used for rearing pups at the study's end.

Puesto La Blanca and Environs

Observations were made at this study area during the 1983 and 1984 breeding seasons. Two main dens were used here, Ash Den Site and Owl Den, both located within 200 m of the house at the edge of the scrub (see Figure 5.5). At both dens I collected pup scan data, so the estimates of the number of pups born are more precise than at the Larreburu

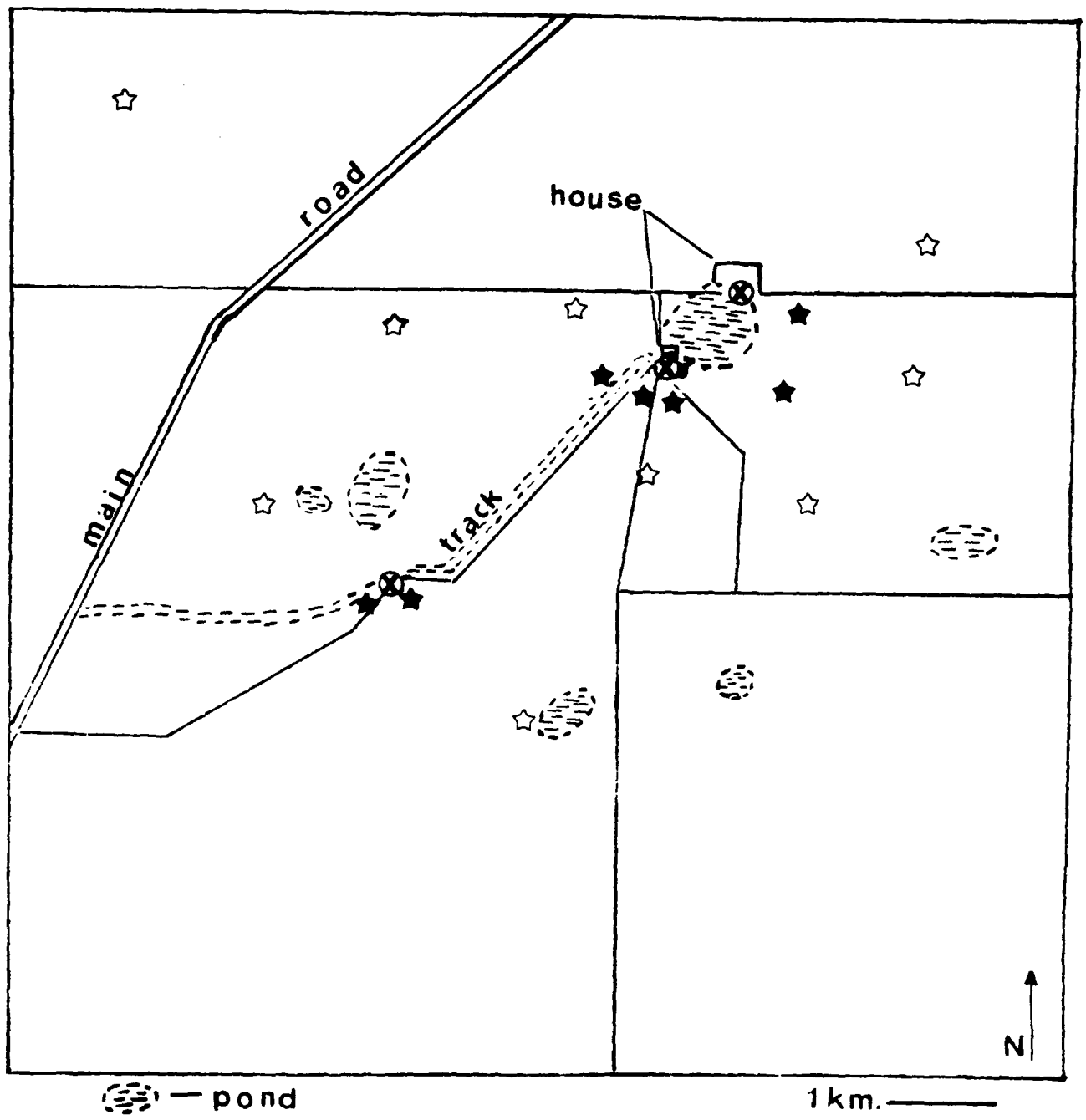


Figure 5.4.--Map of the Estancia Larreburu study area showing the location of all active and inactive dens found in 1981, 1983, and 1984. The open stars mark inactive or abandoned dens, filled stars mark active dens, and circles with x's mark windmills.

Table 5.6.--Sightings of mara pups at Molino Den Site, Estancia Larreburu, during the 1981, 1983, and 1984 breeding seasons.

Date	Number Pups	Comments
	1981	
12.8.81	-	Active?
23.8.81	-	Active?
5.9.81	10	
8.9.81	9	
11.9.81	2	
14.9.81	12	2 in Corral Den
16.9.81	8	
20.9.81	12	2 tiny new born
15.10.81	0	Pups Predated
	1983	
14.10.83	?	Corral Den Only Active
	1984	
25.10.84	-	Inactive

Table 5.7.--Sightings of mara pups at Estancia Den, Estancia Larreburu, during the 1981, 1983 and 1984 breeding seasons.

Date	Number Pups	Comments
	1981	
11.9.81	-	Active
12.9.81	-	Active
13.9.81	-	Active
15.9.81	-	Active
17.9.81	2	1 new born pup
21.9.81	-	Active
22.9.81	2	
24.9.81	4	
25.9.81	3	
26.9.81	3	1 new born pup
1.10.81	3	
2.10.81	2	
5.10.81	7	
6.10.81	2	
9.10.81	7	
12.10.81	8	
13.10.81	7	
27.10.81	2	
30.10.81	2	
2.11.81	4	
4.11.81	4	
6.11.81	2	
	1983	
14.10.83	-	Active
23.10.83	-	Active
	1984	
13.10.84	-	Active?
?.10.84	3	

Table 5.8.--Sightings of mara pups at Airport Den, Estancia Larreburu, during the 1981, 1983 and 1984 breeding seasons.

Date	Number Pups	Comments
	1981	
6.9.81	-	Active
12.9.81	-	Active
13.9.81	1	
19.9.81	-	Active
21.9.81	3	1 new born pup
22.9.81	2	
24.9.81	4	
25.9.81	3	
27.9.81	7	2 new born pups
3.10.81	8	
4.10.81	6	
10.10.81	10	
11.10.81	10	
14.10.81	7	
15.10.81	7	
17.10.81	9	
19.10.81	8	
20.10.81	8	
21.10.81	14	
26.10.81	5	
28.10.81	7	
30.10.81	6	
31.10.81	5	
1.11.81	4	
2.11.81	10	
6.11.81	2	
	1983	
14.10.83	-	Active
18.10.83	-	Active
23.10.83	6	4 Size 3, 2 Size 4 Pups
	1984	
13.10.84	6	

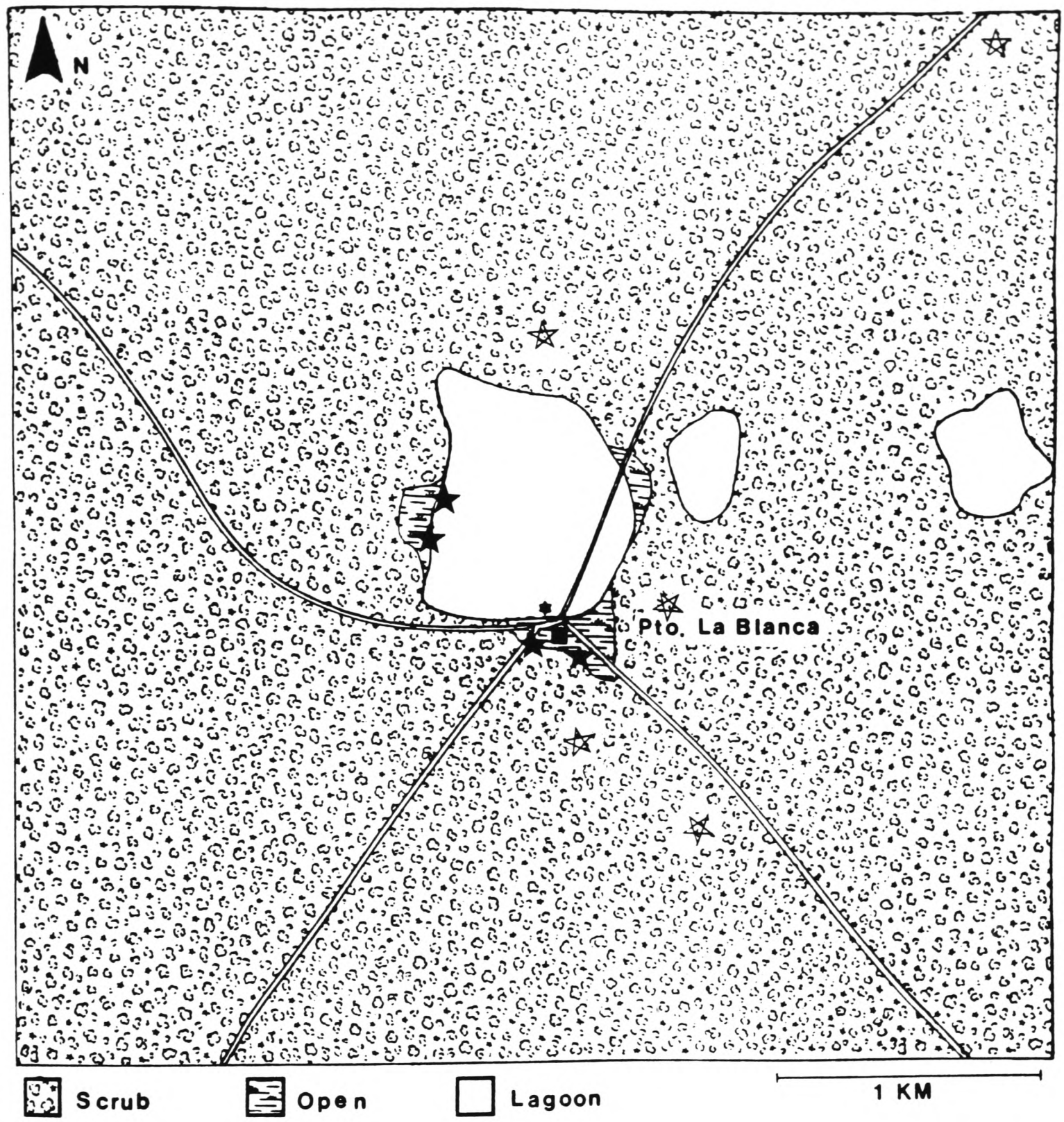


Figure 5.5.--Map of the Puesto La Blanca study area showing the location of all active and inactive dens found in 1983 and 1984. The open stars mark inactive or abandoned dens, filled stars mark active dens, and circles with x's mark windmills.

dens (see above). In 1983, using the pup scan data to make the calculations, at least 48 pups used these two dens (33 at Ash and 15 at Owl, see Table 5.9 and 5.10). In 1984, although at least 19 pups were born here (14 at Ash and 5 at Owl), only 2 may have survived. Whether the pups were killed by disease or a predator is unknown (12 of the Ash Den Site pups disappeared between 4 and 6 October; and the 5 Owl Den pups disappeared between 14 and 16 October). Two other dens were used by pups: Goose Den I and Goose Den II. They were located 200 m apart at the edge of the lagoon, and were about 350 m from the ranch buildings. Pups were not seen at either den in 1984; but in 1983 one pup was seen on two occasions at Goose Den I, and Goose Den II was used by at least three pups. However, I suspect none of these pups survived since both dens seemed to have been abandoned within a month of the pups' first appearances. Weasels (*Galictus cuja*) might have killed the young since 2 were seen at Goose Den II about the time the pups were last sighted there. The den about 200 m south of Ash Den Site was used occasionally by large Ash Den pups which had wandered close to it with their parents. In August of 1984 I found bones from at least 2 pups scattered around this burrow's entrance. The four other dens shown in Figure 5.5 were not used by maras during my stay in the field.

Puesto El Salitral

As at La Blanca, observations were made here during both the 1983 and 1984 breeding seasons. Three main dens were used by maras for rearing pups at this area during the study period: Chicken Den, Corral Den Site and Horse Bones Den Site (see Figure 5.6). All three were located in the open within 300 m of the house. Of the other three dens found in the area (see Figure 5.6) two, located west of the

Table 5.9.--Sightings of each size category of mara pup at Ash Den Site during the 1983 and 1984 breeding seasons.

Date	Total	Size 1	Size 2	Size 3	Size 4	Comments
			1983			
31.8.83	5	5	-	-	-	
3.9.83	5	-	-	-	-	
7.9.83	7	1	-	-	-	
15.9.83	8	3	5	-	-	
19.9.83	6	3	2	-	-	
28.9.83	12	-	1	-	1	
2.10.83	20	4	5	7	4	
4.10.83	18	5	3	-	-	
5.10.83	20	11	3	2	-	
8.10.83	23	10	11	2	-	
13.10.83	15	3	5	5	2	
17.10.83	13	1	7	4	1	
27.10.83	13	-	5	3	5	
28.10.83	11	1	5	3	2	
5.11.83	6	-	-	-	-	
9.11.83	6	-	-	-	-	
10.11.83	10	-	-	10	-	
11.11.83	10	-	-	9	1	
28.11.83	0	-	-	-	-	No maras
8.12.83	2	-	-	-	2	
			1984			
30.8.84	-	-	-	-	-	Active
10.9.84	2	2	-	-	-	
15.9.84	5	4	-	-	-	
17.9.84	6	4	2	-	-	
23.9.84	10	8	2	-	-	
26.9.84	12	8	4	-	-	
27.9.84	11	4	6	1	-	
6.10.84	-	-	-	-	-	All pups dead
27.10.84	-	-	-	-	-	Pair at den
1.11.84	-	-	-	-	-	Pair at den
11.11.84	2	-	-	-	-	
21.11.84	2	-	-	-	-	

Table 5.10.--Sightings of each size category of mara pup at Owl Den during the 1983 and 1984 breeding seasons.

Date	Total	Size 1	Size 2	Size 3	Size 4	Comments
			1983			
26.8.83	4	-	-	-	-	
8.9.83	2	2	-	-	-	
14.9.83	3	2	1	-	-	
20.9.93	3	-	-	-	-	
30.9.83	5	-	-	-	3	
3.10.83	11	1	5	3	2	
7.10.83	8	3	3	2	-	
15.10.83	14	4	3	4	3	
24.10.83	8	-	4	2	2	
1.11.83	6	-	-	4	2	
			1984			
9.10.84	1	-	1	-	-	
14.10.84	4	-	3	1	-	
15.10.84	1	1	-	-	-	
16.10.84	?	-	-	-	-	Pups Dead

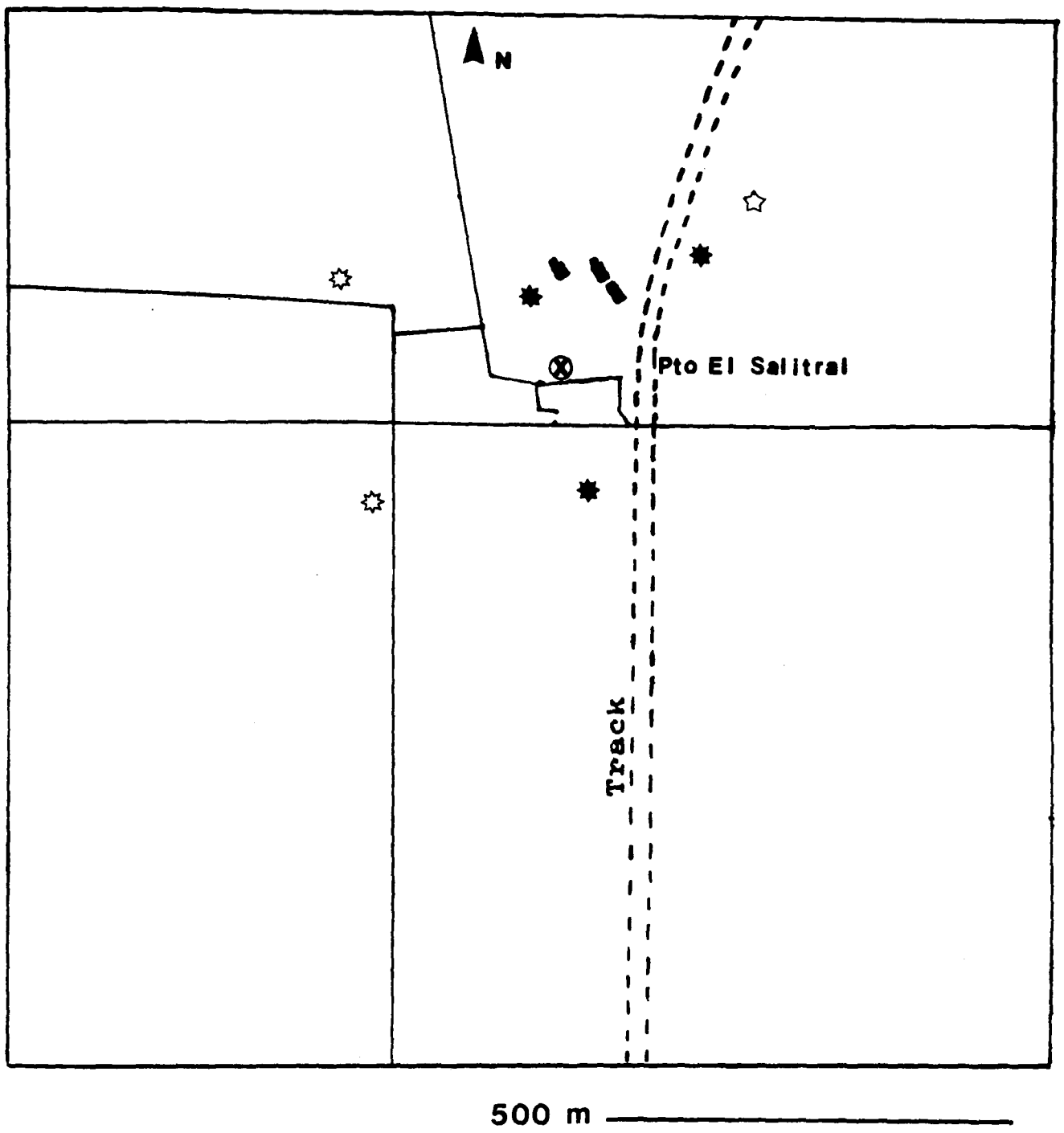


Figure 5.6.--Map of the Puesto El Salitral study area showing the location of all active and inactive dens found in 1981, 1983, and 1984. The open stars mark inactive or abandoned dens, filled stars mark active dens, and circles with x's mark windmills.

house about 300 m, were never seen to be used by pups; and one, located north and east about 100 m from Corral Den Site was occupied by two pups on 3 October 1983. This den may have been used for temporary shelter by larger pups which had wandered from Corral Den Site. In 1983, based on pup scan counts, approximately 34 pups were born here: 8 at Chicken Den, 12 at Corral Den Site, and 14 at Horse Bones Den Site (see Tables 5.11, 5.12, and 5.13). The following year, 1984, 33 pups were born here; 31 at Chicken Den and 2 at Corral Den Site. The Corral Den Site pups probably died a couple days after parturition when that den was flooded.

Other Denning Areas

A further 20 mara dens were found on the Valdés Peninsula away from my main study areas (see Figure 5.7). Four dens were located in two grassy valleys 2 km and 5 km, respectively, west of El Salitral (Puesto Centenario and Grassy Valley Dens in Tables 5.4 and 5.5). Between these dens at least three pups were produced in 1983 and at least 10 in 1984. I saw pups at all but three of the 16 other dens (see Table 5.14). Eight of these were located near estancia buildings in situations similar to my three main study areas. All eight, according to the local shepherds, were used by several pairs of maras. The four remaining dens, which I knew to be active, were all at least 1 km from a human inhabited site. Two were located 5 km north of Puesto El Salitral(see Figure 5.7) about 500 m apart in openings in the scrub. One of these dens was used by at least two pups. The other two known active dens were located near the San Jose Gulf. One was on the edge of a sand dune and had pups from one pair in it in December 1979 (when I made a two month visit to Patagonia). This den had disappeared by 1981. The other was located in sandy soil on top of a sea cliff

Table 5.11.--Sightings of each size category of mara pup at Chicken Den during the 1983 and 1984 breeding seasons.

Date	Total	Size 1	Size 2	Size 3	Size 4	Comments
			1983			
2.8.83	-	-	-	-	-	Den just dug
14.8.83	2	2	-	-	-	
16.8.83	2	2	-	-	-	
26.8.83	5	-	-	-	-	
28.8.83	3	-	-	-	-	
21.9.83	7	2	2	1	2	
27.9.83	8	-	2	3	3	
			1984			
26.8.84	-	-	-	-	-	Active?
3.9.84	1	-	-	-	1	
22.9.84	13	11	2	-	-	
28.9.84	11	-	2	6	-	
7.10.84	19	2	7	10	-	
10.10.84	15	-	2	13	-	
16.10.84	15	-	3	12	-	
19.10.84	19	3	4	12	-	
20.10.84	19	1	6	12	-	
22.10.84	16	-	7	9	-	
24.10.84	16	-	6	10	-	
26.10.84	16	-	4	9	3	
27.10.84	15	-	4	7	4	
28.10.84	15	-	4	6	5	
29.10.84	16	2	5	6	3	
2.11.84	15	2	5	3	5	
11.11.84	15	-	6	8	1	
23.11.84	11	-	2	5	3	

Table 5.12.--Sightings of each size category of mara pup at Horse Bones Den Site during the 1983 and 1984 breeding seasons.

Date	Total	Size 1	Size 2	Size 3	Size 4	Comments
			1983			
4.9.83	2	-	-	-	-	
16.9.83	10	-	7	3	-	
18.9.83	11	-	-	-	-	
3.10.83	14	3	3	7	1	
20.10.83	10	-	1	6	3	
			1984			
1984						Inactive

Table 5.13.--Sightings of each size category of mara pup at Corral Den Site during the 1983 and 1984 breeding seasons.

Date	Total	Size 1	Size 2	Size 3	Size 4	Comments
			1983			
2.8.83	-	-	-	-	-	Just Dug
13.9.83	5	-	-	-	-	
18.9.83	9	1	3	1	2	
3.10.83	9	-	-	-	-	
4.10.83	12	-	6	4	2	
16.11.83	3	-	-	1	2	
			1984			
3.9.84	4	-	-	-	-	Den flooded on 6.9.84

Table 5.14.--Sightings of mara pups at various dens during the 1981, 1983 and 1984 breeding seasons.

Den Site	Date	Number Pups	Comments
	Estancia Larreburu		
Fence	?.10.81	-	
Fence	13.10.84	3	
Fence	22.10.84	4	
Corral	1.10.81	1	
La Anita	.10.81	-	
	Puesto La Blanca		
Goose 1	6.9.83	1	
Goose 1	8.9.83	1	
Goose 1	25.9.84	-	Active?
Goose 1	28.9.84	-	Active?
Goose 2	6.9.83	1	
Goose 2	8.9.83	3	
Goose 2	20.9.83	3	
Goose 2	24.9.83	3	Birth seen
Goose 2	25.10.83	2	Size 2 Pups
Goose 2	.11.83	0	Predated by weasel
High Lagoon	.10.84	?	Active
High Lagoon	11.10.84	0	Predated
	Puesto Centenario		
Main	23.9.83	-	Active?
Main	27.9.83	1	
Main	14.10.83	1	Size 2/3
Main	18.10.84	1	
Valley	23.9.83	-	Active?
Valley	14.10.84	3	
Valley	18.10.84	-	Active?
	Puesto El Salitral		
Grass Valley	20.9.83	2	
Grass Valley	18.10.84	3	
Boliche	18.10.84	3	
Road	3.10.83	2	
	Whale Camp		
Cliff	11.10.84	1	
Cliff	12.10.84	-	Den flooded

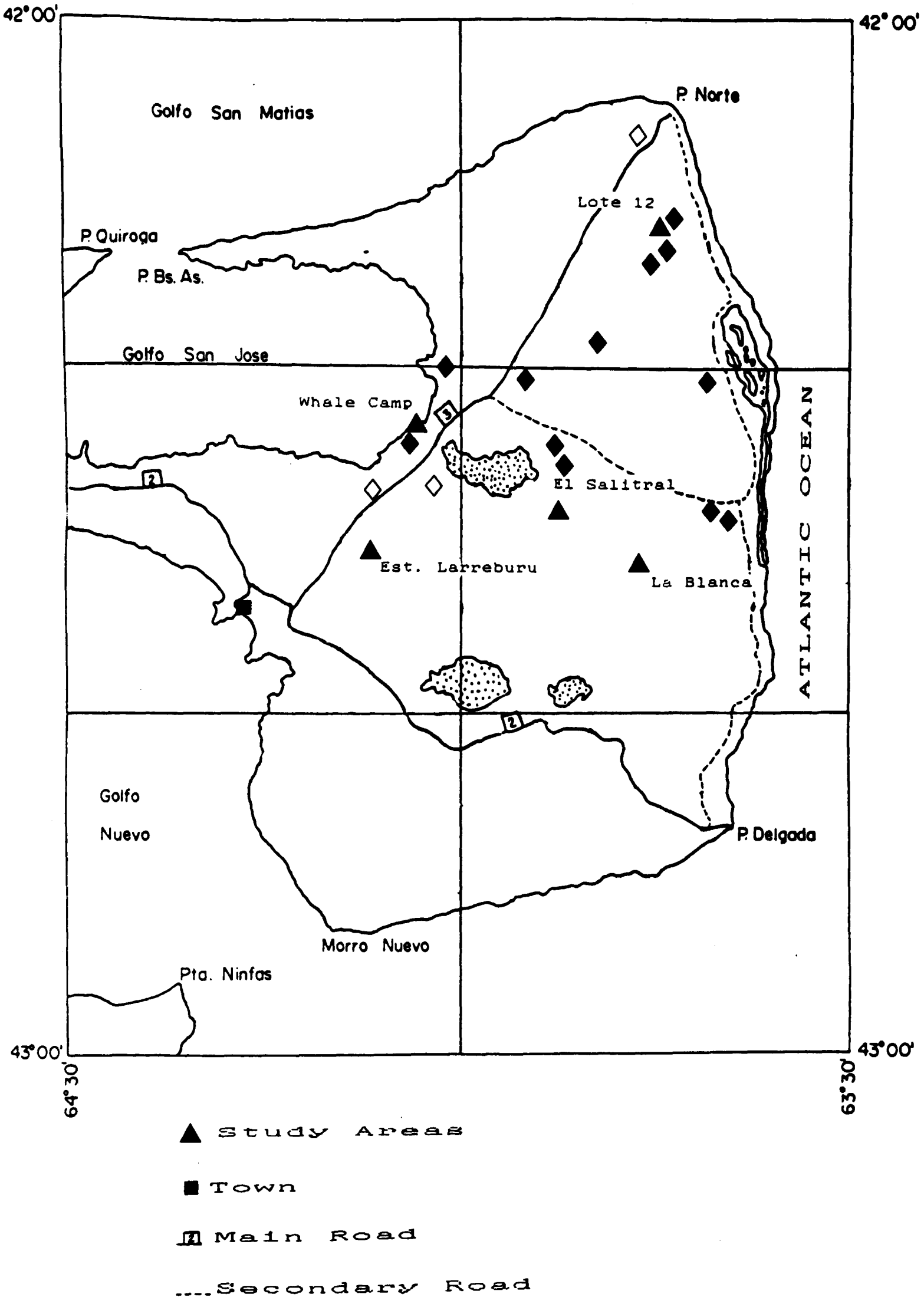


Figure 5.7.--Map of the Valdés Peninsula showing active and inactive dens found in 1979, 1981, 1983, and 1984. The filled diamonds mark dens known to have been used during at least one of these years. Open diamonds mark abandoned or inactive dens. Dens at the Estancia Larreburu, Puesto La Blanca, and Puesto El Salitral study areas are not marked.

about 30 m from the edge. One pair had two pups here in 1984 (P. Thomas, Pers. comm., Dept. Env. Studies, Univ. Calif., Davis). On 12 October the den was flooded in a rain storm and the pups probably died inside.

5.4.3 The Characteristics of Mara Dens

From Table 5.5 (see above), where the habitat of each den is described, it is clear that the dens with the largest membership sizes were all found close to sites of human habitation. This sample is biased since it was easiest to find dens near houses, however these results do suggest that there is something special for maras in the vicinity of human settlements. It is unlikely that this is related solely to specific habitat features associated with human settlements as I know of several abandoned Puestos which are surrounded by equally abandoned mara den sites. These data suggest that the presence of human activity is important to the mara pups' survival. The main benefit is likely to be protection from predators which might be hesitant to go near human sites. At all the isolated dens, at some point during the pupping season the young disappeared prior to when I expected based on the size/age of the pups. However, without additional data on mortality at dens it would be fruitless to speculate more.

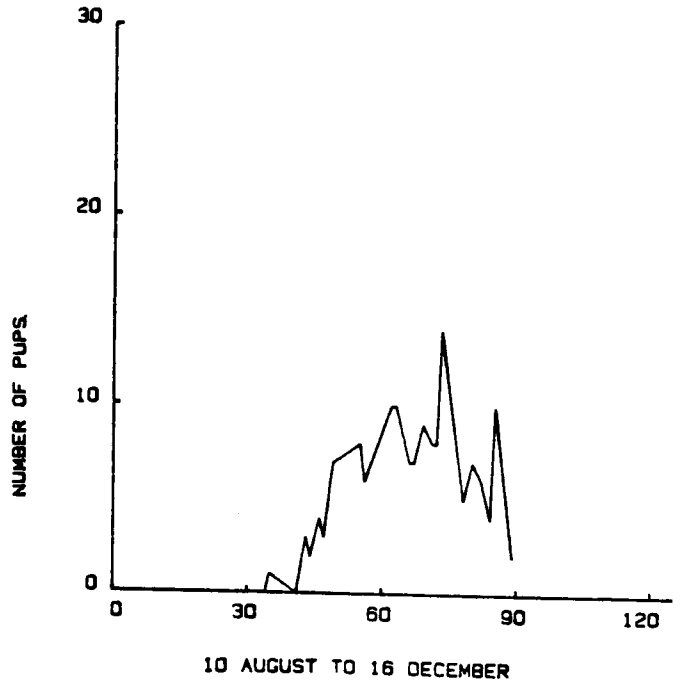
5.4.4 Seasonal and Annual Patterns of Den Usage

The seasonality of breeding has been described in Subsection 5.3.4; here the relative timing of pupping at different dens will be discussed. Figure 5.8 shows plots of the number of pups per day seen at each of the intensively studied dens during the breeding season. The timing of pupping, as reflected in the number of pups sighted at each den per day, appears to be superficially the same between

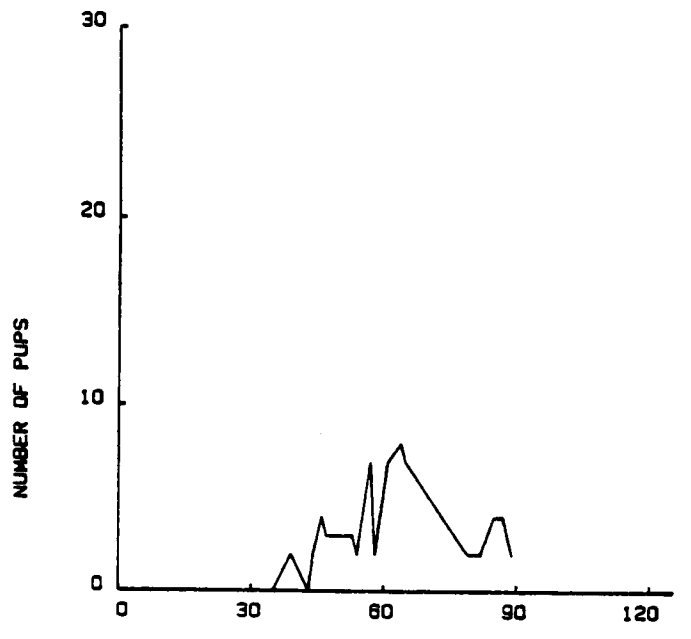
Figure 5.8 (2 Pages).

Plots of the maximum number of pups seen on different days at 9 intensively studied dens during the 1983 and 1984 pupping season. Plots are only shown for the El Salitral and Puesto La Blanca dens.

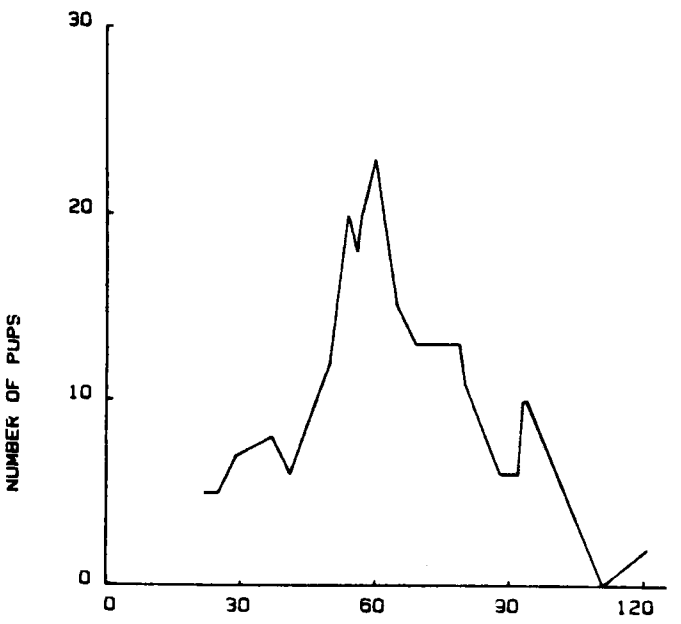
AIRPORT DEN 1981 - NUMBER OF PUPS



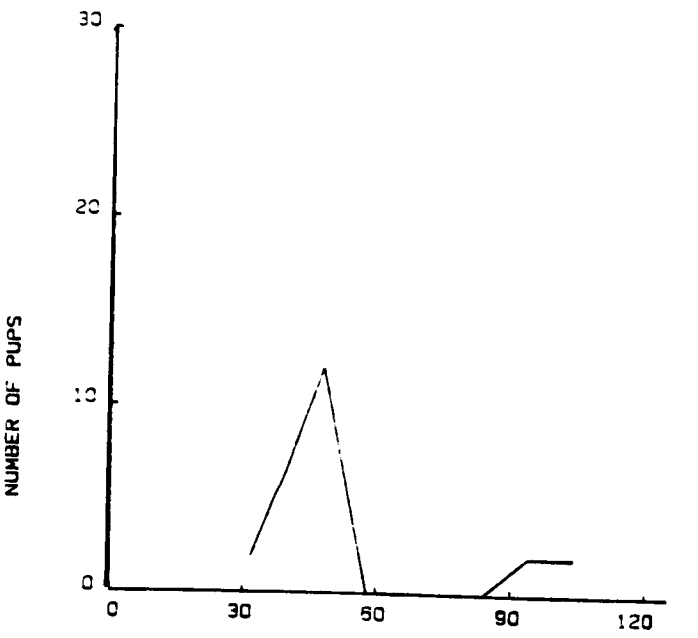
ESTANCIA DEN 1981 - NUMBER OF PUPS



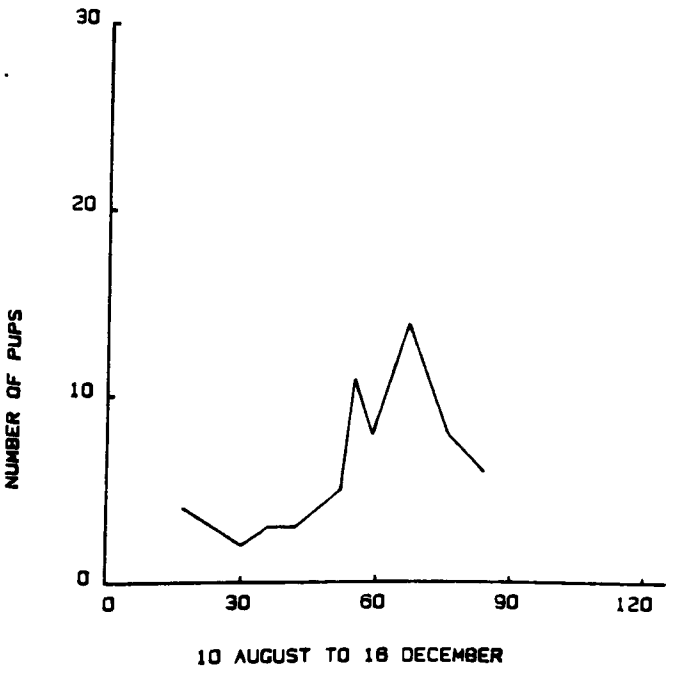
ASH DEN 1983 - NUMBER OF PUPS



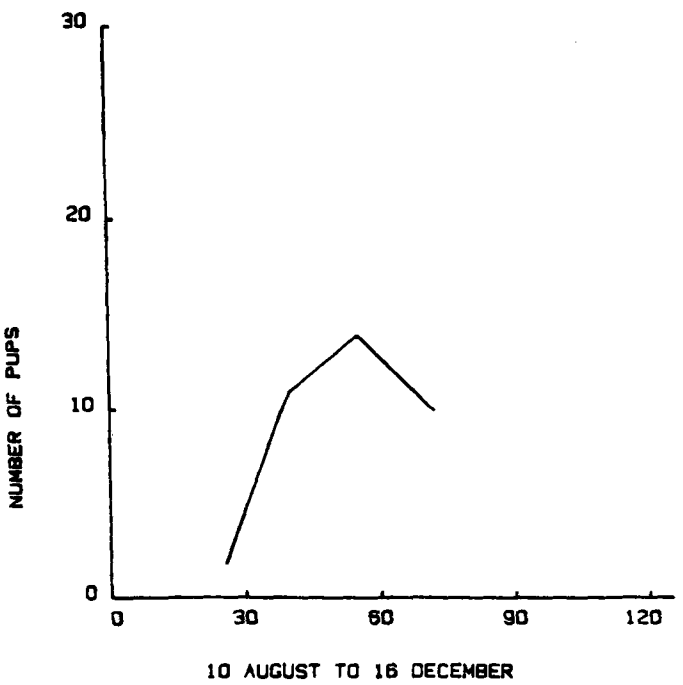
ASH DEN 1984 - NUMBER OF PUPS



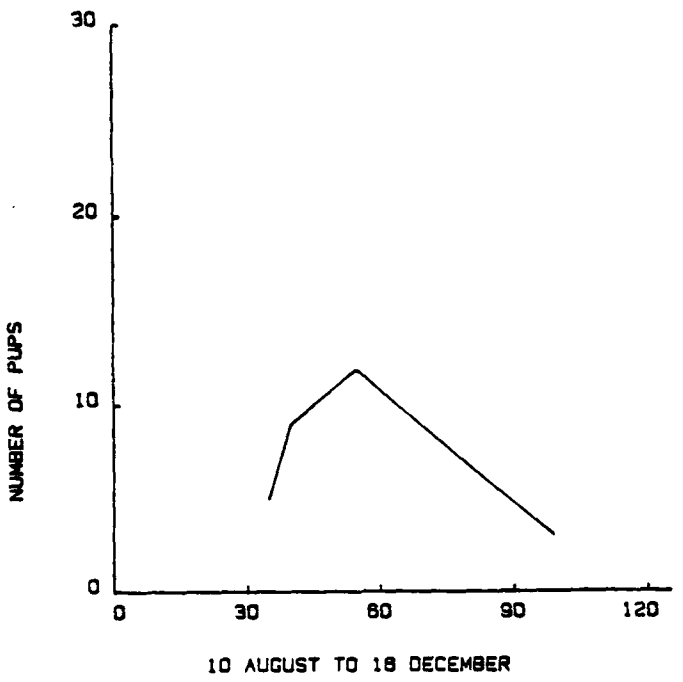
OWL DEN 1983 - NUMBER OF PUPS



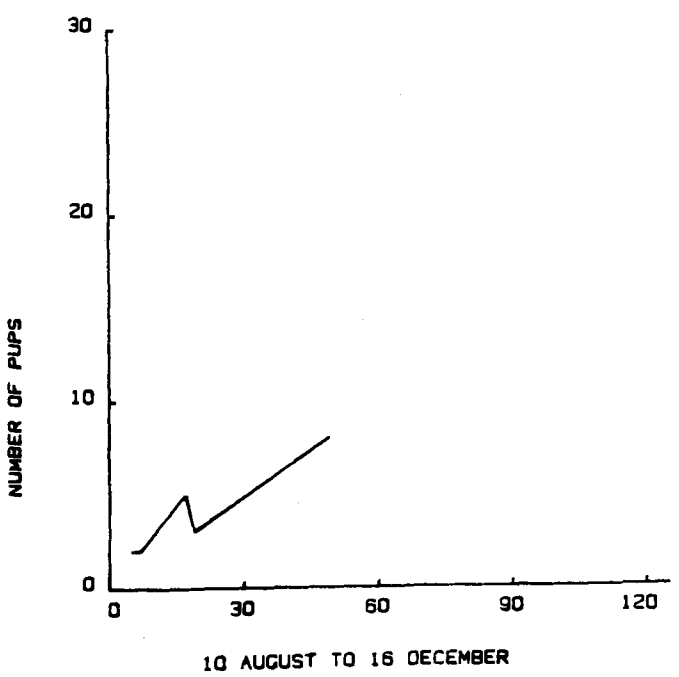
HORSE DEN 1983 - NUMBER OF PUPS



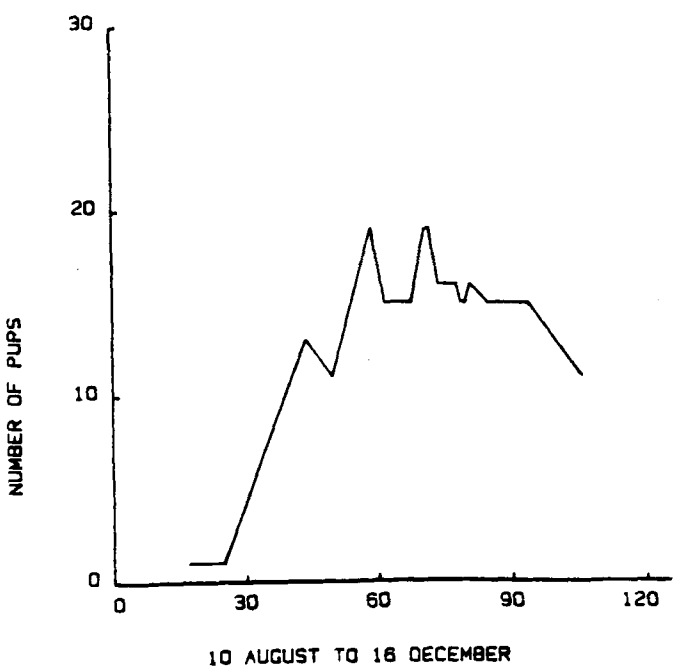
CORRAL DEN 1983 - NUMBER OF PUPS



CHICKEN DEN 1983 - NUMBER OF PUPS



CHICKEN DEN 1984 - NUMBER OF PUPS



dens. However, the plots suggest that the day with the peak number of pups varied between dens (e.g. see Figure 5.8: Ash Den Site and Owl Den in 1983). Below I will test whether there was any pattern to the differences between the timing of pupping at the different dens.

For these analyses only those dens were used where I had estimates of the number of pups at the den most of the way through the breeding season, and where there were no catastrophic die offs of pups: i.e. for 1981, Airport Den and Estancia Den; for 1983, Owl Den, Ash Den, Corral Den, and Horse Bones Den; and for 1984, Chicken Den. The data sets used were constructed from the breeding season day number (starting on 1 August) for each pup sighted in a day intensive observations were made at a den. For each den, Table 5.15 shows the mean day number and the standard deviation. Then, each of the different dens were compared using a t-test (see Table 5.15). The results of these tests showed that the timing of pupping was significantly different in 14 of the 21 comparisons made. Particularly noteworthy is that when dens were compared from the same study area within the same breeding season there were no significant differences: the timing of pupping at Ash Den Site in 1983 was not significantly different from Owl Den in 1983; and Corral Den Site was not significantly different from Horse Bones Den Site in 1983 (Ash vs Owl, $t = -1.47$, NS; Corral vs Horse, $t = 0.30$, NS).

On the basis of these results I suggest two, not necessarily exclusive, hypotheses to explain the difference in timing of pupping at the dens: (i) the differences found were due to between year variation in pupping, and/or (ii)

Table 5.15.--Means and standard deviations of pup sightings at the most intensively studied dens in 1981, 1983, and 1984 and results of t-tests comparing the timing of puppings at the different dens. Study areas: [1] Estancia Larreburu, [2] Puesto La Blanca, [3] Puesto El Salitral. Year: [1] 1981, [3] 1983, [4] 1984. Critical values adjusted for multiple t-tests using alpha/C (C = number of comparisons made).
* $P < 0.05$.

	Mean S.D.	Estancia	Ash	Owl	Corral	Horse	Chicken
Airport[1-1]	67.7 (12.3)	2.6 NS	3.25 *	3.84 *	4.56 *	7.7 *	3.94 *
Estancia[1-1]	62.5 (13.9)		0.09 NS	1.42 NS	2.88 NS	4.59 *	5.42 *
Ash[2-3]	62.3 (19.1)			1.47 NS	2.96 NS	4.98 *	6.73 *
Owl[2-3]	58.6 (17.2)				1.77 NS	2.82 NS	6.23 *
Corral[3-3]	51.4 (18.4)				0.30 NS		6.13 *
Horse[3-3]	50.3 (13.9)						10.27 *
Chicken[3-4]	73.1 (14.5)						

the differences found were due to variation between pupping dates at different denning areas (my three study sites).

1. To test the first hypothesis the data from all the dens in each year were combined: Airport Den Site and Estancia Den in 1981; Ash Den Site, Owl Den, Horse Bones Den Site, and Corral Den Site in 1983; and Chicken Den in 1984. These distributions were then compared using a Kruskal-Wallis analysis of variance which showed that the peak period of den usage by pups was significantly different between years ($H = 133.3$, $df = 2$, $P < 0.005$).
2. To test the second hypothesis the data for each den site studied in 1983 were combined for each study area: Owl Den and Ash Den at La Blanca ($\bar{x} = 61.7$); and Horse Bones Den Site, Corral Den Site, and Chicken Den at El Salitral ($\bar{x} = 46.6$). The data for each study site were then compared using at t-test. As above, these distributions were found to be significantly different showing that the peak of den usage by maras at the different study areas occurred at different times ($T = 7.52$, $P = 0.0000$).

From these results it appears that the timing of pupping varies significantly between years. It seems likely that climactic conditions in different years may be responsible for this variation. The finding that pairs in one area tend to pup together, irrespective of the pupping at other areas in the same season, suggests that there must be advantages to individual pairs in synchronizing the birth of pups at the same study area (discussed in Section 5.8).

5.4.5 Distribution of Den Membership Sizes

At the 17 intensively observed dens (counting dens watched in several years separately) the estimated number of pups varied from 1 to a maximum of 33 (see Table 5.4). Using Formula 5.1 to make the calculations, dens were used by

between 1 and 22 adult pairs of maras. The mean number of pups at a den was 10.94 (± 9.46, median = 16), and the mean number of adult pairs at a den was 6.65 (± 6.13, median = 11; see also Table 5.4). Figure 5.9 is a histogram of the distribution of membership sizes amongst these 17 dens. Clearly the distribution of den membership is not normal. There is, however, a sampling problem with these data as, although I tried to find as many dens as possible, it was easier to find dens located near human settlements (see above). It seems certain that I under-sampled the numerous dens with small membership sizes which appeared to be scattered throughout the scrub. With such uneven sampling it is difficult to draw any firm conclusions other than that most dens appear to be used by 1 to 9 pairs (65% of pups born) with a few dens having much larger memberships.

5.4.6 Breeding Success and Mortality

Estimating the number of pups at a den and obtaining reliable estimates of mortality is difficult (see Subsection 5.4.1), so results presented here should be viewed with circumspection. Table 5.16 summarizes the number of pups born at each of the dens observed and shows estimates of the percentage of pups which died prior to reaching the age of independence (size category 4) from the den. Evidence of predation at the various dens are summarized in Table 5.17. Other potential causes of mortality include disease and hypothermia. From these results it is apparent that mortality can be very high. Of the nine dens upon which I had data, mortality varied from 21% to 100%. Of an estimated 107 pups born, fully 50 appeared to have died before reaching size category 4.

Every den studied used by less than 10 pups had 100% mortality according to my estimates, suggesting that mortality may be closely tied to den membership size. To test what effect den size has on mortality the percent

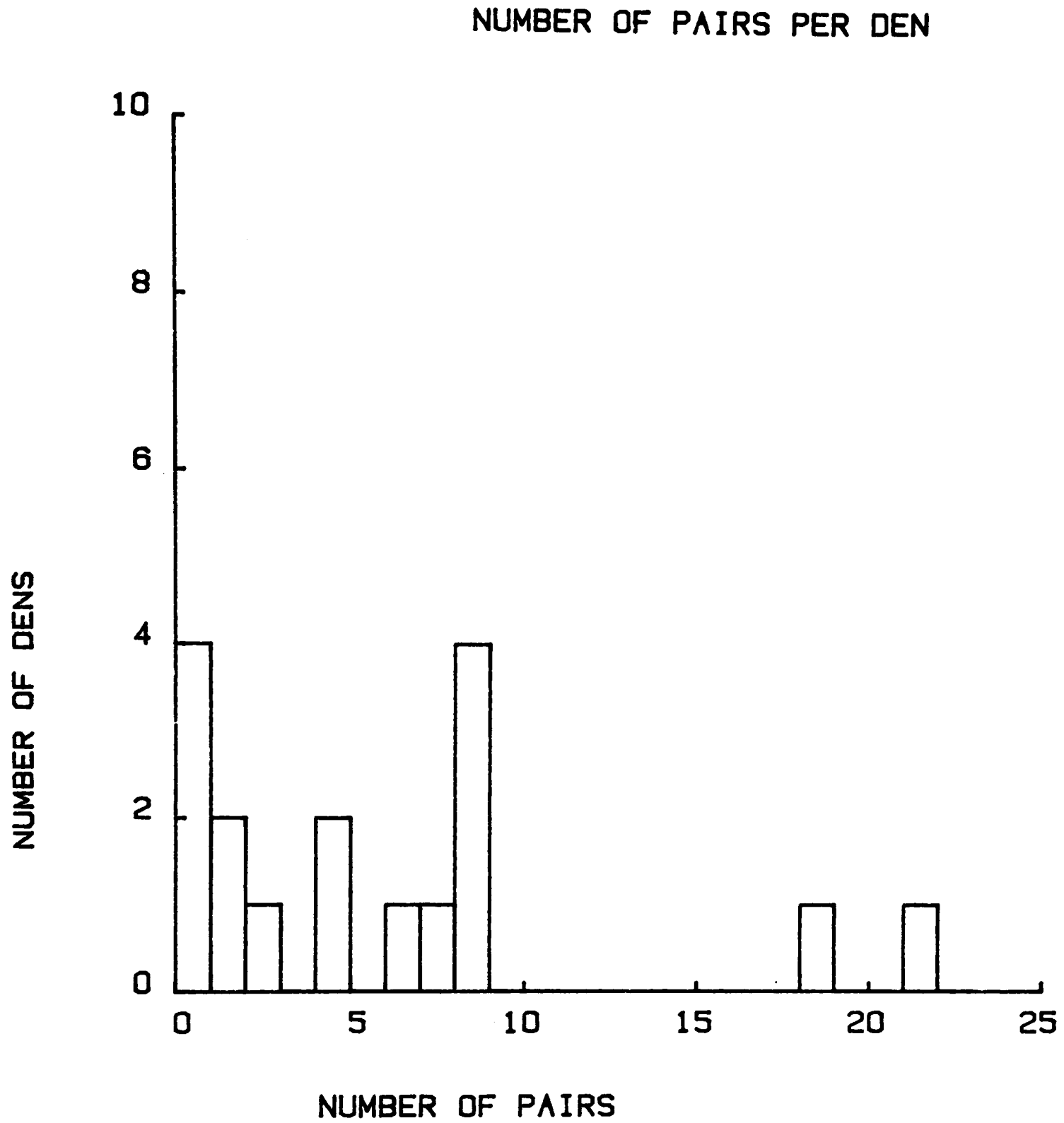


Figure 5.9.--Histogram of the distribution of the number of females (pairs) which gave birth to pups at 17 (counting dens observed in different years independently) intensively observed den sites.

Table 5.16.--The number of adults and pups, and the estimated percent of pups which died prior to reaching the age of independence from the den at each of the intensively studied den sites.

Den Site	Year	Number Adult Pairs	Number Pups	Percent Pup Mortality
----------Estancia Larreburu----------				
Molino	1981	9	14	?
Airport	1981	9	14	?
Estancia	1981	5	8	?
Corral	1981	1	2	100
Fence	1981	1	2	?
La Anita	1981	2	4	?
----------Puesto La Blanca----------				
Ash	1983	22	33	42
	1984	9	14	86
Owl	1983	9	15	21
	1984	3	5	100
Goose I	1983	1	1	100
Goose II	1983	2	4	100
----------Puesto El Salitral----------				
Chicken	1983	5	8	?
	1984	19	31	23
Corral	1983	7	12	?
	1984	1	2	100
Horse Bones	1983	8	14	?

Table 5.17.--Observations and other evidence of predation on mara pups at breeding den sites.

Predator	Number Events	Evidence of Predation
Patagonian Weasel *Galictus cuja*	1	Two seen in vicinity of den immediately prior to the disappearance of pups there.
Hairy Armadillo *Chaetophractus sp.*	2	Fresh armadillo tracks and faeces at time when pups disappeared at two dens. Scrap of fur and bones found near faeces.
Red Backed Hawk *Buteo polysoma*	1	Stooped unsuccessfully on pups by den.
Patagonian Gray Fox *Dusicyon griseus*	1	Foxes seen in the vicinity of a den at the same time that pups disappeared.
Domestic Dogs *Canis familiaris*	2	Seen chasing maras at dens. Found one adult mara killed by a dog. Lots of word of mouth evidence.
Domestic Cats *Felis cattus*	1	Saw a domestic cat stalking pups at a den unsuccessfully.
Humans	many	Lots of evidence from talking to ranchers.

mortality figures for these nine dens were correlated with the number of pups estimated to have been born at the dens. The result was a significant negative correlation ($r = -0.844$, $df = 8$, $P < 0.01$) suggesting that as den size increases mortality rates drop. To test if the correlation found was due to differences between dens with small memberships (under 10 pups) and dens with large memberships (10 or more pups) I correlated the mortality and den membership size estimates for the four dens used by more than 10 pups. No significant differences were found ($r = -0.415$, $df = 3$, N S). Although these data are sketchy, the results suggest that there may be some lower limit to den membership size, perhaps around 10 pups, below which dens cease to be viable. Whether this apparent effect is due to predation, some factor related to disease transmission, or hypothermia (perhaps a minimum number of pups are needed to keep the group warm in the den at night) is unknown.

5.4.7 Associations Between Dens

The question addressed in this subsection is what is the nature of the relationship between maras using different dens located close together. As described above, at each of my study areas maras used a number of dens, often only 100 m or so apart. Below I summarize a range of points:

1. The data on the timing of breeding shows that pupping at the dens at each of my study areas **was** synchronized within years.
2. Pairs sometimes move their pups from one occupied den to another: in 1981 pups were moved from Estancia Den to Airport Den after the latter den was disturbed. Several times in subsequent years I suspected that pups were moved between dens, but without marked animals I could never be sure.

3. At the El Salitral study area all the maras used one den site in 1984, while during the 1983 breeding season they used three different dens. In both years the number of pups produced were approximately equal (37 in 1983 and 33 in 1984).
4. There is considerable spatial overlap between the home ranges of some animals using different dens at the same study area. ELF and PAM used different dens and their ranges overlapped 48 ha (approximately 28% of each animal's range, see Chapter 3). On the other hand, PAM and SYF used the same dens and their ranges overlapped 26.25 ha (approximately 11% of both animal's ranges, see Chapter 3). One marked female might be seen grazing in the vicinity of one den while her pups were located in another several hundred meters away.
5. At each of my study areas the nearest other known concentrations of maras were several km away. Furthermore, in my radio tracking studies (see Chapter 3) I never found animals moving more than 2 or 3 km from their denning site suggesting that there is little interchange between maras at different denning areas.
6. Lastly, at the start of the breeding season maras moved around considerably, apparently investigating the various dens. One of the best examples of this I have seen is summarized in Section 5.3 (above).

From the above it is clear that pairs using one study area are not subdivided into spatially segregated groups with some animals using one den site and others another site. These results suggest that there is considerable interchange between animals using different dens in the same area, and that the animals using dens located close together may form part of a larger social group or community (possibly with many of the individuals closely related). Table 5.18 summarizes the number of pups at each of three study sites over three years of field work. The number of pups born at a study site varied from

Table 5.18.--Comparison between number of pups born and pup mortality at different study sites over three different years. Estancia Larreburu data does not include the Molino Den Site since it was probably too far away for the animals there to associate with the maras nearer the Estancia. The Grassy Valley and Centenario dens are not included with the Puesto El Salital data, nor the Far Lagoon den with the La Blanca date, for the same reasons.

Study Site	Year	Number of Dens Used	Estimated Number of Pups Born	Minimum Pup Mortality
Estancia Larreburu	1981	5	30	?
Puesto La Blanca	1983	4	53	23
Puesto La Blanca	1984	2	19	17
Puesto El Salitral	1983	3	37	?
Puesto El Salitral	1984	2	33	9

19 to 53 with a mean of 34.4 pups (± 12.36, median = 36). The estimates of pups born per year per study site are similar suggesting that these could represent a general herd size for maras breeding around small human settlements. The scattering of dens elsewhere in the scrub, probably used by fewer pairs, suggest that another denning strategy may exist adapted to areas without the benefits (as yet undetermined) of breeding near a human occupied house. Without more data though, further speculation would be unproductive.

5.5 Care of the Young

Mara females nurse their offspring for about 11 weeks (see Section 5.3). This is one of the longest lactation periods in rodents with only two species, both caviomorphs, known to have longer lactation periods: *Hydrochoerus hydrochaeris* has a lactation period of 16 weeks, and *Dasyprocta aguti* has a lactation period of 20 weeks (Weir, 1974; and Eisenberg, 1981). This long lactation period, combined with the lengthy 100 day gestation period, are typical of the caviomorphs which have slow rates of development compared to the myomorph and sciuromorph rodents (Eisenberg, *Op. cit.*). Such a long period of nursing implies that the parent-offspring bond is strong (at least long lasting); and, further, suggests that parental care, in addition to nursing, may be important for pup survival. In this section the nature of mara parental investment in offspring will be described.

I have little data on nursing and parental care once the pups have left the area of the den, so results presented here will focus primarily on the behaviour of mara adults and pups at the intensively observed den sites. The following aspects of how maras care for their young will be discussed: (i) how often parents visit the den and how long

they stay when visiting; (ii) how much do females nurse their young, how this changes as pups grow, and how often do females suckle pups which are are not their own; and (iii), aside from nursing pups, what do adults do at the den and how does this vary between the sexes (see also Chapter 4)?

5.5.1 Methods

Most of the results presented below are based on data collected using the den scan data collection protocol (see Chapter 2). To extract and reformat data several BASIC and FORTRAN programs were written. Three main data subsets were used: (i) arrival and departure of focal pairs at the den, (ii) continuous focal pair sampling, and (iii) instantaneous scans of all adults and pups at the den made at 15 min intervals.

5.5.2 Visits to the Den

Females visit the den during the day to nurse and otherwise care for their offspring. In this subsection results summarizing the duration of time over which females visit the den, the frequency of visits, and how long females stay at the den when visiting will be presented. In general, for these analyses, results for the females and for the pair are similar since males usually accompanied their mates to the den (but see below).

Intensive observations were made at dens between 7:00 in the morning and 20:00 in the evening. Mara adults were never observed visiting dens at night. No significant differences were found in the number of adults (as recorded in den scans) at the dens in the different hours of the day between 8:00 and 20:00 using the Kruskal-Wallis analysis of variance ($H = 14.66$, $df = 10$, NS).

Females visited their pups at the dens for a period of something over 40 days (see Table 5.19). Mara females PJF (in 1983) and LRF (in 1981), the animals for whom I had the best data, were observed nursing pups at dens over periods spanning 44 and 43 days respectively. In PJF's case this is a minimum estimate since when she was first sighted with pups they were in size category 2, and hence must have been at least a week old. Dubost and Genest (*Op. cit.*), in their study in captivity, report that pups were restricted to the area immediately surrounding the den for the first 6 weeks (42 days) of life, which corresponds well with these results.

In captivity, from six weeks old and on mara pups spent the day away from the den with their parents, but continued to return to the den at night for a further 5 weeks (Dubost and Genest, *Op. cit.*). My observations suggest that the same pattern occurs in the wild: at nightfall it was common to see large (category 4) pups running up to and entering a den. Pups of this size were seldom observed at dens with adults. In the morning, parents of size 4 pups would call their presumed young (only 1 or 2 pups would respond) out of the den with a whistle while still out of sight in the scrub (this type of interaction was observed on 4 occasions). During the day, groups of two adults and one to three large pups were often found scattered throughout the scrub within 200 m of a den site.

Breeding female maras appeared to visit the den at least once every day. Table 5.19 summarizes the results on 7 recognizable nursing females. Of the 6 females on whom detailed data were available, all but one visited and nursed their pups every day on which the den was observed during their period of den usage. PJF did not visit the den on 2 days during the 10 days (spanning 44 days) for which I

Table 5.19.--Frequency of visits and the span of days over which mara females nursed their pups at the den.

Den Used	Mara Name	First Seen	Last Seen	Number of Days Den Watched	Number of Days Den Visited	Span of Days
Air	LRF	29.9.81	11.11.81	?	?	43
Ash	ELF	15.9.83	8.10.83	7	7	24
Ash	GCM	15.9.83	28.9.83	2	3	14
Ash	PJF	28.9.83	10.11.83	10	8	44
Ash	TEF	4.10.83	17.10.83	5	5	14
Owl	PUF	3.10.83	15.10.83	3	3	13
Owl	SLF	15.10.83	24.10.83	2	2	10

watched the den. However, on these two days she seemed to have temporarily moved her pups to another burrow located about 100 m away from Ash Den Site in the scrub. On 21% of the days (6:28) female maras visited the den more than once. On every one of these days, however, the first visits had been cut short by some disturbance (usually of human origin).

The length of time that females stayed at the den when nursing pups varied from 5 mins to as long as 9 hrs (Figure 5.10). Of 71 visits to dens by females who nursed pups during the visit the mean length of stay at the den was 1.08 hrs (± 1.17). An analysis of variance showed that there was no significant difference between the length of stay at the den by females nursing different size pups ($F = 0.05$, Factor df = 3, Error df = 67, NS).

5.5.3 Direct Care: Nursing the Young

Normally females nurse only one or two pups at a time, though occasionally as many as 4 pups may suckle simultaneously. Within a given nursing session a female may, for short times, nurse pups which are not her own. Females have as many as 8 teats (Weir, 1974), although I never found more than 6 on a captured animal and never saw more than 4 being used by pups. When several pups are suckling simultaneously they may fight over access to a particular teat (usually the upper pair), suggesting that some teats produce more milk than others. There is no teat order, as has been described in other caviomorphs such as *Myoprocta pratti* (Kleiman, 1974); and a pup will move from teat to teat: seldom staying at one for more than a minute.

Data were collected on 106 visits to dens by nursing females (using the EVR data protocols and an Epson HX20 portable computer, see Chapter 2 and Appendix B). Estimates of nursing times were obtained for 71 of these visits. Females were judged to be nursing when one or more pups were

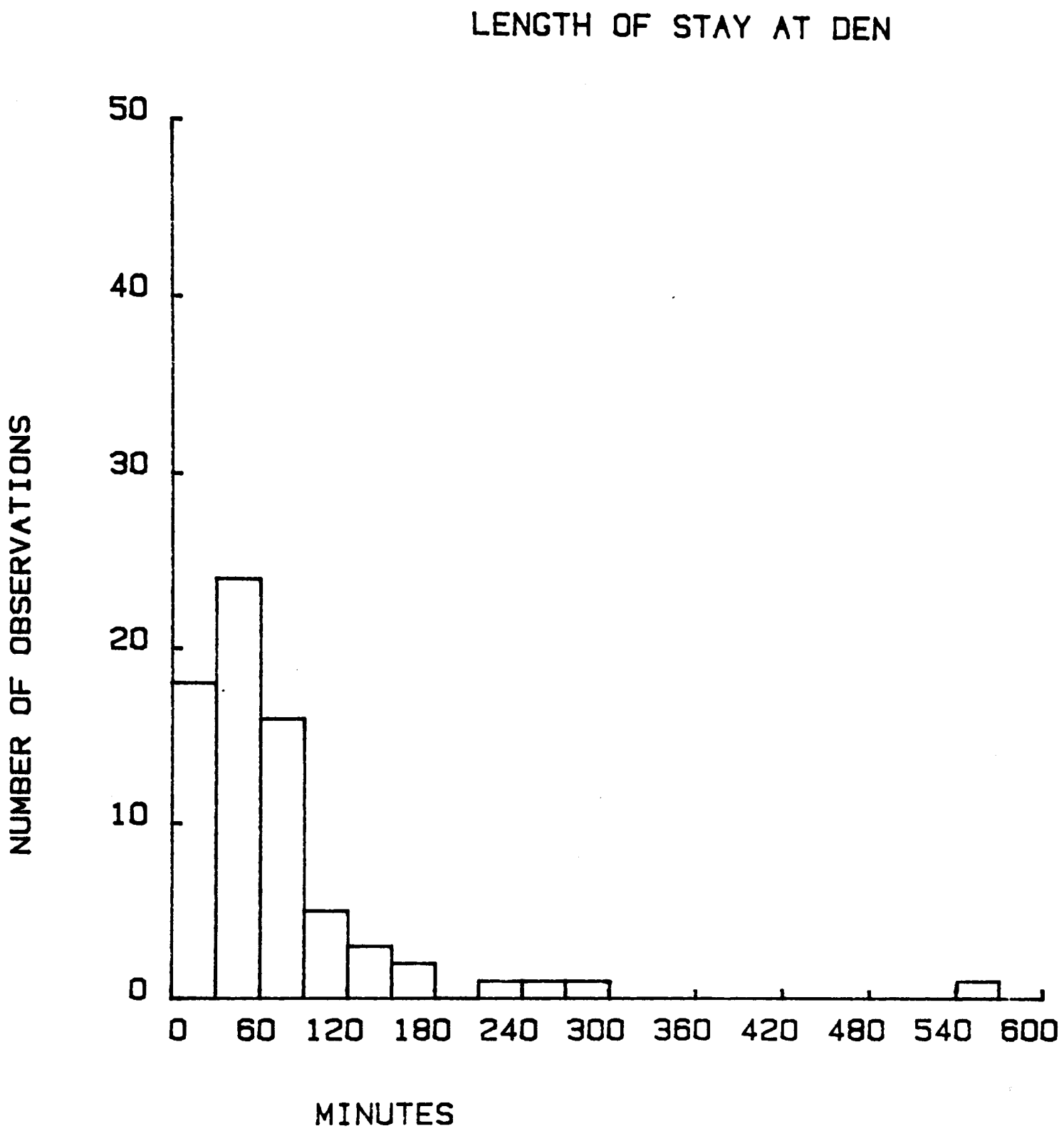


Figure 5.10.--Histogram of the length of time females stayed at den sites when visiting to nurse their pups. Results compiled from 71 den visits at the La Blanca and El Salitral den sites during the 1983 and 1984 pupping seasons.

sucking on a teat. As soon as the last sucking pup lifted its mouth from a teat the clock was stopped. Of these 71 nursing sessions, the average time females spent nursing at least one pup was 0.349 hrs (± 0.288, median 0.27). The minimum and maximum time a female was observed nursing during a visit were, respectively, 0.009 hrs and 1.31 hrs. Nursing would typically be divided into a number of bouts since both females and pups periodically broke off the suckling. The mean number of bouts per session was 9.21 (± 8.28), and the mean bout length was 0.04 hrs. The maximum number of bouts recorded in a session was 34. Using analysis of variance, no significant differences could be found between the time females spent nursing different size/age pups (Source df = 3, Error df = 67, F = 0.25, NS). However, though pups seemed to be sucking whenever they were attached to a teat, nursing time does not necessarily equate directly with the amount of milk obtained by the young: e.g. brown rat pups can remain attached to the mother's teats for long periods even though milk removal is limited to brief intermittent milk ejections (Cross, 1977).

Females, however, often nursed more than one pup at a time. For the 71 nursing sessions monitored, the mean total time individual pups were suckled in one session was 0.513 hours (± 0.456, median = 0.392). The maximum length of time pups were suckled was 2.6 hrs and the minimum was 0.026 hours. These results come from the total time individual pups were nursed by a female during a session: e.g. if two pups were nursed for 0.25 hours simultaneously the total suckling time would be 0.5 hrs. These are over-estimations of the length of time females' nursed their own pups since they include suckling time of pups other than their own.

A serious problem for these analyses was that I was unable to identify pups individually except on the basis of size. Hence, I had great difficult in determining the proportion of the time females spent nursing their own pups versus those of other females. There were usually, however,

pups of various size categories at the dens. Thus, I could test whether females nursed pups of one size significantly more (taking into account the different number of pups of each size category) than pups of another size during a given visit to the den. A Mann-Whitney test was used to compare the amount of time the size of pup nursed most by the female was suckled ($\bar{x}$ 0.480, median = 0.384) against the amount of time pups of other sizes were suckled ($\bar{x}$ 0.0324, median = 0.0). The test showed that these distributions were significantly different ($N = 71$, $W = 7381.0$, $P < 0.000$), and thus that females nursed one size category of pup more than others on any given den visit.

From this result it is clear that females were discriminating between pups, at least on the basis of size, and were thus allowing some pups to suck more than others. Below, in Subsection 5.5.5, I will discuss the mechanism by which females probably identify their offspring, and also present results showing the considerable effort that females make to prevent some pups, presumably not their own, from gaining access to their teats.

To reduce the over-estimation of suckling time due to the inclusion of time when pups not of the same size as a female's own were nursed, data on the size category of pup which a female nursed most during a given session were used to obtain the following results. Females suckled pups that were the size of their own presumptive pups for a mean of 0.48 hrs ($\pm$ 0.437 hrs, see Figure 5.11). Since this is the total time suckled, to arrive at an estimate of the length of time for which each pup was nursed in a session the litter size data obtained by Dubost and Genest (1974) were used to derive the following formula (Formula 5.2) to estimate the length of time each pup was suckled.

Figure 5.11 (Overleaf).

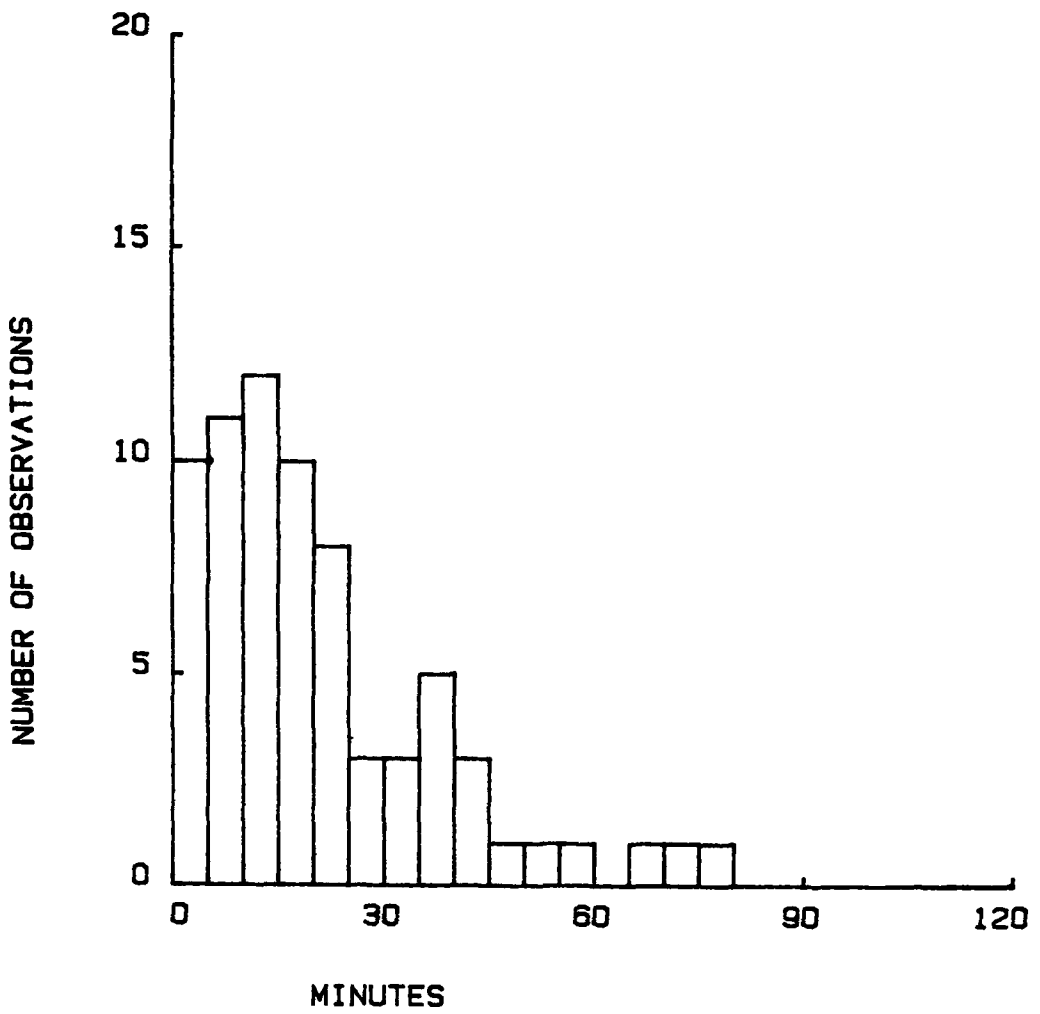
Histograms summarizing the amount of time: females spent nursing pups, pups were suckled overall (accounts for females nursing more than one pup at a time), and individual pups suckled. Data taken from 71 den visits monitored at the La Blanca and El Salitral study areas during the 1983 and 1984 pupping seasons.

A. Total time females spent nursing pups.

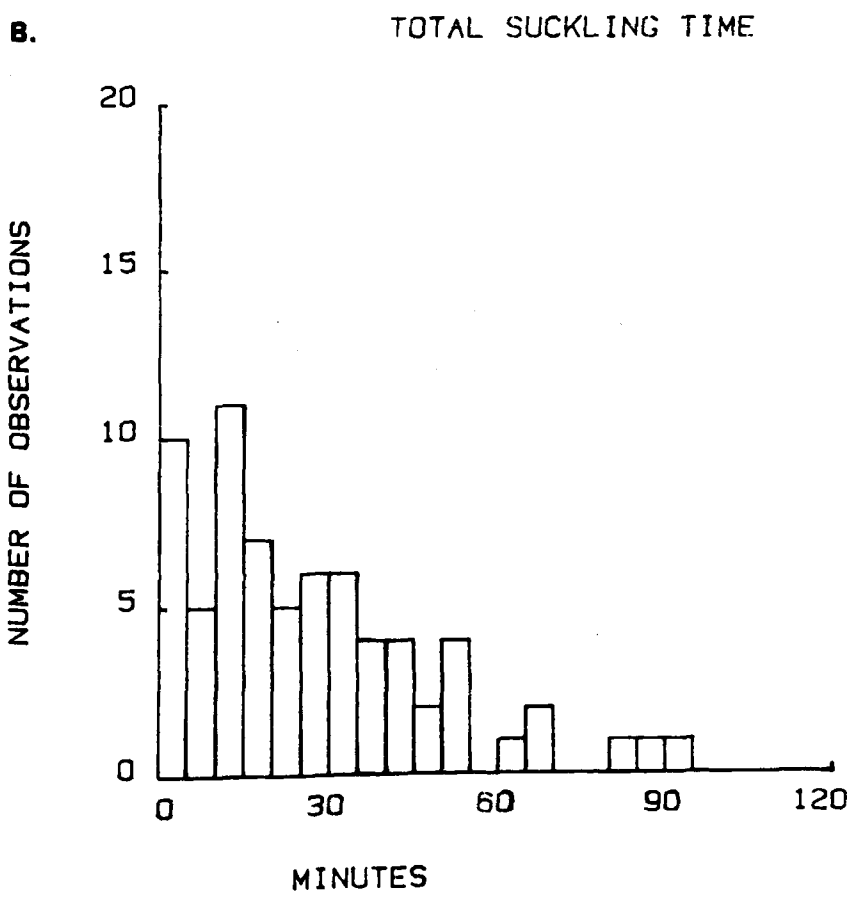
B. Total time pups were suckled.

C. Total time individual pups, presumed to be the nursing females, were suckled.

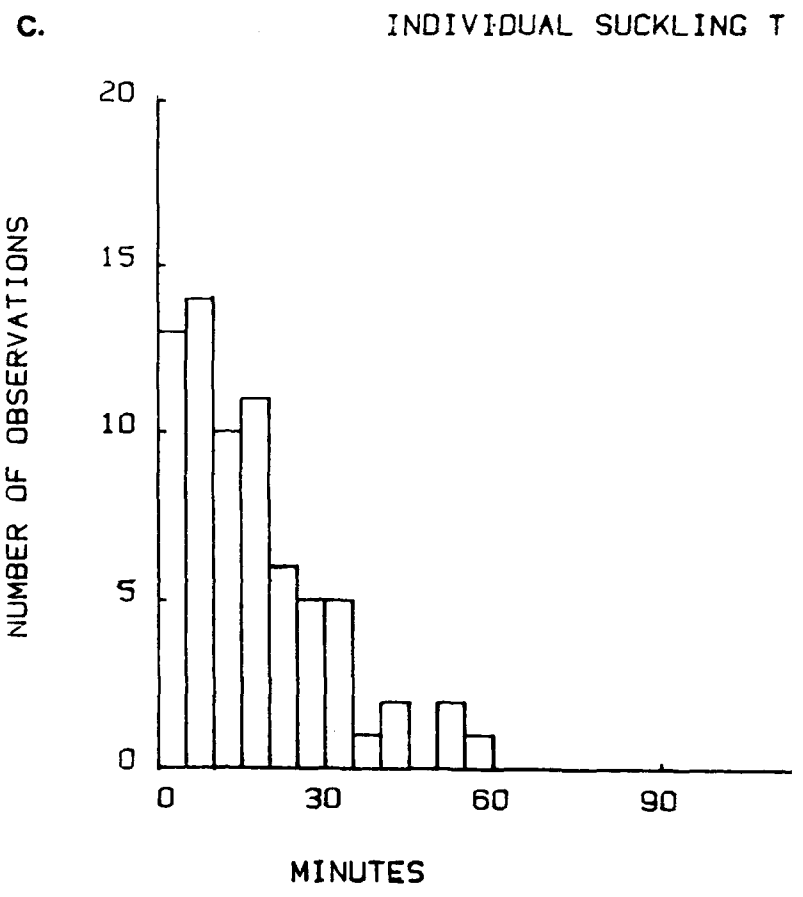
A.


TIME FEMALES SPENT NURSING PUPS
NUMBER OF OBSERVATIONS
20
15
10
5
0
0
30
60
90
120
MINUTES

B.


TOTAL SUCKLING TIME
NUMBER OF OBSERVATIONS
20
15
10
5
0
0
30
60
90
120
MINUTES

C.


INDIVIDUAL SUCKLING T
NUMBER OF OBSERVATIONS
20
15
10
5
0
0
30
60
90
MINUTES

Formula 5.2

IPS = Individual Pup Suckling Time

TOTS = Total Time Main Size Pup Suckled

$$IPS = \frac{(0.70 * TOTS)}{2} + (0.25 * TOTS) + \frac{(0.05 * TOTS)}{3}$$

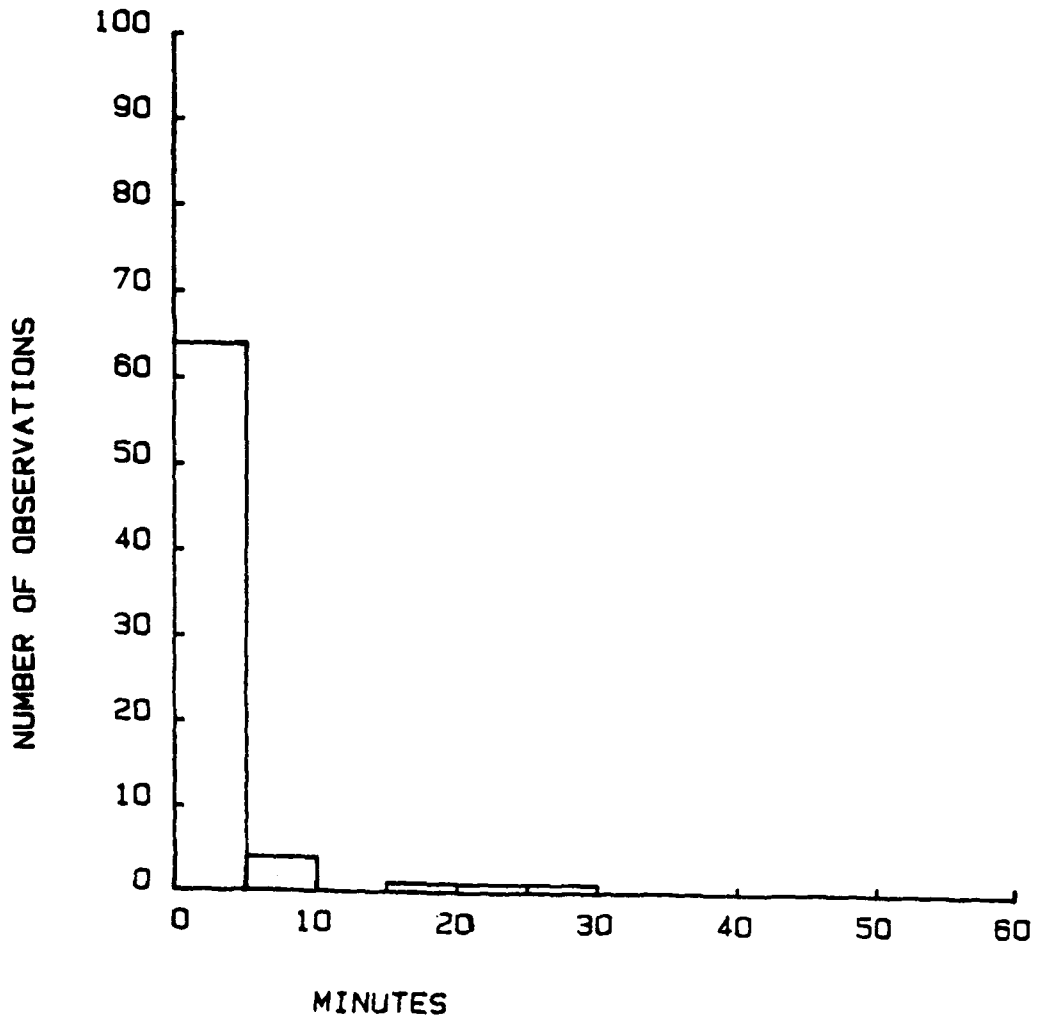
For the 71 nursing sessions on which suckling data were collected, individual pups were nursed by their 'mothers' a mean of 0.296 hrs (± 0.269 hrs) per female visit to the den (see Figure 5.11). A one-way analysis of variance was made on the suckling time data to see if there were any differences in the amount of time each age category of pup suckled, but no significant differences were found (Source df = 3, Error df = 67, F = 0.25, NS).

The simplest estimate of how much time females were sucked on by pups other than their own can be made by considering how long they nursed pups not the same size as their putative pups. The mean length of time which non-main size pups were suckled was 0.0324 hrs (± 0.0828) with a maximum of 0.482 hrs (see Figure 5.12). However in 55% (39:71) of the nursing sessions no non-main size pups were suckled at all. The proportion of the time females suckled main size pups was 0.94 (± 0.11), a substantial proportion of the total (see Figure 5.12). However, this is probably an overestimate since suckling time of main size pups which were not the females' own are included in this estimate.

A significant positive correlation was found between the amount of suckling of non-main size pups and the number of pups at the den on a given day (r_s = 0.458, $P < 0.01$). It is clear from these results that females nurse principally one size of pups on a den visit (presumably their own pups) but that, at least occasionally, they allow pups other than their own to suck substantially.

Maras differ in this from some of their close relatives, many of which practice communal suckling: e.g. *Microcavia australis*, *Galea musteloides*, *Hydrochoerus hydrochaeris* (Rood, 1972; Macdonald, 1981). In these three

A.



B.

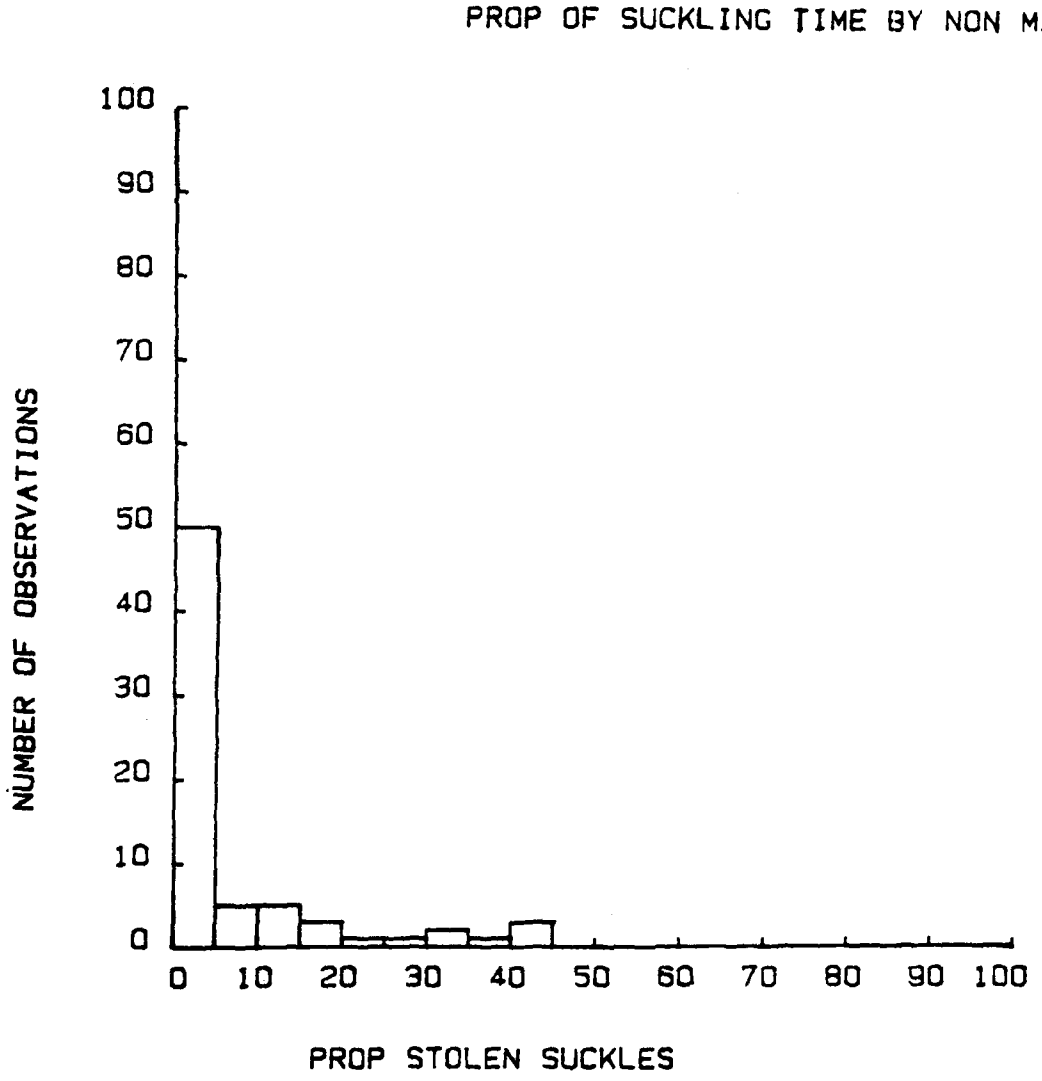


Figure 5.12.--Histograms of the (A) amount of time pups presumed not to be a given females were nursed, and the (B) proportion of the total suckling time these pups were nursed.

species suckling does not appear to be particularly prolonged. However, in *Cavea aperea*, where the nursing period is prolonged and thus presumably more important for pup survival, females behave aggressively towards offspring of other females which try to 'sneak' sucks (Rood, 1972).

5.5.4 Behaviour of Pups Towards Females

As mentioned in the previous sub-section, pups will at least occasionally be suckled by females which are not their mothers. Observations in the field suggest that females make a considerable effort to prevent pups from 'stealing' milk, while at the same time some pups make a considerable effort to obtain milk from females who are not their mothers. When a female approached a den with a large membership it was common for her to be harassed by several pups: up to seven or more would crowd around her all trying to gain access to a teat (see Figure 5.13). Aside from mobbing adults, pups would often try to suck stealthily: sneaking up behind a nursing female and attempting to latch on to a teat near one of her own offspring, apparently in the hope that the female would not detect its presence. Female responses to these pups could be quite violent and included moving away from, chasing, and even biting and shaking a pup (see Figure 5.13, and Table 5.20). Females may sometimes seriously injure pups: on one occasion I saw a female pick up a pup and toss it 0.5 m away, and a number of pups had badly cut up ears presumably from being bitten by females.

Of the 106 nursing sessions recorded, females were harassed by pups to the point of acting aggressively towards them a total of 796 times--a mean of 7.51 times per den visit (see Table 5.20). Nursing bouts were interrupted a mean of 4.11 times, (± 6.12) with one female being interrupted 34 times. With an average of 9.21 bouts (± 12.2) per nursing session (see Subsection 5.5.3) 45% of the

Figure 5.13 (Overleaf).

Photographs illustrating typical interactions between nursing females and pups while at the den.

A Pups mobbing a newly arrived female.

B Female chasing a pup which had been trying to gain access to a teat.

Table 5.20.--Summary of the responses of adult females to the harassing behaviour of mara pups while at the den.

Number of Occurrences	Reaction of Females
425	Chase pup
120	Lunge at pup
80	Bite Pup
171	Move away from pup

nursing bouts were interrupted by the attempts of another pup to gain access to a teat. Outside nursing, females were harassed enough to respond aggressively, either by biting or chasing a pup, a mean of 5.04 times ($\pm$ 6.189, maximum 35) per visit. There was a significant positive correlation between the number of pups at the den and the number of nursing interruptions (r_s = 0.571, N = 70, P < 0.01).

5.5.5 Pup Identification by Females

Females seem to use both smell and sound to identify their own offspring amongst the herd of pups at a den. As mentioned above, when mara pairs arrive at the den the females are often heard to whistle shrilly several times. Whereupon, one or two same size pups usually run up to the newly arrived female. This is one way adults may separate their pups from the herd since only 1 to 3 pups, presumably the whistler's own offspring, normally respond to the whistle (data were not collected on this). For another pup to go to a whistling female it could mean moving away from the den and perhaps missing the arrival of the pup's own mother.

While visiting the den, females carefully sniffed approaching pups before allowing them to suck. They particularly seemed to sniff the pups' rumps, and to a lesser extent their heads and flanks. Table 5.21 summarizes observations of females sniffing pups, and the pups' and adults' reactions immediately afterwards. In 48% of the cases (210:440) females allowed the sniffed pup to suckle. In 15% (66:440) of the cases the female actively prevented a pup from suckling immediately after sniffing it. Preventing the pup from suckling could take the form of the female moving away, biting the pup, or chasing it. The remaining 37% of the cases when pups were observed being sniffed there was no observed reaction: the pup was not nursed after being sniffed nor did the female make an aggressive attempt to

Table 5.21.--Female/pup sniffing behaviour at the den: responses of the pups to being sniffed and the reaction of females immediately after smelling the pup. Data taken from EVR scans. Also shows result of X^2 test of the amount pups of the different size categories were sniffed. The expected values for the X^2 test were calculated on the basis of the number of times pups of each size category were recorded in pup scans on the days in which sniffing behaviour was recorded.

Female Reaction	Pup Response	-Pup Size Category- 1	2	3	4	Total
-	-	59	29	23	1	113
Nurse	-	34	13	14	3	64
Nurse	Raise Rump	64	46	30	6	146
-	Raise Rump	6	9	11	1	27
Move Away	Raise Rump	-	5	1	-	6
-	Hide Rump	12	2	3	-	27
Stop Nursing	-	1	-	-	-	1
-	Stop Suckling	4	-	1	-	5
Chase	-	26	7	11	1	45
Bite Pup	-	4	4	1	-	9
Move Away	-	1	3	1	-	5
Scent Mark	-	-	1	1	-	2
Total		211	119	97	12	

X^2 Test Results:

Pup Size	Observed	Expected	X^2 Statistics
Size 1	211	83	14.05
Size 2	119	133	1.21
Size 3	97	175	5.90
Size 4	12	48	5.20
Total X^2 = 26.36, df = 3, P < 0.001			

keep the pup from sucking.

Pups commonly reacted to being sniffed by a female by raising their rump (see Figure 5.14), proffering it to the female's nose. Of the 179 observations of this behaviour, 82% of the time (146:179) the pup was immediately allowed to begin to suck. Only 6 of the times when a pup raised its rump did the female move away or otherwise reject the pups attempts to gain access to a teat. This result strongly suggests that pups know their own mothers. Further evidence of this could be seen when a pup would approach a female who was not its presumed mother. It would hide its rump by pressing it firmly against the ground (see Figure 5.14). On 8 occasions I saw females turning their rumps towards a pack of approaching pups and enurinate back at them. Perhaps this was a way of communicating the smell of the female to the pups showing them that she was not their mother.

Females sniffed size 1 pups considerably more than the other size categories of pups (see Table 5.12; X^2 = 26.36, df = 3, $P < 0.001$). These small pups stay close to the den and a female attempting to nurse pups of this size may have to contend, particularly at a den with a large membership, with a number of small pups crowding around her all perhaps rather difficult to tell apart (see Figure 5.14).

5.5.6 Non-Nursing Parental Care

In this subsection ways in which adult maras, both male and female, care for their young other than through nursing will be investigated.

How mara adults apportion their time while at the den, and how different this is from what they do away from the den, will be examined below. These data come from instantaneous general scans (see data collection protocols in the Methods Chapter) taken at 15 min intervals. Table

Figure 5.14 (Overleaf).

Photographs illustrating the role of smell in female identification of their own offspring.

A — Female sniffing a mara pup which is raising its rump to the female's nose. This pup was subsequently nursed.

B — Female sniffing a pup which is pressing its rump to the ground. This pup was subsequently chased away.

5.22 summarizes the proportion of scan observations of adult maras behaving in each of six behavioural categories: feeding, sitting or standing, lying, moving, miscellaneous behaviours, and associating with pups (see also Figure 5.15). Maras at the den spent 54% of their time sitting or lying and only 14% of their time feeding, while away from the den they spent 43% of their time feeding and 40% of their time sitting or lying. Males spent 13% of their time feeding at the den against 41% when away from the den; and 73% of their time sitting or lying compared to 46% when away from the den. Females followed a similar pattern spending only 16% of the time feeding at the den against 44% when away from the den. So, in both sexes, the breeding pairs feed less (Males: $X^2 = 75.49$, df = 5, $P < 0.001$; Females: $X^2 = 91.35$, df = 5, $P < 0.001$), sit more (Males: $X^2 = 81.49$, df = 5, $P < 0.001$; Females: $X^2 = 17.21$, df = 5, $P < 0.001$) and, not surprisingly, interact with pups more at the den than away (Males: $X^2 = 19.85$, df = 5, $P < 0.001$; Females: $X^2 = 115.99$, df = 5, $P < 0.001$). The large proportion of time that males spend sitting when at the den is noteworthy as this behaviour category is characteristic of greatest vigilance.

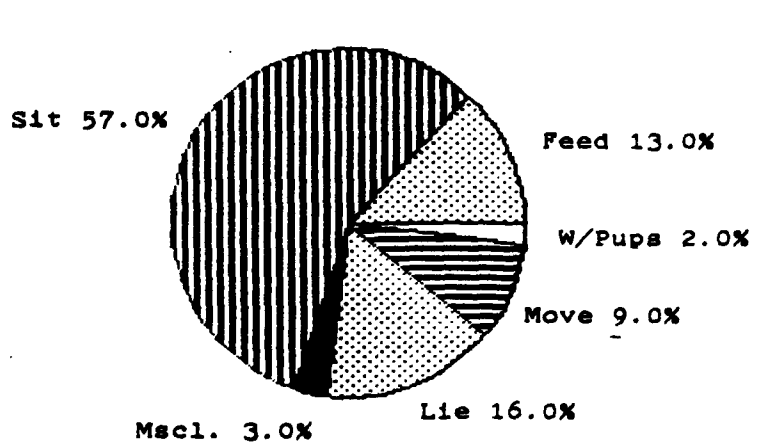
There is little evidence, aside from nursing, of direct parental care (see Table 5.23). There is little parental care reported in other caviomorph rodents--aside from some allogrooming, it consists primarily of guarding the pups (see for example Rood, *Op. cit.*; and Smythe, *Op. cit.*). As Dubost and Genest (*Op. cit.*) have reported, mara adults are almost never seen touching their offspring. I have seen females grooming small pups, and Dubost and Genest (*Op. cit.*) report that females clean the anal regions of the pups when they are small. Males in particular seldom touch pups. It does seems likely, though, that males can recognize their own offspring--in two of the three births observed males made a concerted effort to sniff their own new born pups.

Table 5.22.--Proportion of observation scans of males and females behaving in each of 10 behaviour categories.

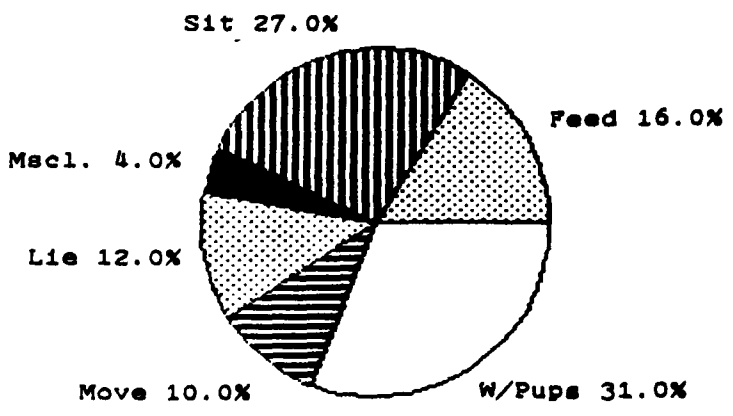
Behaviour Category	Proportion of Obs at den Male	Female	Proportion of Obs not at den Male	Female	Significant Differences
Feed	0.13	0.16	0.41	0.44	1,2,3
Sit	0.57	0.27	0.27	0.18	1,2,3
Miscellaneous	0.03	0.04	0.04	0.04	
Lie	0.16	0.12	0.19	0.17	1
Move	0.09	0.10	0.08	0.08	
Interact w/pups	0.02	0.31	0.002	0.10	1,2,3

All differences with probabilities less than 0.05.
1 - Behaviour of both sexes different at den from away from den.
2 - Males at den different from males away from den.
3 - Females at den different from females away from den.

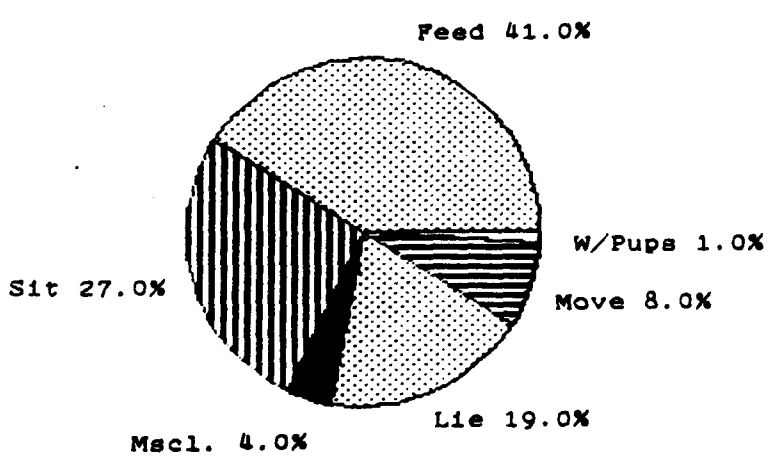
Figure 5.15.--Pie charts showing the behavioural time budgets of males and females at and away from the den.



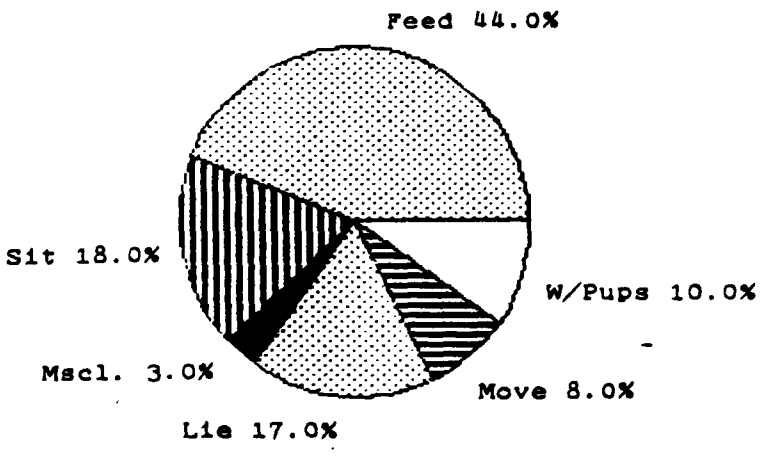
Male Behaviour At Den



Female Behaviour At Den



Male Behaviour In Open



Female Behaviour In Open

Table 5.23.--Number of observations of mara females and males engaging in different pup-associated activities at breeding den sites. Numbers in brackets refer to the number of observations of the behaviour oriented towards each pup size category from size 1 to size 4.

Behaviour Code	Total Females	Total Males
Sniff pup	472 (211,119,97,13)	55 (13,9,15,0)
Groom pup	3	-
Whistle for Pups	42	1
Enurinate on Pups	8	4
Harassed by Pups	120	-
Move Away from Pups	381	22
Chase Pups	627 (266,166,154,16)	21 (7,3,5,0)
Bite Pup	56 (16,34,4,0)	-
Lunge at Pup	124 (20,69,33,1)	-
Stott	15	14

The length of the period maras stay with their young suggests that milk is not the only benefit of the association. Advantages to a prolonged parent-offspring bond could include: (i) adults teaching pups, by example, which food items are safe; (ii) parents teaching pups about the area in which they live; and (iii), at least in the pups' first year of life, parents could provide pups access to safe areas. However, in the absence of much parental care, it seems likely that the main benefits of the extended parent-offspring bond is the protection of the pups from predators.

Predators on pups may include Patagonian gray foxes, weasels, hairy armadillos, red-backed hawks, dogs, and people (see Table 5.17 above). Field notes suggest that adult maras usually react to predators by fleeing, while pups take refuge in the den. On one occasion I saw a male mara chasing a chicken which had wandered near a den. This suggests that mara adults could chase away a small predator which threatened pups. But, the main, or only, form of predator defense at the den must be vigilance; and this is an area where both females and males could invest in caring for their offspring. Males, may have a particularly high potential to protect the pups through vigilance since they spend such a large proportion of their time at the den watching (see above).

Both adult males and females spend some time at the den without their mates (but see Chapter 4). Using the general scan data to examine this, the frequency with which adults of both sexes were alone at the den were compared. Out of 295 scans, 8% (24:295) of the time males were at the den alone, while 33% (96:295) of the times females were at the den alone (no recognizable mate present). Animals were considered alone at the den if their presumed mate was 50 or more m away. Females were at the den without their mates significantly more than males (X^2 = 32.94, 1 df, $P < 0.005$). However, male maras did spend time alone at the den when no

other adults were present, suggesting that this is one way they could care directly for their pups. On three occasions I saw males waiting at a den while their mates were 100 to 200 m off grazing. All three of these times the pups came out of the den and played and grazed, which they would not do if no adults were present (see Section 5.6).

Adults may use stotting to draw danger away from the den. On 8 occasions when I approached a den with mara adults and pups present, the adults first sat alert at the den, while the pups took refuge inside, and then stotted off 20 m or so from the den. Stotting involves jumping up and down on the spot and is usually associated with the presence of a predator (see description in Smythe, 1970). It is a behaviour practiced by some species of antelopes and deer, and its function remains uncertain (but see Caro, 1986a and 1986b). As I walked towards the den the adults would stott and move off a further few meters. They would repeat this several times as I moved closer. This behaviour may have the same function as a broken-winged display in birds (Harvey and Greenwood, 1978); namely, drawing predators away from the nest. I tested whether adult maras stotted more at the den, when fleeing from predators, than when away from the den, but no significant differences were found (X^2 = 0.12, df = 1, NS). This may, however, simply reflect the small sample size.

5.6 The Behaviour of Mara Pups

In this section the behavioural development of mara pups will be discussed. Results will be presented showing: the overall behavioural time budget for pups, how this changes as the pups grow, and how pup behaviour is affected by the presence or absence of adults at the den. Most results presented here refer only to pups in size categories

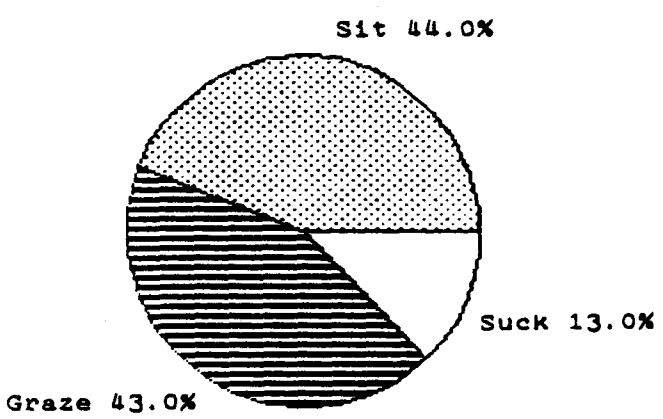
1, 2, and 3. Data on size (category) 4 pups were collected too sporadically to be used in most of these analyses because they spent most of the daylight hours away from the den (see above). For these analyses pup behaviour was classified as being either grazing, nursing, or sitting. In effect I only analyzed the pups' 'states' (see Altman, 1974, and Chapter 2) since other behaviours (e.g. running, frisky hopping, squabbling) were all of very short duration (i.e. 'events').

5.6.1 Behavioural Time Budgets and Development of Pups

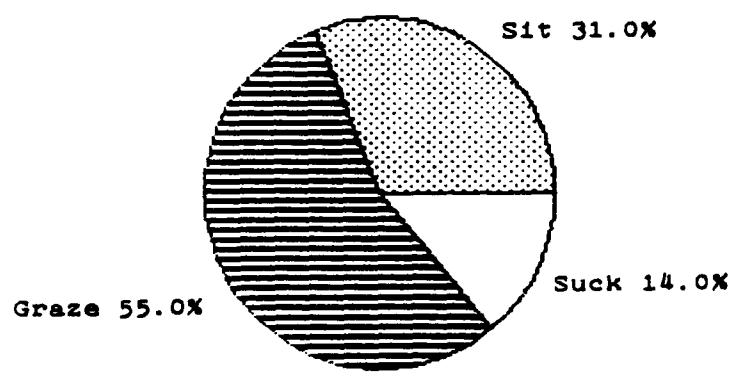
The behavioural time budget of mara pups up to about 6 weeks of age (size categories 1,2, and 3) is shown in Figure 5.16. Overall, pups at the den spent 44% of their time sitting, 43% of their time grazing, and 13% of their time nursing. These results were obtained from taking the average of the proportion of observations of the different size classes of pup engaging in each behaviour category. Below the behavioural development of the pups will be examined in more detail through looking at the following aspects of how their behaviour differs in each of the size/age categories: (i) the proportion of scans they were observed engaging in different behaviours, (ii) the proportion of scans they spend outside the den each day, and (iii) the inter-pup distances between pups in different size classes.

The proportion of observation scans of pups of each size class engaging in different behaviours are shown in Figure 5.16. The results of X^2 tests of whether pups of different sizes engage in each behaviour a different amount are shown in Table 5.24. Summarizing these results: (i) the proportion of scans pups spent suckling does not change between size categories 1 and 3 (X^2 = 1.22, d.f. = 2, NS); (ii) the proportion of scans of pup grazing decreases from size class 1 to 2 to 3 (X^2 = 56.41, d.f. = 2, $P < 0.001$);

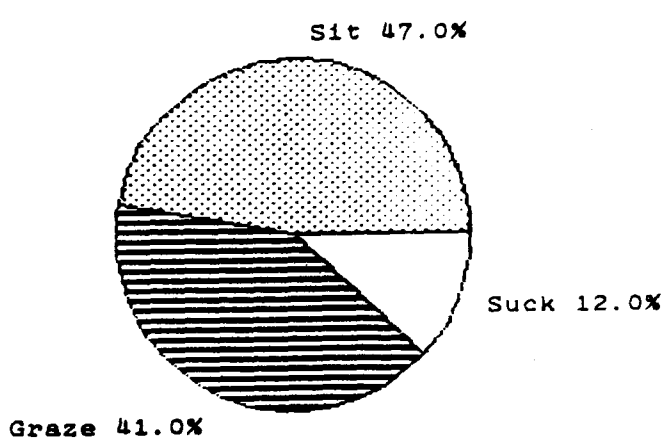
Figure 5.16.--Pie charts showing the behavioural time budgets for pups overall, and for pups in size/age categories 1, 2, and 3.



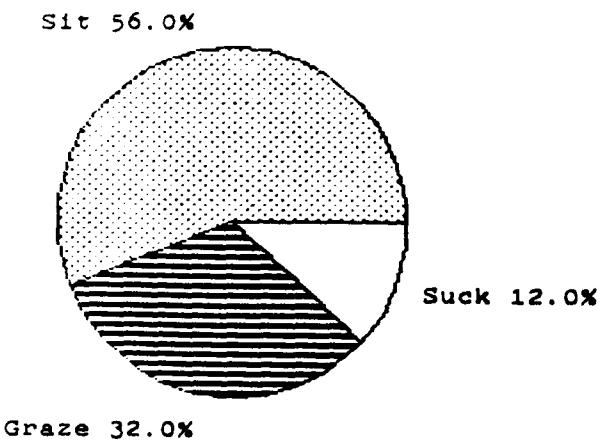
Overall Pup Behaviour



Size 1 Pup Behaviour



Size 2 Pup Behaviour



Size 3 Pup Behaviour

Table 5.24.--The proportion of observation of different age classes of mara pups engaging in different behaviours. Differences found using the X^2 test on the number of observations in each behaviour category. Data taken from pup scans selected at 30 minute intervals to limit auto-correlation.

Behaviour Category	-Pup Size Categories- 1	2	3	X^2	Significant Differences Between Sizes
Sitting	0.31	0.47	0.56	49.28	$P < 0.001$
Grazing	0.55	0.41	0.32	56.51	$P < 0.001$
Suckling	0.14	0.12	0.12	1.22	N.S.
Total X^2 =				106.41 (4 df)	

and (iii) the proportion of scans pups of different age classes spent sitting increases from size class 1 to 2 to 3 (X^2 = 49.28, d.f. = 2, P < 0.001).

Below, the amount of time pups of different sizes spend outside the den is examined. For each day data were collected at a den, the total number of times each size category of pup was recorded in a pup scan was divided by the number of pups of that size at the den (see Section 5.4). These numbers could then be averaged across all the days in which den-scan data were collected to provide the following results: individual size 1 pups were seen a mean of 5.298 times per day (± 4.367), size 2 pups were seen a mean of 8.291 times per day (± 6.046), size 3 pups were seen a mean of 9.423 times per day (± 7.415), and size 4 pups were seen a mean of 4.660 times per day (± 4.149). These distributions were then compared using a Kruskal Wallis analysis of variance and were found to be significantly different (H = 8.689, df = 3, P < 0.05). The pattern that emerges is that as individual pups grow from size 1 to size 3 they spend increasing amounts of time in the open around the den. By the time they reach size category 4, approximately 6 weeks old, the amount they are seen declines since they spend most of the day away from the den.

A similar pattern emerges when one examines how close pups of different size categories stay to other pups (see Table 5.25). While collecting pup scan data the nearest pup distance for each pup was recorded (in mara lengths distance code) every 10 minutes. The distance between pups was divided into four categories: 0 to 2 mara lengths, 2.1 to 5 mara lengths, 5.1 to 10 mara lengths, and greater than 10 mara lengths. The number of times that pups of each size were seen in each inter-pup distance category was totalled and compared using the X^2 test. The differences were found to be highly significant (X^2 = 108.32, d.f. = 9, P < 0.001) showing that smaller pups spend more time close to other young (regardless of size category) than larger pups.

Table 5.25.--The proportion of pup scan observations of mara pups of different age categories at different nearest pup distances. X^2 tests were made on the different cells to detect which differences were significant between different age classes of pups. * is P <0.05, ** is P < 0.001

Distance to Nearest Pup in Mara Lengths	-Pup Size Categories- 1	2	3	4
0 - 2	0.96 *	0.91	0.83	0.73 *
2 - 5	0.03 **	0.06 **	0.10 *	0.17 **
5 - 10	0.01 **	0.03	0.05	0.07 **
10 <	0.0 *	0.001 **	0.02 **	0.03 *

Reviewing the results of this subsection, the following were the most important findings: as pups grow older they spend more time out of the den, wander farther from other pups, and spend proportionally less of their time outside the burrow grazing and more time sitting. This last result, may be particularly important since sitting is the behaviour category where the pups are most vigilant--i.e. not distracted by grazing or nursing.

5.6.2 Effects of Adult Presence on Pup Behaviour

Here I will be looking at how pup behaviour changes at the den both when adults are present and absent, and with varying number of adults. These analyses will provide results showing both the degree of behavioural cohesion and coordination between adults and pups, and how pup behaviour may be adapted to the risk of predation.

The den-scan data were used (see Chapter 3 for data collection methodology) for these analyses. To insure independence between scans, which in the field were made at 10 min intervals, a minimum independence interval of 1.08 hr was used to select the 163 scans used for these tests. A 1.08 hr interval was chosen since this is the mean length of time females stay at the den (see Section 5.5.2). This limits the auto-correlation from scan to scan which would exist if several scans were included in the data set from the same female's visit to the den. The variables compared under the different conditions were: the number of pups visible outside the den, the average distance of the pups from the den, and the proportion of the visible pups engaging in suckling, grazing, and sitting.

The Mann-Whitney test was used to compare the number of pups in sight, the proportion of the pups engaging in different behaviours, and the proportion of pups at different distances from the den when adults were present

and absent from the den. The following results were obtained:

1. Significantly more pups were visible at the den during scans when adults were present ($\bar{x}$ = 5.61, ± 3.69) than during those when adults were absent ($\bar{x}$ = 1.29, ± 2.55) from the den (W = 14691.0, P < 0.000).
2. When pups were outside the den their numbers did not differ significantly whether adults were present or not (present: $\bar{x}$ = 4.57, ± 4.11; absent: $\bar{x}$ = 4.29, ± 2.48; W = 16896.5, NS).
3. The proportion of the pups outside the den which were sitting was significantly higher when no adults were at the den than when adults were present (present: median = 0.5; absent: median = 0.75; W = 16279, P < 0.0130). There was not, however, a significant change in the proportion of pups grazing (present: median = 0.0; absent: median = 0.25; W = 16552.5, NS).
4. Pups not with adults stayed significantly closer to the den when adults were absent from the den than when adults were present (present: $\bar{x}$ = 3.12, ± 4.72, absent: $\bar{x}$ = 1.385, ± 0.771; W = 11550.5, P < 0.0000).

To investigate how increasing numbers of adults and pups at the den affects pup behaviour the Spearman rank correlation was used to obtain the following results:

1. As the number of adults at the den increases so does the number of visible pups (r_s = 0.206, N = 163, P < 0.005). This is true independent of time of day, a possible confounding variable, since there were no significant differences between the number of adults (or pups) out of the den in different hours of the day between 8:00 and 19:00 (see Section 5.5 above).

2. Proportionally more of the visible pups suckle as the number of adults at the den increases (r_s = 0.313, P < 0.001).
3. The proportions of pups grazing and sitting do not change significantly as the number of adults at the den increases (Grazing: r_s = -0.120, Sitting: r_s= 0.012).
4. The proportion of pups suckling, grazing and alert does not change as the number of pups at the den increases (Suckling: r_s = 0.119, Grazing: r_s = 0.145, Alert: r_s = -0.010; none are significant).

The pattern shown from the above results is that pups are greatly affected by the number and, particularly, the presence and absence of adults at the den. When adults were absent from the den fewer pups ventured out, and those that did stayed closer to the den than when adults were present. Furthermore, in the absence of adults, when pups were out they mostly sat around the den entrance (see above). Pups seemed little affected by the actual number of adults present since their behaviour (grazing and sitting) did not change with more adults at the den. What is important is that at least some adults are present; thus, pup behaviour in the absence of adults (mostly sitting by or in the den mouth) seems highly adapted to the risk of predation. These results suggest that the risk of grazing away from the den without adults present to warn the pups of danger was high.

5.7 Interactions Between Adults at the Den

The behavioural relationships between adult maras have been described to some extent in Chapters 3 and 4. Here, I will be looking at two aspects of the way adult pairs interact at the den: (i) the nature and number of aggressive interactions between pairs; and (ii) how the

number of adults at the den affects queuing time: the length of time between a pair's arrival at a den and the start of nursing.

Aggressive behaviour between pairs usually took the form of the male of one pair approaching another pair to attempt to sniff or mount the other female. Virtually all aggressive interactions were ended by one male chasing the other off and the two pairs eventually going separate ways. I never saw a male take over (keep separate from its mate) the female of another pair for more than a few minutes (see also Dubost and Genest, *Op. cit.*). An aggressive interaction could carry on for up to an hour, and might include a number of component interactions. For the sake of independence, a single aggressive interaction was counted for each interaction separated by more than an hour from another 'fight' between the same individuals. I have not attempted to analyze interaction rates statistically--there were too many conflicting variables. However, the following findings were made: 95% (239:252) of the aggressive interactions observed occurred during the main part of the pupping season, 15 August to 30 November; of these, 74% (186:252) occurred in the month of September; and of all the interactions observed, 89% (224:252) took place in the vicinity of breeding den sites. The month of September is when the majority of the pups are born, and hence many females may have been coming into a post-partum oestrus (see Section 5.3). This could explain the high rate of interactions between pairs since males could be attempting to mate polygynously if the opportunity presented itself.

My impression in the field was that pairs arriving at the den spent a certain amount of time queuing, waiting 20 to 30 m from the pups and den, while a previously arrived pair was at the den with the young. Of 71 closely monitored den visits, in 87% (62) pairs queued for less than 10 mins. The mean queue time was 0.092 hrs ($\pm$ 0.16, median = 0.034). Queuing could be a cost for pairs using dens with large

memberships: they might need to spend long times at dens waiting to tend their pups. However, as the results presented below show, there seems to be little relation between queueing time and the number of adults at a den.

1. There was not a significant correlation between the amount of time a pair had to queue at the den before nursing pups and the number of adults at the den prior to the female's arrival (r_s = -0.014, N = 62, NS).
2. There was not a significant difference in queue time between the amount of time females waited between arriving at the den and starting to nurse, when other adults were already present and when no adults were present (W = 1108.0, P = 0.9307).
3. There was not a significant correlation between the queue time and the maximum number of adults at the den during a female's stay (r_s = -0.135, NS, N = 71).

5.8 Tests of Hypotheses

Having described the denning system, I will now seek an evolutionary explanation for why maras have adopted a communal denning system. I propose the following three, not necessarily exclusive, hypotheses:

1. Mara pairs use communal dens because there is a shortage of den sites, and groups are simply aggregations lacking functional advantage.
2. Den sites are not limiting, so pairs use communal dens because of an advantage in collective denning.
3. Limitation or scarcity of the den sites cause pairs to use communal dens (as in 1 above), but maras have subsequently evolved behavioural traits to capitalize on these aggregated conditions.

Below, each of these hypotheses will be examined in detail.

5.8.1 Hypothesis 1: Den Sites are Limiting

Possible reasons for den sites being limited are: (i) the ground is suitable for digging in only a few places; (ii) maras are unable to dig dens efficiently; and (iii) dens must be near a particular resource such as open ground, food, or water for energetic reasons or for safety from predators. Each of these possibilities will be assessed in turn below:

1. From Figures 5.4, 5.5 and 5.6, maps of the active and inactive den sites found at my three study areas, one can see that a large number of unused dens were located around each study site (19 unused dens compared to 14 used dens). The wide distribution of these dens shows that maras are able to construct dens over a wide area.
2. Of 23 dens found at the 3 study areas, 4 (17%) were dug during the period of field work. This shows conclusively that maras can easily construct new dens if and when they please.
3. The distribution of dens which were used show a distinct pattern: most of the 20 'active' dens (12, or 60%) were located within 500 m of a human inhabited, or at least regularly visited, site. This strongly suggests that these kinds of sites must have qualities important for successful breeding (see Section 5.4 above). However, around each of these sites there were a number of available den sites out of which maras used only one or two.

These results show clearly that dens are not limiting, and further that maras actively chose to den communally. The best illustration of this comes from the El Salitral study area where 4 dens were used in 1983 compared to 2 in 1984 (see Section 5.4), despite the fact that

approximately equal numbers of pups were born each year (37 in 1983 and 33 in 1984).

5.8.2 Hypothesis 2: Collective Denning

With the rejection of the hypothesis that limited den site availability forces maras to den communally, it seems likely that pairs must group together when breeding because of an advantage in collective denning. Possible advantages of collective denning are:

1. Lower likelihood of individual offspring being chosen from the group by a predator because of the large number of young to choose from.
2. Reduced risk of predation at the den, either or both through enhanced vigilance and strength of numbers.
3. Pups help each other by their greater corporate vigilance or collective strength (possibly aided by larger pups helping smaller ones).
4. Communal suckling may be an advantage either, because some females actively suckle some babies other than their own, or all females will adopt an orphan or a very hungry baby for at least some time. Obtaining, or 'stealing', milk from another female may be important for some pups' survival, and critical if a pup's mother dies.
5. Adult presence at the den sites during the day is vital for babies to be out during the day. The young need to be out as much of the day as possible to feed, exercise, and play/learn.

Any of the above predictions may be true, and none of them is necessarily an exclusive explanation of why maras den communally. Below each will be assessed in turn.

Predator Swamping

Banding together at communal dens appears to reduce the likelihood of a given female's pup being taken by a predator. From examining the mortality estimates for dens with different mara membership sizes (see Table 5.16, and Section 5.4) the data suggest that, if dens were not hit by a catastrophic disease or predation, the mortality figures for dens with larger memberships may be less than those for dens used by fewer animals. However, the sample size is too small and unevenly collected to be certain if this is a real effect. Further evidence that maras are responding to predation risk in this way is the synchronization of pupping at the same study area within years (see Section 5.4)--a similar pattern (Darling, 1938) has been described for seabirds as a response to predator pressures: i.e. 'predator swamping' (see review in Wittenberg, 1981).

Group Defense and Vigilance

Despite the example mentioned (see Subsection 5.5.6) of a mara chasing a chicken, I have seen little evidence that mara adults, either singly or as a group, are capable of defending the den from predators. Further, most predators (see Table 5.17) are as dangerous to the adults as to the pups. The best defense maras have against predators would seem to be vigilance, so that pups would have time to take refuge in the den and adults to run away. As mentioned in Section 5.2, one advantage of group living is that individuals can spend more time engaging in productive behaviour, such as grazing, and less time guarding. If mara adults cooperate in communal vigilance at the den, one should see the following:

1. Increased numbers of adults should be vigilant as the number of mara adults at the den increases.
2. Proportionally fewer adults should be vigilant, and a greater proportion should be feeding, resting, and nursing young as the number of adults at the den increases.

The data for these analyses come from the general scan data set. Scans were selected at 1.08 hr interval, the mean length of stay at the den by nursing females, to reduce the problem of auto-correlation between scans. Only scans collected at least 30 mins before or after a human disturbance were used. The Spearman rank correlation was used to test how the behaviour of adults at the den changes with different numbers of adults present. The following results were found:

1. The number of adults alert increases as the number of adults at the den increases (r_s = 0.765, N = 202, P < 0.001).
2. Proportionally fewer of the adults are alert as the number of adults at the den increases (r_s = 0.323, N = 168, P < 0.001).
3. Proportionally more adults are resting as the number of adults at the den increases (r_s = 0.359, N = 168, P < 0.001).
4. The proportion of the adults nursing does not change significantly as the number of adults at the den increases (r_s = 0.083, N = 168).

These results follow the predictions made. They show considerable evidence that groups of mara adults sharing a den coordinate their activities closely: as the number of adults at the den increases individual maras are able to spend more time grazing and resting, and less time predator scanning, while the safety of the group increases with more animals watching at any one time. Groups of adult maras at

communal dens clearly cooperate more than if they were simply aggregations of individuals.

Cooperation Amongst Pups

As already seen in Section 5.6, mara pups do not appear to coordinate their activities to the same extent as adults. The proportion of pups grazing or alert is apparently unaffected by the number of young around the den. Older pups do appear to be more attuned to the risk of predation since they spend a greater proportion of their time out of the den sitting (the most vigilant behaviour category) than do younger ones. However, the proportion of time these older pups spend sitting is not correlated with the number of pups present (see in Section 5.6).

The best evidence for coordination between pups was that there was not a significant difference between the number of pups out of the den (on the few occasions when they came out in the absence of adults) when adults were present and the number of pups out when adults were absent (see Section 5.6). This suggests that pups coordinate their activities to the extent that they only come out of the den as a group. Individual pups can then take cover amongst the others since the chance of any single pup being taken by an individual predator may be reduced (see Section 5.2). Further, although they do not appear to coordinate their scanning behaviour, pups may benefit from the safety of having more eyes watching. This could be augmented by the advantage that large pups, which spend more time sitting (watching) than smaller ones, could (in effect) be protecting the younger animals

These results suggest that pups do coordinate their behaviour to a limited extent; and thus, may benefit from communal denning. However, these results are not nearly as

compelling as those already presented showing the amount adults coordinate their behaviour around dens.

Importance of Communal Nursing

Many aspects of this have already been covered in Section 5.5. To summarize:

1. Females go to great efforts to limit the amount they suckle offspring of other pairs: they have been seen biting, chasing, or otherwise preventing pups which were presumed not to be their own up to a maximum of 34 times during a single nursing session ($\bar{x}$ 7.51 per visit to the den).
2. Females have been seen nursing pups which were presumed not to be their own up to a maximum of 0.482 hrs (compared to a $\bar{x}$ of 0.06, $\pm$ 0.11) during a den visit.
3. On 2 October 1983 two tiny apparently orphaned or abandoned pups (no female arrived to nurse them over several days) were observed being nursed by several females. I have no evidence to show whether or not these pups survived; but it is possible that suckling under these circumstances could at times be critical to an orphaned pup's survival.

Thus, though communal suckling is uncommon, it may occasionally be important for pup survival. However, it seems unlikely that communal suckling, though it may be an advantage, is the main reason maras den communally. In fact, the energetic costs of preventing pups not one's own from gaining access to a teat may be high: on 2 occasions (15.9.83 at Ash Den and 5.9.81 at Molino Den Site) I saw females leave the area of the den after continual harassment by pups, apparently without having nursed their own

offspring sufficiently since they returned later in the day.

Cooperative Den Guarding

To test the hypothesis that the presence of adults is necessary to allow pups to spend as much time out of the den as possible two predictions were made: (i) if pups are dependent on adult presence, there should be a strong correlation between pup activities and the presence and/or number of adults at the den; and (ii) den members should maximize the number of hours at least some adults are at the den.

The first part of this hypothesis has already been investigated in the section on pup behaviour (Section 5.6). There it was shown that: (i) the number of pups out of the den increases as the number of adults at the den increases; (ii) in the absence of adults, pups spend proportionally more time sitting than grazing than when adults are present; and (iii) as the number of adults present increases pups wander farther from the den. These results suggest a high degree of coordination between the activities of the pups and the presence, absence, and number of adults at the den.

If mara adults maximize the time they spend at the den and if dens are of different crêche sizes, one would expect the following to be true: (i) adults should maximize the number of hours a day during which at least some are present at the den, and (ii) at dens with fewer pairs, individual adults should spend more time at the den than those at dens with larger memberships.

To test whether adults maximize the time that they are at the den, the proportion of scans with adults present was correlated with the maximum number of pups at the den that day. The result was a significant positive correlation

(r_s = 0.573, N = 38, P < 0.001) showing that as den membership size increases (as shown by the number of pups) adults are at the den a greater proportion of the day. At dens where membership exceeds 10 pups (about 6 pairs) the proportion of the day in which adults are at the den levels off at about 90% of the observation scans (see Figure 5.17).

The second prediction, that individual adults at dens with smaller memberships should spend more time at the den than members of larger communes was tested as follows. A significant negative correlation was found between the time pairs spent at the den and the number of pups at the den during the observation day (r_s = -0.249, N = 93, P < 0.02). In addition, the length of visits to the den data were divided into two groups: one for dens which averaged more than 10 pups present per den observation session (median length of stay 0.667 hrs, N = 32), and one for those which averaged fewer than 10 pups (median length of stay 1.0423 hrs, N = 66). A significant difference was found between these groups using the Mann-Whitney test (W = 1943, P < 0.0066) showing that animals at dens with smaller memberships stayed at the den longer than adults stayed at dens with larger memberships. This is probably a disadvantage for animals at dens with small memberships since staying at the den may be energetically costly for adults--they do not spend as much time feeding at the den as away from the den (see Figure 5.15 above).

Thus, to a greater or lesser extent, these results suggest that every one of the possible advantages of collective denning mentioned at the start of this subsection have some validity. The evidence that adults are cooperating in guarding the den is particularly compelling.

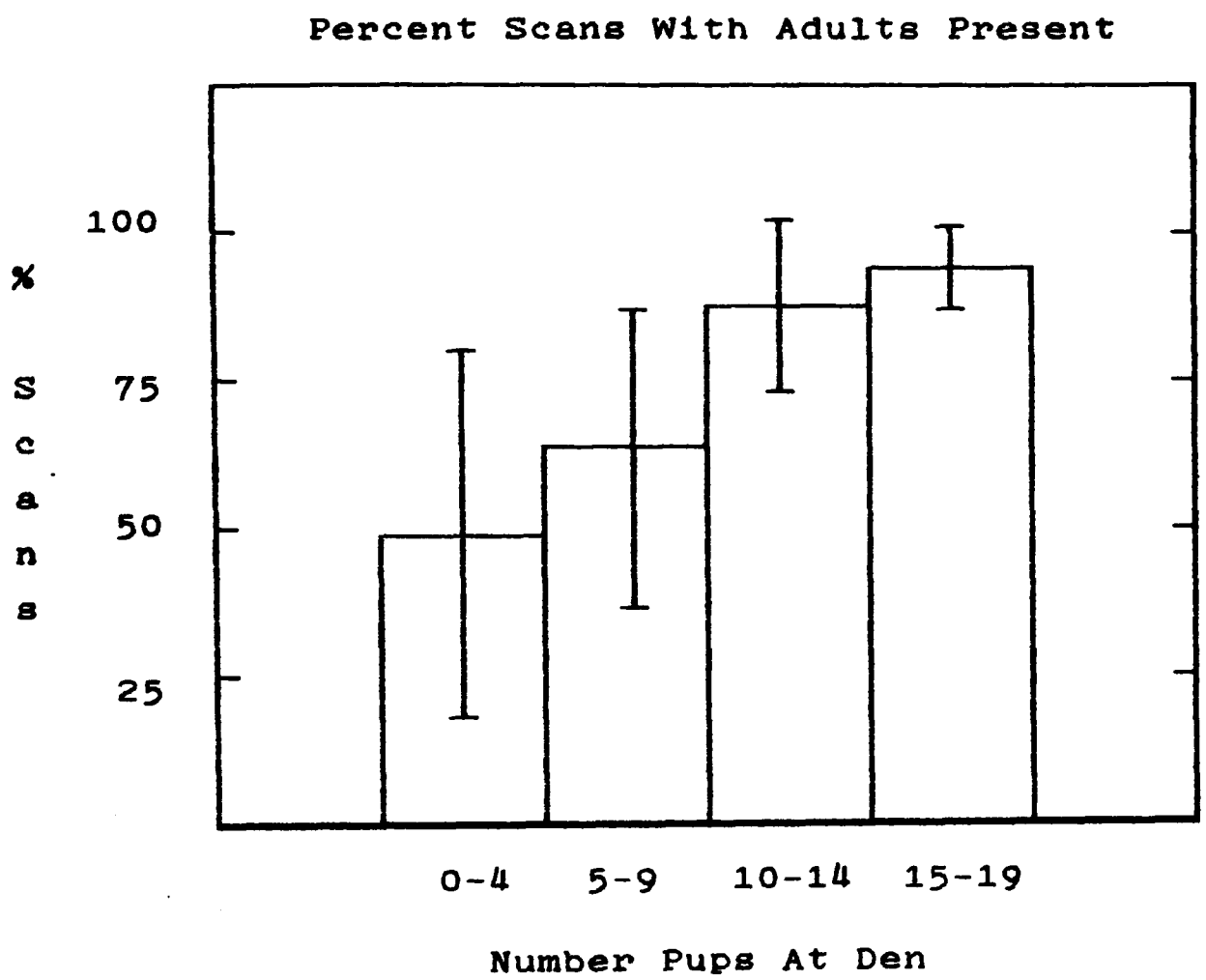


Figure 5.17.--Histogram illustrating the proportion of scans during the day in which mara adults were at dens with different membership sizes as reflected in the number of pups at the den. Error bars mark the standard deviations.

5.8.3 Hypothesis 3: Den Sites are Limited but Maras Cooperate

This hypothesis is really a combination of the other two. We have seen above that den sites appear not to be limited, with the proviso that maras may prefer to use dens located near human settlements; and we have seen that adult maras sharing a communal den coordinate their activities to a large extent. The question, then, is whether the advantages of cooperation are the reasons maras den communally, or whether they have evolved cooperation after being forced into communal denning. To some extent this is a chicken or egg question today, since the answer lies in evolutionary history. The results presented above suggest that the main reason maras den communally is that there are distinct advantages in banding together. Particularly strong evidence for this is that where there were several usable den sites (see Figures 5.4, 5.5, and 5.6) maras clearly choose to use only one or two of the available sites. However, without more data on the evolution of the mara's social system it is difficult to draw other than tentative conclusions from these results.

5.9 Summary and Discussion

In this chapter the main aspects of the mara's denning system have been described, and several hypotheses as to why maras den communally have been tested. The main discussion of these results will be saved for Chapter 6; however, the most important points made are summarized below:

COMMUNAL DENNING

1. Breeding Biology: The mara's gestation period is about 100 days. Litter sizes vary from 1 to 3, with 75% of litters consisting of 2 young. Pups are nursed for approximately 11 weeks--one of the longest lactation periods known in rodents. The majority of pups are born in September and October, although newborn pups are seen between August and January. Most females in the study area produce one litter a year. However, at least some females have a post-partum oestrus. Foetuses resulting from these matings probably come to term only if the female's current pups die or environmental conditions are particularly favourable. I suggest that allowing a second litter to develop while nursing may be an insurance against pup loss (a similar strategy is used by wallabies, see Kaufman, 1974).
2. Ecology of Denning: The pups are born in the mouths of dens which are virtually never entered by adults. Individual dens are used by one or more adult pairs for raising young. Data were collected on 29 mara dens. A total of 710.42 hrs were spent observing maras at 8 dens at 3 study areas over 3 pupping seasons. Dens fell into two categories: (i) dens used by one or two pairs in small openings in the scrub, located 1 km or more from the nearest neighbour (data on these dens were not collected); and (ii) denning areas, or communities, of several dens located within 400 m of each other. Denning communities were usually centered on large openings in the scrub (often lagoons) near small human settlements (1-5 inhabitants). It is speculated that the human presence may deter predators, and that this may be important for pup survival.

2.1. Number of Pups Per Den: Between 1 and 33 pups (litters from 1 to 22 adult pairs) were estimated to have been born at the various studied dens. Most dens (15 out of 17) were used by under 10

mara pairs. However, 35% (64:183) of the pups estimated to have been born were at dens used by 10 or more pairs. Pup mortality was high, with 47% (50:107) of the pups born at 9 intensively monitored dens dying before reaching 6 weeks of age. All pups born at dens used by 10 or fewer pups probably died. Causes of pups mortality may include predators such as weasels, armadillos, foxes, birds of prey, and humans. Other cause of pup mortality may be disease and hypothermia.

2.2. Denning Areas: At different denning areas, females gave birth to between 19 and 53 pups at 2 to 5 dens. The timing of parturition by different females at different dens in the same area was more synchronized than between areas, or the same area in different years. The denning areas studied were all at least 2 km from the nearest known neighbouring area. Results of radio tracking (see Chapter 3) show that maras seldom move between denning areas. Thus, it seems likely that many of the animals at one denning area are related. The results suggest that mara pairs sharing a denning area may be considered as a single social unit or herd.

3. Growth and Behaviour of Mara Pups: Pups spend all their time in, or within 20 m of, the den for the first 6 weeks of life. After 6 weeks the pups leave the area with their parents during the day, only returning to the den at night. After about 11 weeks the pups cease to use the den. Data on pup behaviour were only collected on animals up to 6 weeks of age. Pups spend 44% of their time sitting, 43% grazing, and 13% nursing. As pups grow older they spend proportionally more of their time sitting and less time grazing. Smaller (size 1) pups were out of the den less during the day than the larger (older) ones, and stay closer to other pups.

When no adults were at the den, pups almost never ventured out of the den mouth; and when they did they stayed within 5 m of the den, sitting or grazing. When at least one adult is present, pups spend proportionally less time sitting, more time grazing, and wander farther from the den than when no adults are present. The proportion of pups engaging in different behaviours is unaffected by the actual number of pups or adults at the den--the decisive factor is that at least one adult is present.

4. Nursing the Pups: Adult pairs visit the dens once a day (usually) between 7:00 and 20:00 to tend their pups. The mean length of stay at a den was 1.08 hrs. There were no significant differences between the length of time which females stayed at dens when nursing pups of different sizes. Females nursed pups a mean of 0.349 hrs per den visit. Nursing was typically divided into several bouts ($\bar{x}$ 9.21, max = 34). Females often nursed more than one pup at a time. It was difficult to estimate how long females nursed their individual offspring since pups of other pairs were continually trying to gain access to the teats. Females nursed each of their own presumed pups (the size of pups nursed the most) a mean of 0.296 hrs per den visit. No significant differences were found in the amount pups of different sizes/ages (up to 6 weeks) were nursed.

5. Communal Suckling and Pup Identification: In 45% (32:71) of the nursing sessions monitored, pups presumed not to be a given females gained access to the teats. Pups of other pairs were suckled a mean of 0.032 hrs per den visit ($\pm$ 0.083, max = 0.48 hrs), 0.11 of the time females nursed each of their pups. Females go to a considerable effort to prevent pups from 'sneaking' sucks, and chase off, and even injure, pups presumed not to be their own. Fully 45 % of nursing bouts observed were interrupted by pups trying to 'steal' milk.

Females were observed behaving aggressively towards pups a mean of 4.11 times per nursing session. They appeared to identify their offspring from smelling the pups' sides and rumps--pups raised their rumps to their presumptive mother's nose, and not to others, when attempting to gain access to a teat. Females also whistled to draw their presumed pups out of the den. There was a significant positive correlation between the amount of time females nursed pups presumed not to be their own and the number of pups at a den. The loss of milk to 'stolen' sucks, and the time spent preventing milk stealing clearly are costs of communal denning. In some other caviomorph rodents, communal suckling is common (e.g. capybaras: Macdonald, 1981); mara females go to a considerable effort to prevent it, but nevertheless some pups may gain a substantial amount of milk in this way.

6. Non-nursing parental care: The long lactation period (which may be as much to maintain the parent-offspring bond as to provide nutrition to the pups), particularly relative to the much shorter one of most rodent species, suggests that the parent-offspring bond is important for pup survival. There is very little direct parental care other than nursing (e.g. almost no allo-grooming). Analysis of adult time budgets at the den showed that they feed less and sit more (particularly males) at the den than when away from the den. Since sitting is the most vigilant behaviour category, the fact that males at the den spend 57% of their time sitting suggests that they may be playing a guarding role. Adults are unable to defend the pups from predators so their main role must be to warn the young of danger, allowing them time to enter the den before a predator arrives. Also, stotting at the den may be a distraction display used to draw predators away from the pups. Thus vigilance is probably the main contribution that adults, and males in

particular, make towards non-nursing parental-care.

7. Relations Between Pairs At The Den: Mara males were seen engaging in aggressive interactions, or fights, around dens 224 times. These interactions usually took the form of one male trying to approach and temporarily usurp another male's female. Interactions were of short duration and, invariably, mates were never separated for more than a few minutes by another male's actions. The interaction rate outside the period when females were coming into oestrus was low. Most of the aggressive interactions (74%) seen between male maras occurred in the vicinity of dens during the month of September. Most pups are born at this time, and so many females must have exhibited post-partum oestrus. This would be an opportunity for males to copulate with females other than their mates, and thus probably explains the high interaction rate at this time of year.

8. Test of Hypotheses: Three possibly interrelated hypotheses were presented as to why maras den communally, these were: (i) they do so because den sites are limited; (ii) they do so because of the advantages of collective denning; or (iii) they were originally forced to den communally because den sites were limited, but have since adopted a range of behaviours to take advantage of their enforced aggregated condition. These hypotheses were evaluated as follows:

8.1. Results suggest that den sites are not limited and that maras can easily dig new dens. Further, the results show that given a choice of several unused dens, maras were choosing to use ones already occupied by other maras.

8.2. Every one of the possible benefits suggested for why maras den communally were supported. The most important results were: (i) As the number of adults at the den climbs the number of adults sitting (the most vigilant behaviour) increase

while the proportion sitting declines--thus, individually, maras were able to spend more time resting or grazing when more adults were present, while benefiting from increased vigilance (and hence safety from predators) overall at the den. (ii) Pup survival at dens with larger memberships was higher than at dens used by few pairs, possibly because of a 'selfish herd' effect. (iii) Despite the efforts of females to prevent pups which were not their offspring from suckling, some infants nevertheless are able to 'steal' milk. This may play an important role in the survival of some, particularly orphaned, pups. (iv) Adults were present more of the day at dens with larger memberships than at dens with smaller memberships, while individually they spent less time at the dens. This last point must benefit pups since most pups come out of the den when any adults are present, and thus at dens used by many pairs the pups have more time to graze and play. Adults may also benefit since they spend less time at dens used by many pairs, and hence spend more time on their own ranges where they enjoy higher grazing and resting rates than at the den.

8.3. The last possibility was hard to evaluate because the answer lies in evolutionary history. With all the advantages of denning in groups shown, and the fact that soil conditions make den digging easy for maras, it would appear likely that communal denning was adopted because of its inherent advantages. However, it is also possible that the mara has descended from a group living ancestor from which it has developed the system of monogamous pairs living apart from others except during the pupping season. Under these conditions communal denning could be a hold over from a

previous era. Evidence for this last possibility is slim, but it is noteworthy that the mara's closest relatives, the other members of the family Caviidae, are all group living (further discussed in Chapter 6).

The driving force favouring communal denning in maras appeared to be predation pressure. This is similar to the system described for the weaverlike bird *Bubalornis albirostris* where each pair uses its own chamber in a large thorny communal nest which serves to deter predators (see Section 5.2). Unlike the groove-billed anis, where the main beneficiaries of the reduced predation risk are the adults (which, through communal nesting, minimize the time they spend individually at the highly dangerous nest site), in maras it seems likely that the pups benefit the most through cooperative den guarding. One point I have not investigated for lack of data is the effect of disease or parasites on the denning system--evaluation of this will have to await further field study.

Chapter 6

Final Discussion

In this concluding chapter I will bring together the various results presented above to create a synthesis of the mara's behaviour and ecology which answers, as far as I can, the questions set out in the introduction: why are maras monogamous, and why do they den communally? Against this background I will then consider in depth how the mara's social system compares, first with those of other species of rodents, and second, with unrelated but morphologically, ecologically, and behaviourally similar species.

6.1 The Mara and its Environment

In this summary I will review the strategies maras have adopted in response to the environmental and ecophysiological constraints to which they are subject. First the constraints on the mara will be listed; and then I will discuss the following adaptations: (i) breeding seasonality, (ii) ranging patterns, (iii) the pair-bond, and (iv) denning behaviour. This division between ecophysiological constraints and behavioural adaptations is convenient, but at least partly artificial, since both are features of a complex adaptive syndrome, which probably evolved simultaneously.

The environmental constraints on the mara are of three types:

1. Seasonal fluctuation in resource availability tied to most precipitation occurring in the fall and winter (March to July, see Chapter 2).

2. Unpredictable and wide dispersion of food (see Chapter 3).
3. Predation pressures on pups and adults (see Chapters 3 and 5).
4. The scarcity of open ground, and possibly small human settlements, for denning (see Chapter 5).

These are matched by three basic ecophysiological constraints:

1. The mara's food habits as highly selective grazers choosing only the most nutritious food items (see Chapter 3).
2. The body size of about 8 kg (see Chapter 2 and Appendix A), and light morphology adapted to cursorial movements.
3. The mara's reproductive physiology with long gestation (100 days) and lactation periods (77 days; see Chapter 5, and Dubost and Genest, 1974). This is probably due to the mara's phylogeny since all the caviomorphs have exceptionally long gestation and lactation periods for rodents (see Weir, 1974).

Seasonality of Breeding

In captivity mara's produce three to four litters a year (Dubost and Genest, 1974) while in the wild, at least on the Valdés Peninsula, most females probably produce only one litter a year (see Chapter 5). Seasonal fluctuation in environmental conditions in the wild must prevent maras from breeding throughout the year. Most births occur in September and October, before the summer dry season, and after the fall and winter rains (see Chapter 2 for details of seasonal patterns in precipitation). This timing

suggests either, or both of, the following: (i) the cold and wet winter weather may not be favourable for the pups to survive despite the presumed abundance of food at that time of year, and (ii) females may depend on stocking up energy as fat during the rains which they then use to get them through the long lactation and gestation periods. The consequences of breeding seasonality for the social system will be discussed below in the context of monogamy and communal denning.

Ranging Habits

Here I will address the following two questions: (i) what is the distribution of food resources and how is this related to mara ranging behaviour, and (ii) what are the spatial relationships between pairs of maras.

My data on the distribution of food resources for the mara are limited, and the main points will have to be inferred from observations of actual ranging patterns. Evidence is presented in Chapter 3 showing that maras are almost exclusively grazing animals, and that grasses probably make up a larger proportion of their diet than herbs (see Subsection 3.5.3). Also, results of vegetation sampling (see Subsection 3.2.5) suggest that, despite an appearance of uniformity, the distribution of grasses and herbs are unpredictable and irregular. The ranging behaviour of nine radio-collared maras was characterized by the following (see Chapter 3 for details):

- Ranges were not stable in size or location, and radio-collared animals constantly moved into patches (50 X 50 m cells) which they were not known to have visited before.
- The prevailing range size for two radio-collared maras at any given moment measured about 35 ha; while over a

year maras may cover an area of 200 ha (see Subsection 3.3.2).

- Pairs stay within one general area with their movements rotating around a central core.
- Mara pairs stayed for less than 50 mins in 80% of the (50 X 50 m) cells entered.
- During a given day pairs traveled up to 6326 m (X 1953 m), and spent 46% of their time grazing (an underestimate since it does not include time spent searching for food items).

The pattern of resource distribution suggested from these results is that the food in any given 50 X 50 m cell is quickly consumed since the animals spend so little time in each patch (< 1 hr); and that, since the animals were continually moving into new areas, resources are probably widely dispersed in an unpredictable and irregular manner. With an unpredictable pattern of resource distribution what keeps a mara pair in one general area? I suggest either, or all of the following:

1. They utilize a cropping regime to increase productivity (as suggested for other grazing species by McNaughton, 1979).
2. They must restrict their movements so as to stay in proximity to a good den site for pupping.
3. Familiarity with the locality is important for the animals to know:

    3.1. The location of different food resources (this might be particularly important if maras were selecting for diversity in their diet as do some primates; see Hladik, 1977).

    3.2. The location of cover as a means to evade predators.

4. The presence of other maras in the surrounding area restrict a pairs movements.

In the absence of more data it is difficult to distinguish between these possibilities; however, since scrub areas between den sites appeared sparsely populated by maras it is likely that the need to stay near a denning site must be an important factor restricting animals' movements.

What is the nature of the spatial relationships between mara pairs? When looked at over three monthly periods neighbouring mara's ranges may overlap up to 33% of their total area. However, the spatial correlation (see Section 3.5) between neighbouring maras was very low suggesting that, despite the range overlap, mara pairs were avoiding each other. Future studies may reveal that different mara pairs living adjacently are actually occupying floating territories, as has been reported for red foxes (see Doncaster, 1985; for other examples see Chapter 3). It seems likely that this putative spacing pattern would be tied to the ephemeral nature of food resources--with the food in any given (50 X 50 m) cell exhausted within an hour of a pair's arrival, competition between pairs foraging in close proximity is probably high and would thus favour animals staying widely spaced (see Jarman, 1974; and below). This pattern seems to break down during the driest part of the year, January and February, when large groups of up to 70 maras may be seen gathered together on dry lagoon beds (see Chapter 3). Maras very rarely drink, so they must depend on the moisture on and in plants to survive. At this time of year the grass and herbs in the scrub are extremely dry. I conjecture that the vegetation on the lagoons has a higher water content than the vegetation in the surrounding scrub due to the water table probably being closer to the surface; and thus, that maras prefer the lagoon vegetation at this time of year as a means of maintaining their water balance.

Final Discussion

The Monogamous Pair Bond

In Chapter 4 I presented data showing that maras are monogamous in the wild, and tested several hypotheses as to why mara's have adopted this social system which is so uncommon in mammals. My evidence for monogamy in maras in the wild is of two kinds: (i) 63% of the groups seen consisted of one male and one female, and (ii) the extreme degree of behavioural coordination between paired maras suggests that a strong pair-bond must exist. The two critical factors leading to monogamy in maras are, I argue, (i) the dispersion of food resources, and (ii) the brevity of the female's period of sexual receptivity. The salient points of the argument are reviewed below:

- As suggested above, the sparse distribution and unpredictable nature of food resources plays a pivotal role in mara spacing behaviour by forcing the animals to space out to avoid competing for the rapidly exhausted food resources in any one location. In these circumstances it is hard to avoid the conclusion that several animals feeding together would interfere with each other, and that this interference would increase at least in linear proportion to group size, and it would probably increase exponentially. Therefore, foraging considerations alone might favour maras being solitary. On the other hand, with maras spending on average 46% of their time feeding (see Chapter 3), during which time their heads are lowered and thus their ability to detect predators severely limited, it seems probable that they could be more vigilant, and hence safer, foraging in groups. Evidence for groups having higher vigilance than solitary animals has been shown in Klipspringer (Dunbar and Dunbar, 1980), Ostrich (Bertram, 1980), and meerkats (Pers. comm. D.W. Macdonald). A group of 2 or 3 maras might be the optimal compromise. While this argument may provide a

plausible explanation for observed group sizes, it has no direct bearing on the sex ratio of group members. Foraging groups might, for example, consist of single sex units. Therefore, the distribution of food alone would not necessarily lead to monogamy.

- The mara's oestrous period lasts for only a few hours; and the oestrus which leads to most births occurs in May and June, a time of year when groups of maras are widely dispersed (see Chapters 3 and 5). This short period of sexual receptivity, combined with the wide dispersion of females due to the distribution of food resources is, I argue, the critical factor favouring monogamy in maras. Firstly, the energetic costs for males of finding widely dispersed females would be very high; and, secondly, males would be forced into time consuming and energetically costly fights with other males over oestrous females. Under these circumstances the risk, for a male, of being at the wrong place at the right time would be high. Thus, female spacing patterns make it economically difficult for one male, however powerful he may be, to monopolize several females: the would be polygamist would simply exhaust himself between searching for females in oestrus, and fighting over the few he found. Also, selection on females may have acted to favour short oestrous periods as a way of 'forcing' monogamy on the males. Males, under these conditions, probably do best by securing one female; and to guarantee securing her the relationship must be stabilized well in advance. Having got caught in this system, due to resource dispersion, the males do best by maximizing their female's productivity through being highly vigilant, as will be discussed below (see also Chapter 4).

Once staying with one female for an extended period is favoured for a male, a range of factors have probably

acted together to enhance the benefits of monogamy. The most obvious feature of the pair-bond is the extreme degree of behavioural coordination between the male and female, 57% of the time they are doing the same thing, which may help the pair stay in contact (see Chapter 4). Further, and more important, there is a clear division of labour between the sexes. Because of the energetic demands of gestation and lactation (which are exceptionally long for rodents, see above) during the breeding season female maras spend a larger proportion of the day feeding (40%) than males (27%). On the other hand, males, with their reduced need to feed, spend more time sitting, the behaviour associated with highest vigilance; and also maintain contact with their mates (see Chapter 4). Thus females would be at higher risk from predation if grazing alone than in the company of a male. Males enhance their monogamous condition through watching for their females to maximize their safety (they also may guard the pups, see Chapter 5) and the amount of time they spend feeding, so that their joint offspring will have the full benefits of energy input from the female. The strength of the pair-bond in maras is remarkable since in captive situation, where opportunities for males to mate with several females exist, they still tightly maintain their monogamous bonds (see Dubost and Genest, 1974).

Communal Denning

During the breeding season groups of between 1 and 22 pairs of maras congregate at single den sites to raise their pups. The pups stay at the den for a period of about 6 weeks (after which they return to the den at night for a further 5 weeks), during which time their parents visit every day for about an hour to nurse the young (see Chapter 5 for details of parental care). Not only were dens used by

several pairs of maras, but dens were very clumped in distribution: several dens tended to be located within a few hundred meters of each other to form denning communities, usually centered on large openings in the scrub. The question of why maras den communally is a complex problem since the answer involves both the ecology of denning, and the mara's breeding biology and system of parental care. In Chapter 5 I tested three hypotheses as to the possible advantages to maras of denning communally. The available evidence suggests that communal denning is associated with increased protection from predators for pups and adults accrued through denning in groups of several pairs. The argument can be summarized as follows:

- There were numerous unused den sites at all three study areas, and maras dug new dens in each area during my stay in the field (see Sections 5.5 and 5.8). Thus, den sites are not limited, and so maras appear to choose to den communally.
- Pup mortality at dens was high, with 47% of the pups born at nine intensively monitored dens dying before reaching 6 weeks of age. These data, despite acknowledged sample bias, suggest that pup survival was higher at dens with larger memberships than at dens used by few pairs (see Subsection 5.4.6). It is not clear what proportion of the mortality was due to predators or disease, however, I present evidence that predators on mara pups include weasels, foxes, armadillos, and humans.
- As the number of adults present at a den increases, the number of adults sitting (the most vigilant behaviour category) increases while the proportion of adults sitting declines (see Section 5.8); thus, individually, adult maras were able to spend more time resting or grazing when more adults were present, while at the same time benefiting from higher safety from predation through increased vigilance overall at the den.

Final Discussion

- Despite the efforts of females to prevent pups which were not their own from obtaining milk, some young, nevertheless are able to 'steal' some suckles (see Section 5.5). This may play an important role in the survival of some, particularly orphaned, pups.
- Adults were present for more of the day at dens with larger memberships than at dens with smaller memberships, while individually they spent less time at the dens (see Section 5.8). This may be important for adults since they spend little time grazing around the den (see Subsection 4.6.3), and may benefit from spending as little time there as possible so that the females can graze to fulfill their high energetic needs (see above). It also may be safer for the adults when they are away from the highly conspicuous den sites.
- Pups almost never come out of the den except when adults are present, and when they do come out in the absence of adults the predominate behaviour is to sit by the den entrance (see Subsection 5.6.2). When adults are at the den, most or all of the pups present come out to graze and play, even when their own parents are absent. Thus, as the number of pairs at a den increases, individual pups are able to spend proportionally more time in the open, grazing and playing. This is important for the pups so that they can mature and leave the den as quickly as possible.

With these results it appears that a reduced risk of predation is a major advantage to why marag den communally. I detected little movement of animals between denning areas, so it seems certain that many of the animals sharing a denning area are related. Thus this system, which involves different pairs, in effect, sharing guard duty at the dens, may be enhanced by kin selection.

There may, however, be a second denning strategy (on which I collected no data) since I found 4 isolated pupping dens in the scrub each probably used by only one or two

pairs. I have no data on pup survival at these dens, but it seems likely that these sites provide safety to the pups through being highly cryptic. In the absence of more data further speculation would serve no useful purpose.

With these results I suggest two possible routes in the evolution of the mara's social system with its combination of communal denning and monogamy:

1. From an essentially monogamous starting point it has become advantageous for the maras to crêche their young. This could have happened either, because of existing pressures, or because of pressures that existed in the recent past.

2. Ancestral maras were even more group living, and hence probably polygynous. Then their habitat changed to favour monogamy (by becoming more patchy and unpredictable), but some of the advantages of the crêche remained. In this case one might consider monogamy as being imposed on a more gregarious system, rather than vice versa.

Distinguishing between these possibilities is difficult due to the lack of data on the mara's evolution. However, the latter possibility seems more probable, if only because coloniality is so widespread in the mara's caviomorph relatives regardless of their niche or habitat (Kleiman, 1977). Another point in favour of the second possibility is that the greater the advantages of communal denning the more likely that maras evolved monogamy after communal denning since the advantage of being in larger groups would demand foraging further afield by the members because of the patchy distribution of food. This would lead to the females being widely spaced out, and eventually to monogamy.

6.2 Comparison With Other Mammals

In this section I will be comparing the mara's adaptations with those of other large caviomorph rodents (those which weigh close to a kilo or more), a selected group of ruminant species, and hares. Several authors have made passing reference to the mara's morphological and behavioural convergence with the lagomorphs, and some species of ungulates (see for example Genest and Dubost, 1974; and Smythe 1970). Now, for the first time, it is possible to consider these comparisons in the light of data on mara behaviour in the wild. Summaries of morphological, behavioural, and ecological data on these selected species of rodents, ruminants, and lagomorphs are shown in Table 6.1. The questions I hope to address in this discussion are what does the mara share in common with each of these diverse groups of mammals, and what do these similarities tell us about the selective pressures leading to monogamy in mammals. The comparison with ruminants and lagomorphs may also shed some light on the phenomenon of convergent evolution.

Before beginning I must voice a note of caution regarding comparisons of this kind. The pressures which have led to a given species adopting a specific morphological or behavioural pattern are not necessarily those to which it is subject today. To fully understand a species' morphology and behaviour one must have an idea of both current and past pressures. Data on the factors affecting a species evolution in the past are usually unknown, and therefore any conclusions are inevitably tentative.

Table 6.1 (Overleaf)--Some morphological, ecological, and behavioural traits of the larger (≥ 0.3 kg) Caviomorph rodent species, the most cursorial lagomorphs (and hence similar to maras) for which good data are available, and the few ruminant species which are monogamous.

References: [1] this thesis [2] Dubost and Genest, 1974 [3] Rood, 1972 [4] Rood, 1970 [5] Lacher, 1981 [6] Herrera, 1986 [7] Smythe, 1978 [8] Gosling, 1981 [9] Kleiman, 1971 [10] Kleiman, 1974 [11] Weir, 1974 [12] Pearson, 1948 [13] Enders, 1935 [14] Weir, 1970 [15] Osgood, 1943 [16] Montgomery and Lubin, 1978 [17] Kingdon, 1982 [18] Dubost, 1984 [19] Dubost, 1980 [20] Dunbar and Dunbar, 1974 [21] Dunbar and Dunbar, 1980 [22] Hofman and Stewart, 1972 [23] Tilson and Tilson, 1986 [24] Monfort and Monfort, 1974 [25] Jungius, 1971 [26] Hendrichs, 1975 [27] Nowak and Paradiso, 1983 [28] Cowan and Bell, 1986 [29] Graf, 1985 [30] Boutin, 1980 [31] Pearson, 1951 [32] Tilson, 1980 [33] Monaghan and Metcalfe, 1985 [34] Lechleitner, 1958 [35] Frylestam, 1980 [36] Frylestam, 1986 [37] Boutin 1984 [38] Broekhuizen and Maaskamp, 1982.

Codes

Habitat	S - steppe or scrub (bare ground between plants), Grs - grasslands, Sv - savannah (grassland with scattered trees), F - forest, Of - open forest, Arb - arboreal, Rc - rock outcrops, nrW - near water, Aq - aquatic, Ub - ubiquitous.
Diet	Gz - grazer, Br - browser, Fr - fructovore, Gh - general herbivore, Sd - graminivore.
Group Size	P - pair, F - family, C - colonial, S - solitary, Sc - social.
Range Type	Ft - floating territory, T - territory, H - undefended home range, Ovh - overlapping home range.
Activity	D - diurnal, N - nocturnal, C - crepuscular.
Mating System	Mng - monogamous, Prom - promiscuous, Poly - polygynous, Hi - dominance hierarchy.
Anti-predator	Fl - flight, Cv - cover.

Species	Weight (kg)	Habitat	Diet	Group Size	Home Range Size (ha)	Home Range Type	Activity Patterns	Mating System	Anti Predator Behaviour	References
CAVIOMORPH RODENTS										
Dolichotis patagonum Mara	6-16	S	Gz/Br	P	35 (use) 200 (year)	FT	D	Mng	Fl	1,2
Cavia aperea Wild Guinea Pig	0.70	S	Gz/Br	C	0.12-0.14	Ovh	C	Prom	Cv	3
Galea musteloides	0.49	S	Gz	C	0.40		D	Prom	Cv	3
Kerodon rupestris Rock Cavy	1.0	Rc	Br	C			D ?	Poly/Hi	Cv	5
Microcavia australis Desert Cavy	0.3	S	Br	C	0.22-0.39		D	Prom	Cv	3,4
Hydrochoerus hydrochaeris Capybara	35-64	Aq/Sv	Gz	1-40	10-20	T	C	Pl/Hi	Water	6,27
Dasyprocta agouti Central American Agouti		F	Fr	S/P	1-2	T	D/N	Mng	Cv	7,13
Myocastor coypus Coypu	5-10	Aq	Gh	C			N	Poly	Cv/Water	8
Myoprocta sp. Acouchi	0.6-1.3	F	Fr	C			N		Cv	9,10
Agouti paca Paca	6.3-10.0	F/nrW	F/H	S/P			N		Cv	10,13
Lagostomus maximus Plains Viscacha	8.0	S	Gz/Sd	15-50			C/N	Prom	Cv	10,11
Lagostomus peruanum Mountain Viscacha	0.9-3.0	S/Rc	Gh	4-75			D	Prom	Cv	12,31
Chinchilla sp. Chinchilla	0.5-0.8	Rc	Gh	100			C/N		Cv	14,15
Capromys ingrahami Hutia	0.7	F/Rc/Arb	Br	S		H	N		Cv	10
Coendu prehensilis Coendu	0.9-5.0	F/Sv/Arb	Gh	S	8-38		N	Poly	Quills	16,27
ANTELOPES										
Cephalophus monticola Blue Duiker	3.5-9	Of	Br	P	2.5-4.0	T	D	Mng		17,18,19
Oreotragus oreotragus Klipspringer	10.9-12.2	Sv/Rc	Br	P	6-9	T	D/N	Mng	Fl	20,21,32
Madoqua kirkii Kirk's Dikdik	5.5	S	Br	P	7-8.4	T	D/N	Mng		17,22,23,26
Ourebia ourebi Oribi	18	S/Sv	Gz	P/F	20-45	T		Mng	Fl/Cv	17,24
Redunca arundium Southern Reedbuck	50-80	Sv/Reeds	Gz	P	35-60	T	C	Mng	Fl/Cv	17,25,26
HARES										
Lepus americanus Snowshoe Hare	1.0-1.7	F	Br	S/Sc	3-10	H	D/N	Poly	Cv	28,29,30,37
Lepus europaeus European Hare	3.5-4.3	Grs	Gz	S/Sc	12-300	H	N/C	Poly	Fl/Cv	28,35,38
Lepus californicus Black-tailed Jack rabbit	2.2-2.7	S/Grs	Gz	S/Sc	145	H	D/N	Poly	Fl/Cv	28,34

6.2.1 Maras as a Caviomorph Rodent

Caviomorph rodents have a wide variety of social systems and live in a wide range of habitats (see review in Kleiman, 1974; and Lacher, 1981). They range from colonial plains dwelling species like the plains viscacha (see Weir, 1974) to mainly solitary forest species like the agouti (see Smythe, 1978). Below I list the most striking comparisons between maras and the other caviomorphs (for references see Table 6.1):

1. Maras have by far the largest home range size of any of these species. Looking at the prevailing range size (30-35 ha) the only species with a home range of a similar size is the coendu ($\leq$ 38 ha).
2. Maras are the most cursorial species, relying mainly on speed to escape from predators instead of retreating to an earth (e.g. plains viscachas), thick cover (e.g. agoutis), or water (e.g. capybaras).
3. With the possible exception of the paca, maras are the second largest of these species (6-16 kg) with only the capybara weighing more (35-64 kg).
4. All the rock and steppe dwelling species (including the mara) are diurnal or crepuscular, with the exception of the crepuscular and nocturnal plains viscacha; while the forest and water dwelling species are all primarily nocturnal.
5. The savannah dwelling species, other than the mara, all live in colonies and have a promiscuous or polygynous mating system. Even maras form colonies during the pupping season, as reviewed above. In contrast, all the forest dwelling species are primarily solitary.
6. The only other species which is definitely monogamous is the agouti, *Dasyprocta aguti*. They are animals of dense tropical rain forest with one male and one female sharing a territory; however, the paired animals are

rarely together and they live a mainly solitary existence.

Thus, while maras share being primarily diurnal with most of the other plains dwelling caviomorphs, in all other features of their ecology they are strikingly different. Maras can be seen as unique amongst the caviomorph rodents, for which data are available, in their ecology, morphology, and behavioural adaptations.

6.2.2 Maras and Ruminants

The similarities between maras and ruminants which previous authors have noted are as follows:

- Morphological: Unlike most rodents, maras fall well within the range of linear dimension and weight embraced by ungulates. Maras have the long legs, particularly the powerful hind legs, and general body form of a small ungulate. Further, the paws are reduced in size and hoof like (see Dubost and Genest, 1974).
- Escape Behaviour: Maras usually rely on flight to escape from predators, and can attain speeds of at least 60 kmh for short stretches. Also, and most remarkably, maras use stotting as part of their predator evasion repertoire, a characteristic ungulate escape behaviour, the function of which is as yet unclear (see Smythe, 1970; and review in Caro, 1986a).

Rather than review the social organization of all species of ungulates (see reviews of ungulates in Geist, 1974; and antelopes in particular in Jarman, *Op. cit.*), I will here look at just those species which are known to have a strong monogamous pair bond, and ask the question of what these species have in common with each other and with maras. In the literature I have found only 5 species which

are known to maintain tight year round monogamous bonds in the same manner as maras. These are: (i) klipspringer (*Oreotragus oreotragus*), (ii) Kirk's dikdik (*Madoqua kirkii*), (iii) oribi (*Ourebia ourebi*), (iv) southern reedbuck, (*Redunca arundium*), and (v) blue duiker, (*Cephalophus monticola*, see Table 6.1 for references). Aside from a social system where pair-bonded males and females are usually in contact with their mates, all five of these species share most of the following ten characteristics (see Table 6.1 for references):

1. They live in relatively open habitat, either steppe or grassland, with the exception of blue duiker which lives in open forest.
2. Living in pairs is probably an anti-predator adaptation which, at least in klipspringer and blue duiker, allows the female and male to invest more, respectively, in caring for the young, and guarding the female and young from predators.
3. Their main escape strategy is to flee to dense cover or rocks, although they also rely on speed and dodging to escape.
4. Reedbuck, klipspringer, and oribi are all occasionally observed in bands comprising several family units. These large groupings do not persist for long and are usually associated with a seasonal and localized abundance of food.
5. There is little or no sexual dimorphism.
6. Blue duiker, klipspringer, and Kirk's dikdik were classified in Jarman's (1974) class 'a' feeding style: concentrate selectors feeding very selectively on a wide range of plants, using particular plant parts only, and typically remaining in one vegetation type and in one small home range throughout the year. Oribi and southern reedbuck were classified in Jarman's (*Op. cit.*) class 'b' feeding style: also highly selective though less so than class 'a', usually feeding entirely on a

range of grass species or browse (oribi concentrate on young grass shoots), and remaining in one vegetation type and one home range throughout the year.

7. Jarman (*Op. cit.*) has described the pattern of food distribution for these species as follows: the food items for class 'a', and to a lesser extent class 'b', are spatially scattered small distinct items separated by varying distances from the next similar acceptable item.
8. Four of these five species are known to be diurnal. This is probably an adaptation to their open habitat, since their main predator defense is early detection so that they can either flee or hide (see Dubost, 1980). Other small ruminants rely on crypsis to evade predators (e.g. musk deer; Green, 1985).
9. All are territorial.
10. Four are relatively small: varying from 4 to 9 kg for the blue duiker and Kirk's dikdik, to 10 to 15 kg for klipspringer, to 14 to 21 kg for oribi. The southern reedbuck is the exception as it weighs between 50 and 80 kg, though even this species is not big compared to the many ruminant species weighing over 100 kg.

These characteristics contrast markedly with other ruminants which are typified by the following traits:

The smaller species such as muntjac, duiker, sunni, steenbok and grysbok, are all solitary with groups almost never comprising more than a lone female and her offspring (see Green, 1985, for review of these species). Some of these species may be facultatively monogamous (Kleiman, 1977) with females sharing a territory with a male but almost never coming into contact. But most are polygynous with a male's territory probably overlapping that of several females (e.g common duiker, Dunbar and Dunbar, 1979). They are concentrate selectors (in

Jarman's class 'a' feeding style), as are 3 of the above species, and most live in dense forest on permanent territories. These species are mostly nocturnal and rely on crypsis to escape predators. Females tend to be larger than the males; which Ralls (1976) has suggested may be related to competition for food being higher amongst females than males because of the energetic demands of reproduction.

The larger ruminants are, in general, open plain dwellers. There are too many variations of their social systems to list here (see reviews in Jarman, *Op. cit.*; and Geist, *Op. cit.*), but they tend to live in groups of several or many females with one or more accompanying males, and their mating systems are invariably polygynous. In food habits they range from Jarman's comparatively selective class 'b' feeding styles (discussed above), to the often migratory class 'd' which moves in pursuit of grass in the optimum condition, to class 'e' which feed unselectively on a wide range of grasses and browse and move seasonally within a large home range. Jarman (*Op. cit.*) has shown a strong trend in increasing body size in the different species from class a to the class e feeding styles.

Thus, the monogamous ruminants which maintain year round pair-bonds seem to fall into the middle ground between the small solitary ruminants and the group living ones. With these comparisons made it is clear that there are numerous similarities between the truly monogamous ruminants and maras. In the list of characteristics of these species, maras match every one perfectly except for the ungulates' strict territoriality. This difference may be explained by the maras need to stay near a communal den site, which forces pairs into tighter contact than might be preferred for purely foraging purposes. Further, my data suggest that

pairs are avoiding each other in time, in effect occupying floating territories (see above), even if their ranges do overlap considerably. It has often been suggested that social organization is more flexible than either ecology and morphology (e.g. Monaghan and Metcalfe, 1985); thus, it seems likely that the selective pressures which have led to monogamy in maras are similar to those in the ruminants since the adaptations made by both groups are strikingly similar.

6.2.3 Maras and Lagomorphs

Maras have often been compared with the lagomorphs since their long ears and habit of sitting lend them the appearance of large hares (*Lepus*). One of their common names in english is the Patagonian hare, which is also the translation of the common Argentine name for them: *Liebre Patagónica*. Below I summarize data on the ecology and behaviour of hares to allow a comparison to be made (again see Table 6.1 for references).

1. Hares weigh up to 5 kg.
2. They normally inhabit grasslands, steppe or forest.
3. As a means of evading predators, hares depend on flight (they can attain speeds of 80 kmh) as well as crypsis.
4. Hares are concentrate selectors, feeding mainly on grasses and herbs.
5. They may be active during the day and night.
6. Daily movements of hares vary between 1.6 and 16.2 ha, but they may occupy ranges of up to 300 ha.
7. Most species of hares are solitary except during the breeding season; though European hares will occasionally band together to forage in groups under certain patterns of food distribution (see Monaghan and Metcalfe, 1985). The mating system is polygynous with males fighting over and chasing females.

8. They rarely use dens and the young are often born in the open.

These data come from hares living in a variety of environments, however introduced European hares, *Lepus europeaus*, were abundant at all my study areas and nothing I saw there disagreed with the description of their behaviour and ecology made above. Judging from these results, hares share few behavioural or ecological features with maras. In fact, hares seem much more similar to the generally smaller non-pair-bonded ruminants described above than they do to maras.

6.3 Concluding Remarks

The most striking feature of these comparisons is that maras emerge as a species with a unique combination of traits: their combination of monogamy with communal denning is so far unknown in any other species of mammals. Despite this, their similarity with the monogamous ruminants is striking in a wide range of ecological, morphological and behavioural adaptations. This remarkable degree of convergence between maras and the monogamous ruminants is a notable example of the long term effects of natural selection. One wonders then, whether some day maras will not abandon their communal dens to become even more like an antelope, or whether antelopes will take up communal denning.

Appendix A

MARA WEIGHTS AND MEASUREMENTS

When maras were captured for the purposes of attaching radio-collars and plastic identification collars the following measurements were recorded: (i) hind foot length, (ii) total length, (iii) and weight. Measurements and weights were obtained on a total of 23 adult maras: 15 females and 8 males. The results are summarized below:

Mara Weights: The heaviest animal recorded was a pregnant female who weighed 9.8 kg. The lightest was a female who weighted 6.6 kg. The mean weight of the 23 animals weighed was 8.12 kg (± 0.75).

Differences in Weight Between Males and Females: The mean weight for the 8 males captured was 7.73 kg (± 0.62), and for the 15 females it was 8.33 kg (± 0.74). No significant differences were found between the weights of males and females using the t-test (T = 2.05, P = 0.057). All but four of the females weighed were captured during periods when they were likely to be pregnant or lactating: 1 was pregnant, 1 was lactating, and the other 2 may have been pregnant. Two near term foetuses taken from a dead female weighed 0.358 kg and 0.345 kg, respectively. It thus seems likely that the weighed females might have been 1 kg or so heavier than their non-pregnant weight. Future investigations may show that on average males weigh more than non-pregnant females.

Skeletal Size--Hind Foot Length: Hind foot lengths were obtained on 25 maras (10 males and 15 females). The mean length was 17.2 cm (0.91). No significant differences were found between the hind foot lengths of males and females using a t-test (T = 0.00, P = 1.0).

Skeletal Size--Total length: Total lengths, measured along the body, were obtained on 19 maras (7 males and 12 females). The mean total length was 75.28 cm (± 3.56). Males averaged 77.71 cm (± 3.09), and female averaged 73.87 cm (± 3.11). Males were found to have a significantly greater total length than females using a t-test (T=2.59, P < 0.02).

The suggestion from these results is that males may be slightly larger (greater total length and possibly heavier weight when weights of non-pregnant females are used) than females. However, without more data these results should be taken as strictly preliminary.

Appendix B

EVREC: An Event Recorder Program for the EPSON HX20

In this appendix a program listing and description is provided for the EVREC MICROSOFT BASIC Program written for the EPSON HX20 portable microcomputer for recording behavioural field data on maras. The HX20 proved to be an extremely versatile and effective tool for collecting behavioural data. It was also remarkably tough--it withstood hundreds of hours of use in sometimes freezing conditions. It even went through several dust storms with out having any serious problems. EVREC was written to record behavioural observations on maras using the Event Recorder data collection protocol discussed in Chapter 2. The EPSON HX20 used had only a 16 kbyte memory, so there was a premium on space and the program was written in as concise form as possible. Because of the limited memory, few error checking routines were included in the program, and it was designed to be as simple as possible to minimize problems. The machine's real time clock was used for all behaviour times. This has the disadvantage that times were only accurate to a second.

Program Listing

```
10 TITLE "EVREC"
20 WIDTH 20,4,1:CLEAR 150,11000:DEFFIL 13,0:ISP$=""
30 DEF FNTIM=VAL(LEFT$(TIME$,2))+(VAL(MID$(TIME$,4,
          2))/60)+(VAL(RIGHT$(TIME$,2))/6000)
40 CLS:PRINT" Evrec Program":PRINT" AB Taber":
          PRINT" Type Return":INPUT"",DUM$
50 CLS:INPUT"Menu:  1)Strt 2)Cont3)Evr  4)Edt
          5)Key 6)Copy 7)End ";FC%:
          IF FC%<1 OR FC%>7 GOTO 50
60 ON FC%GOSUB 90,130,180,290,360,400,540
70 IF FC%=1 OR FC%=2 THEN FC%=3:GOTO 60
80 GOTO 50
90 CLS:INPUT"LOCATION ";LOC$
100 OBD$=MID$(DATE$,4,2)+LEFT$(DATE$,2)+
          RIGHT$(DATE$,2):STIM=FNTIM
110 PUT%0,STIM,OBD$:PUT%,FNTIM,LOC$,:LIN%=2
```

```
120 RETURN
130 CLS:PRINT"CONTINUE INPUT"
140 GET%841, STIM,DAT$
150 LIN%=VAL(DAT$)
160 RETURN
180 CLS
185 LOCATE 0,0:PRINT"@ Menu  X Back Line"
190 LOCATE 0,3:PRINTLIN%;">";:A$=INKEY$
200 IF A$="@" THEN DAT$="END":GOTO 250
210 IF A$="X" OR A$="x" THEN LIN%=LIN%+1:GOTO 185
220 IF A$=ISP$ AND FNTIM>OSCN+0.25 THEN LOCATE 1,1:
        PRINT"SCAN NOW":GOTO 185
230 IF A$=ISP$ GOTO 185
240 PRINT A$;:INPUT"",DT$:DAT$=A$+DT$:
        IF LEFT$(DAT$,3)=SCN THE OSCN=FNTIM
250 GOSUB 560
260 IF LEFT$(DAT$,3)="END" THEN PUT%841,STIM,
        STR$(LIN%):RETURN
270 IF LIN%>800 THEN LOCATE 0,1:PRINT"ALERT ";
        841-LIN%;" LINES LEFT"
280 LIN%=LIN%+1:GOTO 185
290 CLS
291 LOCATE 0,0:PRINT"1 Move 2 Get 3 Alter  4 Menu
        Choice":CHS%=VAL(INKEY$):
        IF CHS%<1 OR CHS%>4 GOTO 291
300 IF CHS%=4 THEN RETURN
310 IS CHS%=1 THEN LIN%=LIN%+1
320 IF CHS%=2 THEN LOCATE 0,3:INPUT"Line Num ";Lin%
330 GOSUB 580
340 IF CHS%=3 THEN INPUT"New Data";DAT$:GOSUB 570
350 GOTO 291
360 CLS:PRINT"KEY CODING ROUTINE":KEYLIST
370 INPUT"KEY NUMBER";FKN%:INPUT"STRING";FK$
380 KEY FKN%,FK$
390 RETURN
400 CLS:PRINT"DATA COPY"
410 INPUT"COPY DATA TO TAPE(1) OR PRINTER(2)";CHS%:
        IF CHS%<1 OR CHS%>2 GOTO 410
420 INPUT"FILE NAME";FILN$:LIN%=0
430 LPRINT"FILENAME = ";FILN$:IF CHS%=2 GOTO 480
440 PRINT"TAPE COUNT=";TAPCNT:INPUT"OK Y/N";IAN$
450 IF IAN$="N" OR IAN$"n" THEN INPUT"NEW TAPE
        COUNT ";TC%:WIND 0:WIND TC%
460 LPRINT"TAPCNT = ";TAPCNT
470 OPEN"O",£1,FILN$
480 GOSUB 580
490 IF CHS%=1 THEN PRINT£1,TM,DAT$
500 IF CHS%=2 THEN LPRINT USING"£££ ££.££££ &";
            LIN%,TM,DAT$
510 IF LEFT$(DAT$,3)><"END"THEN LIN%=LIN%+1: GOTO 480
520 IF CHS%=1 THEN CLOSE£1: LPRINT"END TAPCNT = ";TAPCNT
530 RETURN
540 CLS
550 END
560 TM=FNTIM
```

```
570 PUT%LIN%,TM,DAT$
580 GET%LIN%TM,DAT$
590 LOCATE 0,2;PRINT USING"£££ ££.£££££";LIN%,TM,DAT$
600 RETURN
```

Line by Line Comments on Program

10 - 80 — Initializing routines. Line 30 turns the EPSON TIME$ function into a real number. Line 50 is the main program menu with the options being: (1) start observation session, (2) continue old session, (3) change from edit mode to data input mode, (4) initiate edit mode, (5) code function keys to any string, (6) copy data to tape or microprinter, (7) end program.

90 - 120 — Start observation session: input observation site, and the program automatically codes the date and start time.

130 - 160 — Restart an observation session. The last line number used is retrieved from line 841 in the RAM file. This could be changed in a machine with a larger memory.

180 - 280 — Main data input subroutine. Includes code to continuously check the time using the INKEY$ function so as to determine when it was time to do a general scan. Flashes "Scan Now" every 15 minutes, though this can be adjusted (line 220). Originally I had the program beep when it was time to do a scan using the SOUND command. This sound was occasionally audible to the observed maras so I subsequently removed the line.

290 - 350 — Subroutine to edit existing data in the RAM file. Functions are (1) move (display) the next line, (2) get a data record specified by line number, (3) alter the current data record, (4) return to main program menu.

360 - 390 — Subroutine to code function keys.

400 - 530 — Subroutine to transfer data to microcassette or to print data on the built in printer.

540 - 550	Ending Subroutine.
560 - 600	Subroutine to store and retrieve data from RAM file: called by several of the above subroutines.

Appendix C

Birth Protocols

Birth protocols for the three mara females observed giving birth during the 1983 and 1984 breeding seasons at the El Salitral and La Blanca study areas.

14 August 1983

An unknown pair was observed giving birth at Chicken den at Puesto El Salitral. This was the first time I saw pups this year, and perhaps one of the first births of the 1983 breeding season.

10:58 Pair arrives and female immediately goes to mouth of den while male sits 1 m away. Female difficult to see as only head and back visible above den's mouth. -- 11:20 Pair moves 30 m away to another den site used by burrowing owls. -- 11:25 Pair back at main den and female grazes while male sits nearbye. -- 11:28 Another pair approaches den but are chased off by male. After chase male returns to female, zig-zag displays and anal drags. The new pair sits 50 m away from den. Male sits alertly. -- 11:32 Pair goes back to owl's den and the female stands in the den's mouth. -- 11:45 Pair trotts a few meters from the owl's den. -- 11:46 The female approaches the new pair. Then the male heads her off back towards the owl den, away from the other pair. Both males zig-zag display towards their respective mates.-- 11:50 The pair trotts back to the owl's den and the female disappears inside. -- 12:00 The female walks towards the original den and then back to the owl den. -- 12:06 Both animals are at main den. -- 12:10 Female stands in the den mouth and the male sniffs her genitals. -- 12:15 The female disappears into the den mouth. The male waits outside. -- 12:20 Female sits with her nose down in den and then stands and digs at the mouth of the den. -- 12:20-12:50 Female alternates sitting in the den mouth with digging. -- 12:55-13:35 Female is mostly out of site in the den mouth. She alternates sitting and standing. During this time she gives birth to two pups. --

13:36 A quivery little pup appears by the side of the female. The pups ears are erect but it can barely walk. The male approaches den and sniffs pup. -- 13:39 Pup goes towards male 1 m from den. Male sniffs pup and then it goes back into den. -- 13:40 Female nurses the pup in den mouth. male sits nearbye. -- 13:45 Female nursing two tiny pups. -- 13:54 One pup totters over to male 1 m away. He sniffs the pup and then jerks away. Pup resumes suckling with other one. -- 14:00-14:15 Female mostly out of sight in the den mouth with the pups. -- 14:15 Female grooms pups. -- 14:20 Female nursing both pups. male grazes 5 m away. -- 14:28 Pup goes towards male. Male jerks away and then pups go back into den. -- 14:35 Female leaves den and grazes 1 m away. Pups grazing inside den mouth. -- 14:36 Male zig zag displays towards the female and then briefly half mounts her. The pups are out of view in den. -- 14:40 Female presents her genitals to the male and the male zig zag displays. -- 14:45 pair moves off chin-rump-following. -- 14:46 Male urinates on the female who presents genitals. -- 14:50 Male and female graze about 100 m from den. -- 14:55 Male anal drags. -- 14:59 male mince steps towards the female and half mounts her. The female walks away and then pair disappears into the scrub.

15 September 1983

The radio collared female ELF was seen to give birth to one pup in the mouth of Ash Den. The den was already active with at least 8 pups already in it.

09:55 ELF and male (EL1) walk to den with the female leading. -- 09:59 Male goes into den mouth and 8 pups emerge. -- 10:00 ELF and EL1 stand and sniff pups in the den's mouth. -- 10:10 Both move away from den and ELF sniffs pups while her mate sits nearbye. -- 10:15 ELF lies down and her mate sits. -- 10:20 ELF sits and sniffs pups which are trying to suckle. -- 10:30 ELF goes into den mouth and begins to dig. -- 10:32 ELF leaps out of den and walks over to hide and examines it from about 10 m away. I stop breathing. -- 10:35 ELF goes back to den and sits near mate. -- 10:38 EL1 goes towards a new pair. The males face off and then EL1 chases the new pair's male away. The new pair sits 30 m from den. ELF and EL1 sit by den. -- 10:41-10:45 EL1 runs towards the new pair and chases the male 3 times. -- 10:46 Another pair arrives and the new female whistles. EL1 chases them away. -- 10:50 ELF lies in den mouth, EL1 sits alert next to her. The other two pairs sit 30 m from den. -- 10:51 EL1 again chases one of the new males who has attempted to approach the den. EL1

bites at and rips some hunks of fur out of the other male's coat. -- 10:55 ELF and EL1 sit at den. ELF is in den mouth. -- 11:03 EL1 chases an approaching male away. -- 11:07 ELF walks away from den and EL1 follows. Both other pairs immediately go to den and are surrounded by pups. -- 11:10 ELF and EL1 graze 20 m from den. -- 11:18 EL1 chases both new pairs away from den. ELF goes back into den mouth. - - 11:20 ELF digs at den mouth and EL1 sits alert about 10 m away. -- 11:25 Four adults and two pups all are around the den mouth. ELF lies in den mouth and some of the other females nurse their offspring. -- 11:40 ELF stands and digs in den mouth. Other animals have moved 10-30 m away. -- 11:45-11:50 ELF stands in den mouth. -- 11:51 ELF chases one pair away from den a few meters. -- 11:55 ELF gives birth to one pup. First I see two contractions and then pup comes out in bag. The female licks the bag off the pup and then pup wriggles a bit. Then the pup crawled down into the den mouth. From birth to when pup disappeared in den took about 20 seconds. All the other pairs have disappeared, probably as a result of the peon's yelling. -- 12:00 ELF stands in den mouth with her nose down with pup out of site inside. EL1 lies 1 m away from den. -- 12:05-13:04 ELF sits mostly out of site with pups in den mouth. EL1 spends most of time lying nearbye. -- 12:50 EL1 chases one pair away 5 m then returns to lie by den. -- 13:04 ELF chases one pair and then another away from den. --1308 ELF is nursing one tiny pup but having difficulties with another larger pup which continually tries to suckle. -- 13:10-13:25 ELF sits in den mouth and nurses pup. -- 13:25 ELF chases a size 2 pup away. EL1 chases another pair away from den and then trotts back to den and lies down. -- 13:30 ELF lies out of site in den mouth with her own tiny pups and three other medium size pups. -- 13:35 EL1 chases a pair away 40 m. He sniffs the other female's rump as she presents genitals. -- 13:36 EL1 chases the pair two times. -- 13:40 ELF sits outside den mouth 1 m. -- 13:41 EL1 again chases a pair. -- 13:43 ELF lets the new born pup and a size 3 pup suckle. She then sniffs size 3 and chases it away. -- 13:43 ELF nurses size 1 and two size 3 pups. EL1 off chasing other pairs again. -- 13:51 EL1 chasing again. There are only two other females near the den now and no other males because of EL1's chasing. -- 13:52 A size 3 pup suckles ELF although she has repeatedly chased it off. -- 13:53 EL1 off into the bushes chasing another male. -- 13:55 ELF is nursing a size one and size 3 pups. EL1 sits by den. -- 13:57 EL1 chases a single male in a great 100 m sweep through the scrub, then he runs back to the den. -- 14:04 ELF again permits size 3 pups to suckle although she has moved away from it and bitten the pup once. EL1 off chasing solitary male again. -- 14:05 ELF nursing size 1 and size 3 pups by den. -- 1410 EL1 chases single male 100 m from den and then returns to ELF. -- 14:15 ELF lies by den, her pup is out of site in den. EL1 again chasing solitary male. -- 14:20 EL1 twice chases an unmarked pair 30 m from den. the male zig-zags towards mate. --

14:25-14:45 ELF and EL1 lie and sit by den. -- 14:45-15:18 EL1 chases animals away from den 10 times. ELF sits and stands by den and sniffs a size three pup once. Her pup is out of view in den. -- 15:18 ELF walks away from the den with EL1 following. EL1 zig-zag displays at ELF as she presents genitals and enurinates back at him. Then both disappeared into the scrub with EL1 chin-rump-following.

15 September 1984

SYF gives birth at the main Ash den. There were already several pairs in residence.

10:25 SYF shows up at the den and is declared a focal pair for event recorder scans. -- 10:38 SYF is in the mouth of the den. SY1 (SYF's mate) chases mara CAM away from den. -- 10:42 SYF in the den mouth chases some pups. -- 10:45 SYF sits about 5 m from the den and SY1 grazes. Four tiny pups sit outside den mouth. -- 10:50 SY1 chases CA2 and then turns and runs back to SYF. CA2 pair queues. -- 10:51 CAM runs towards the den. SY1 runs towards CAM and turns him away. -- 10:53 SY1 chases CA2 away from the den and from SYF. -- 10:54 SYF sits and SY1 sits alert near den as CAM pair approaches. -- 10:55 SY1 again chases CA2 away from the den. CAM runs towards CA2 after chase. SY1 is keeping the other pairs away from his female at the den giving her peace in which to give birth. -- 10:57 CAM pair leaves with one tiny pup, taking it away to nurse it in peace from SY1's chases. -- 10:58 A new pair arrives and SYF chases them away. -- 11:00 SYF grazes about 30 m from the den while her mate sits nearbye. - - 11:02 The new male runs towards SYF and SY1 and then SY1 chases them off. SYF and mate now about 20 m from den. -- 11:03 SYF now grazing. -- 11:06 SYF and mate now at the old Ash den entrance. SYF goes into den's mouth. -- 11:09 SYF and SY1 go towards the main den. SYF trotts and SY1 stotts towards the den. The pair at the den chases SY1 away. -- 11:15 SYF grazes about 10 m from den and SY1 sits alert. Then SY1 runs towards the den but is chased away by the male of the pair which is in possession of the den. The two males face off and chase. SYF lost control when she wandered off to look at the old den. -- 11:17 SYF gives birth to one pup about 10 m from the den's mouth in the open air. SY1 sniffs his "own" pup after first facing off briefly with SYF. Then both the male and female lick the pup. -- 11:19 SYF sniffs the pup twice. She is about 5 m from the den with her pup. -- 11:21 SYF leads the pup towards the den. The pup can barely walk and staggers to the den which is about 10 m away. It looks incredibly fragile and tiny out in the

open. -- 11:24 CAM pair reappears and go towards the den. SY1 chases them off and this time remains in control of the den. SYF moves to the den mouth with the tiny pup. CA2 stays near den while CAM wanders off grazing. -- 11:33 CAM stotts towards the den. SY1 chases CAM and CA2 away from the den. He first chases CA2 off and then CAM runs to join her. -- 11:34 SYF, who is now in the den mouth, gives birth to another pup. -- 11:36 SYF digs deep in the mouth of the den and then lies down in den mouth -- 11:41 SYF twice chases a pup. -- 11:41-12:09 SYF mostly out of site in den mouth with pups. -- 12:10 SYF nurses two tiny pups. Then briefly breaks off nursing to chase a pup away. -- 12:11 SYF digs in den mouth then she sniffs a pup and moves 5 m from the den with a tiny pup tottering after her. Then SYF goes back to the den entrance and chases pups, digs and sits, all partly obscured from view. -- 11:36 Another male stotts towards the den leading his female. SY1 runs towards the interlopers. The male zig-zag displays towards the female, the two males face off, and then SYF chases them off. The new female looks pregnant. -- 12:46-13:09 SY1 chases the new pair three times as the female repeatedly tries to approach the den. -- 12:48 SYF eats the afterbirth. -- 13:12-13:30 SYF combines nursing with chasing off pups. She chases pups 5 times and although nurses principally her new-born pups some other small pups occasionally steal suckles. -- 13:30 SYF moves away from den and grazes while her mate sits nearbye. -- 13:37 SYF and mate move away from area into scrub.

Appendix D

Paper in Notes from the Mammal Society No. 48

Taber, A.B. and Macdonald D.W. 1984. Scent dispensing papillae and associated behaviour of the Mara, *Dolichotis patagonum*, (Rodentia, Caviomorpha). Notes from the Mammal Society No. 48. J. Zool., Lond. 203, 298-301.

References

Ables, E.D. 1969. Home range studies of red fox *Vulpes vulpes*. J. Mammal. 50, 108-120.

Alexander, R.D. 1974. The evolution of social behaviour. Annu. Rev. Ecol. Syst. 5, 325-383.

Altman, J. 1974. Observational study of behaviour: sampling methods. Behaviour. 49, 227-267.

Amlaner, C.J. 1980. The design of antennas for use in radio telemetry. In: C.J. Amlaner and D.W. Macdonald (eds), A Handbook on Biotelemetry and Radio Tracking. Pergamon Press, Oxford. Pp 251-262.

Axelrod, R. and Hamilton, W.D. 1981. The evolution of cooperation. Science (Wash., D.C.) 211, 1390-1396.

Barkstrom, B. 1981. What time does the sun rise and set? Byte, 6, 94-114.

Beltramone, C. 1981. Rasgos fisiographicos de Peninsula Valdes. Centro Nacional Patagonico, Chubut, Argentina. Contribution 46.

Bertiller, M.B., Beeskow, A.M., and Irisarri, M. del P. 1981. Caracteres fisonomicos y floristicos de la vegetacion del Chubut. 2. La Peninsula Valdes y el Istmo Ameghino. Centro Nacional Patagonico, Chubut, Argentina. Contribution 41.

Bertram, B.C.R. 1978. Living in groups: predators and prey. In: J.R. Krebs and N.B. Davies (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford. Pp 64-96.

Bertram, B.C.R. 1980. Vigilance and group size in ostriches. Anim. Behav. 28, 278-286.

Bhadresa, R. 1986. Faecal analysis and exclosure studies. In: P.D. Moore and S.B. Chapman (eds), Methods in Plant Ecology (2nd edition). Blackwell Scientific Publication, Oxford. Pp 61-72.

Bick, G.H. and Bick, J.C. 1965. Demography and behaviour of the damselfly, *Argia apicalis* (Say), (Odonata: Coenagriidae). Ecology, 46, 461-472.

Boutin, S. 1980. Effect of spring removal experiments on the spacing behaviour of female snowshoe hares. Can. J. Zool. 58, 2167-2174.

Boutin, S. 1984. Home range size and methods of estimating snowshoe hare densities. Acta Zool. Fennica 177, 275-278.

Braun-Blanquet, J. 1932. Plant Sociology: The Study of Plant Communities. McGraw-Hill, New York.

Broekhuizen, S. and Maaskamp, F. 1982. Movement, home range and clustering in the European hare (*Lepus europeaus*). Z. Saugetierk. D. 47, 22-32.

Bruning, D.F. 1974. Social structure and reproductive behaviour in the greater rhea. Living Bird 13, 251-294.

Bucher, G.C. 1937. Notes on life-history and habits of *Capromys*. Mamm. Soc. Cuban Hist. Nat. 'Filipe Poey', 11. 93-107.

Caro, T.M. 1986a. The function of stotting in Thomson's gazelles: some tests of the predictions. Anim. Behav. 34, 663-684.

Caro, T.M. 1986b. The functions of stotting: a review of hypotheses. Anim. Behav. 34, 649-662.

Carr, G.M. and Macdonald, D.W. 1986. The sociality of solitary foragers: a model based on resource dispersion. Anim. Behav. 34, 1540-1549.

Clutton-Brock, T.H. and Harvey, P.H. 1977. Primate ecology and social organization. J. Zool. (Lond.) 183, 1-39.

Clutton-Brock, T.H. and Harvey, P.H. 1979. Comparison and adaptation. Proc. R. Soc. Lond. B. Biol. Sci. 205, 547-565.

Clutton-Brock, T.H. and Harvey, P.H. 1980. Primates, brains, and ecology. J. Zool. (Lond.) 190, 309-323.

Clutton-Brock, T.H. and Harvey, P.H. 1984. Comparative approaches to investigating adaptation. In: J.R. Krebs and N.B. Davies (eds), Behavioural Ecology (2nd edition). Blackwell Scientific Publications, Oxford.

Clutton-Brock, T.H., Guiness, F.E. and Albon, S.D. 1982. The Red Deer: Behaviour and Ecology of Two Sexes. Chicago University Press, Chicago.

Cordero, G. and Ojasti J. 1981. Comparison of capybara pupulations of open and forested habitats. J. Wildl. Manage. 45, 267-271.

Cowan, D.P. and Garson, P.J. 1985. Variation in the social structure of rabbit populations: causes and demographic consequences. In: R.M. Sibly and R.H. Smith (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford. Pp 537-555

Cowan, D.P. and Bell, D.J. 1986. Leporid social behaviour and social organization. Mammal Rev. 16, 169-179.

Crook, J.H. 1964. The evolution of social organisation and visual communication in the weaver birds (Ploceinae). Behaviour Suppl. 10, 1-78.

Crook, J.H. 1977. On the integration of gender strategies in mammalian social systems. In: J.S. Rosenblatt and B.R. Komisaruk (eds), Reproductive Behaviour and Evolution. Plenum Press, New York. Pp 17-38.

Crook, J.H. and Gartlan, J.S. 1966. Evolution of primate societies. Nature (Lond.) 210, 1200-1203.

Cross, B.A. 1977. Comparative physiology of milk removal. Symp. Zool. Soc. Lond. 41, 193-210.

Cumming, D.H.M. 1975. A field study of the ecology and behaviour of warthog. Museum Memoir No. 7, Trustees of Nat. Mus. and Monuments of Rhodesia. Pp 1-179.

Darling, F.F. 1938. Bird Flocks and the Breeding Cycle: a contribution to the study of avian sociality. Cambridge University Press, Cambridge.

Darwin, C. 1860. The Voyage of The Beagle. Doubleday and Co., New York.

Davies, N.B. 1978. Ecological questions about territorial behaviour. In: J.R. Krebs and N.B. Davies (eds). Behavioural Ecology. Blackwell Scientific Publications, Oxford. Pp 317-350.

Dawkins, R. 1976. The Selfish Gene. Oxford University Press, Oxford.

DeGroot, P. 1980. Information transfer in a socially roosting weaver bird (*Quelea quelea*: Ploceinae): an experimental study. Anim. Behav. 28, 1249-1254.

Don, B.A.C. and Rennolls, K. 1983. A home range model incorporating biological attraction points. J. Anim. Ecol. 52, 69-81.

Doncaster, C.P. 1985. The spatial organisation of urban foxes (*Vulpes vulpes*) in Oxford. D.Phil. thesis, Oxford.

Dubost, G. 1968. Les niches ecologiques de forets tropicales Sud Americanes et Africaines, sources de convergence remarquables entre rongeurs et artiodactyles. Terre Vie 1, 3-28.

Dubost, G. 1980. L'ecologie et la vie sociale du cephalophe bleu (*Cephalophus monticola* Thunberg), petit ruminant forestier africain. Z. Tierpsychol. 45, 205-266.

Dubost, G. 1984. Comparison of the diets of frugivorous forest ruminants of Gabon. J. Mammal. 65, 298-313.

Dubost, G. and Genest, H. 1974. Le comportement social d'une colonie de maras *Dolichotis patagonum* Z. dans le Parc de Branfere. Z. Tierpsychol. 35, 225-302.

Dunbar, R.I.M. 1982. Intraspecific variations in mating strategy. In: P.P.G. Bateson and P.H. Klopfer (eds), Perspectives in Ethology (Volume 5). Plenum Press, New York. Pp 385-431

Dunbar, R.I.M. 1984. The ecology of monogamy. New Sci. 1419, 12-15.

Dunbar, R.I.M. and Dunbar, E.P. 1974. Social organization and ecology of the Klipspringer (*Oreotragus oreotragus*). Z. Tierpsychol. 35, 481-493.

Dunbar, R.I.M. and Dunbar, E.P. 1979. Observations on the social organisation of common duiker in Ethiopia. Afr. J. Ecol. 17, 249-252.

Dunbar, R.I.M. and Dunbar, E.P. 1980. The pairbond in Klipspringer. Anim. Behav. 28, 219-229.

Dunn, J.E. and Gipson, P. 1977. Analysis of radio telemetry data in studies of home range. Biometrics 33, 85-101.

Eaton, R.L. 1974. The Cheetah: The Biology, Ecology, and Behaviour of an Endangered Species. Van Nostrand Reinhold, New York.

Eisenberg, J.F. 1981. The Mammalian Radiations. Chicago University Press, Chicago.

Eisenberg, J.F. and Mckay, G.M. 1974. Comparison of ungulate adaptations in the New World and Old World tropical forests with special reference to Ceylon and the rain forest of Central Ameica. In: V. Geist and F.

Walther (eds). The Behaviour of Ungulates and its Relation to Management. I.U.C.N. Publ. Ser. No. 24. Pp 585-602.

Emlen, S.T. and Oring, L.W. 1977. Ecology, sexual selection and the evolution of mating systems. Science (Wash., D.C.) 197, 215-223.

Enders, R.K. 1935. Mammalian life histories from Barro Colorado Island, Panama. Bull. Mus. Comp. Zool. Harv. Univ. 78, 383-502.

Estes, R.D. 1976. The significance of breeding in synchrony in the wildebeest. E. Afr. Wildl. J. 14, 135-152.

Ford, R.G. and Krumme, D.W. 1979. The analysis of space use patterns, J. Theor. Biol. 76, 125-155.

Frame, G.W. 1984. Cheetahs of the Serengeti, male-female differences in habitat exploitation. In: D.W. Macdonald (ed), The Encyclopaedia of Mammals (volume 1). George Allen and Unwin, London. Pp 42-43.

Frylestam, B. 1980. Growth and body weight of European hares in southern Sweden. Holarctic Ecology 3, 817-826.

Frylestam, B. 1986. Agricultural land use effects on the winter diet of brown hares (*Iepus europeaus* Pallas) in southern Sweden. Mammal Rev. 16, 157-161.

Geist, V. 1974. On the relationship of social evolution and ecology in ungulates. Am. Zool. 14, 205-220.

Genest, H. and Dubost G. 1974. Pair living in the mara (*Dolichotis patagonum* Z.). Mammalia 38, 155-162.

Goldsmith, F.B., Harrison, C.M., and Morton, A.J. 1986. Description and analysis of vegetation. In: P.D. Moore and S.B. Chapman (eds), Methods in Plant Ecology. Blackwell Scientific Publications. Pp 437-524.

Gosling, L.M. 1981. The Coypu. In: C.L. Boyle (ed), R.S.P.C.A. Book of British Mammals. Collins, London. Pp 129-135.

Gosling, L.M. and Petrie, M. 1981. The economics of social organization. In: C.R. Townsend and P. Carlow (eds), Physiological Ecology. Blackwell Scientific Publications, Oxford. Pp 315-345.

Gould, S.J. and Lewontin, R.C. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc. R. Soc. Lond. 205, 581-598.

Graf, R.P. 1985. Social organisation of snowshoe hares. Can. J. Zool. 63, 468-474.

Grafen, A. 1984. Natural selection, kin selection and group selection. In: J.R. Krebs and N.B. Davies (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford. Pp 62-84.

Green, M.J.B. 1985. Aspects of the Ecology of the Himalayan Musk Deer. Ph.D. thesis, Cambridge University, Cambridge.

Greig-Smith, P. 1983. Quantitative Plant Ecology, 3rd Edition. Buttersworth, London.

Hamilton, W.D. 1964. The genetical evolution of social behaviour. I, II. J. Theor. Biol. 7, 1-52.

Hamilton, W.D. 1971. Geometry for the selfish herd. J. Theor. Biol. 31, 295-311.

Harvey, P.H. and Greenwood, P.J. 1978. Anti-predator defense strategies: some evolutionary problems. In: J.R. Krebs and N.B. Davies (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford. Pp 64-96.

Hendrichs, H. 1975. Changes in a population of dikdik, *Madoqua (Rhynchotragus) kirki* (Gunther, 1880). Z. Tierpsychol. 38, 55-69.

Hendrichs, H., and Hendrichs, U. 1971. Dikdik und Elefanten Okologie und Soziologie zweir afrikanischer Huftiere. R. Piper. and Co., Munich.

Herrera, E.A. 1986. The Behavioural Ecology of the Capybara, *Hydrochoerus hydrochaeris*. D.Phil. thesis, Oxford University, Oxford.

Hladik, C.M. 1977. Chimpanzees of Gabon and Chimpanzees of Gombe: some comparative data on the diet. In: T.H. Clutton-Brock (ed.), Primate Ecology. Academic Press, London. Pp 481-501.

Hofer, H. 1986. Patterns of resource distribution and exploitation by the red fox (*Vulpes vulpes*) and the Eurasian badger (*Meles meles*); a comparative study. D.Phil. thesis, Oxford University, Oxford.

Hofmann, R.R. and Stewart, D.R.M. 1972. Grazer or browser: a classification based on the stomach structure and feeding habits of East African ruminants. Mammalia 36, 226-240.

Hoogland, J.L. 1979. Aggression, ectoparasitism and other costs of prairie dog (Sciuridae: *Cynomys* sp) coloniality. Behaviour 69, 1-35.

Hoogland, J.L. and Sherman, P.W. 1976. Advantages and disadvantages of bank swallow (*Riparia riparia*) coloniality. Ecol. Monogr. 46, 33-58.

Hough, N.G. 1980. Ranging behaviour of a maturing red fox. In: C.J. Amlaner and D. W. Macdonald (eds). A Handbook on Biotelemetry and Radio Tracking. Pergamon Press, Oxford. Pp 691-696.

Jarman, P.J. 1974. The social organisation of antelope in relation to their ecology. Behaviour 48, 215-267.

Jarman, P.J. 1982. Prospects for intraspecific comparisons in sociobiology. In: King's College Sociobiology Group (eds), Current Problems in Sociobiology. Cambridge University Press, Cambridge. Pp 323-342.

Jarvis, J.U.M. 1973. The structure of a population of mole rats, *Tachyoryctes splendens* (Rodentia: Rhizomyidae). J. Zool. (Lond.) 171, 1-14.

Jennrich, R.I. and Turner, F.B. 1969. Measurement of non-circular home range. J. Theor. Biol. 22, 227-237.

Jungius, H. 1971. The biology and behaviour of the reedbuck (*Redunca arundinum* Boddart, 1785) in the Kruger National Park. Mamm. Depicta. Paul Parey, Hamburg.

Kaufmann, J.H. 1974. Social ethology of the whiptail wallaby, *Macropus parryi*, in northeastern New South Wales. Anim. Behav. 22, 281-369.

Kenward, R.E. 1978. Hawks and doves: factors affecting success and selection in goshawk attacks on wood-pigeons. J. Anim. Ecol. 47, 449-460.

Kingdon, J. 1982. East African Mammals (volume IIIc). Academic Press, London.

Kirchshofer, R. 1960. Uber das Harnspritzen der grossen Mara (*Dolichotis patagonum*). Z. Saugetierk. D. 25, 112-127.

Kirchshofer, V.R. 1960. Das grosse Mara. Entwicklung eines nagers zu einem Steppenlaufer, Umsch. Wiss. Tech. 60, 198-201.

Kleiman, D.G. 1971. Behaviour of the acouchi. Z. Tierpsychol. 29, 259-278.

Kleiman, D.G. 1974. Patterns of behaviour in Hystricomorph rodents. Symp. Zool. Soc. Lond. 34, 171-209.

Kleiman, D.G. 1977. Monogamy in mammals. Q. Rev. Biol. 52, 36-69.

Kleiman, D.G. 1981. Correlations among life history characteristics of mammalian species exhibiting two extreme forms of monogamy. In: R.D. Alexander and D.W. Tinkle (eds), Natural Selection and Social Behaviour. Blackwell Scientific Publications, Oxford. Pp 332-344.

Krebs, J.R. 1978. Optimal foraging: decision for predators. In: J.R. Krebs and N.B. Davies (eds), Behavioural Ecology. Blackwell Scientific Publications, Oxford. Pp 23-63.

Krebs, J.R., MacRoberts, M.H. and Cullen, J.M. 1972. Flocking and feeding in the great tit *Parus major*--an experimental study. Ibis 114, 507-530.

Krebs, J.R. and Davies, N.B. 1981. An Introduction to Behavioural Ecology. Blackwell Scientific Publications, Oxford.

Kruuk, H. 1964. Predators and anti-predator behaviour of the black-headed gull, *Larus ridibundus*. Behavioural Suppl. 11, 1-129.

Kruuk, H. 1972. The Spotted Hyaena. University Chicago Press, Chicago.

Kruuk, H. and Macdonald, D.W. 1984. Group territories of carnivores: empires and enclaves. In: R.M. Sibly and R.H. Smith (eds.), Behavioural Ecology, Ecological Consequences of Adaptive Behaviour. Blackwell Scientific Publications, Oxford. Pp 521-536.

Kufner, M.B. 1983. Impacto de los herbivoros silvestres en el algarrobal mendocino y su competencia con el ganado. Report to: Consejo Nacional de Investigaciones Cientificas y Tecnicas, Buenos Aires, Argentina.

Lacher, T.E. 1981. The comparative social behaviour of *Kerodon rupestris* and *Galea spixii* and the evolution of behaviour in the caviidae. Bull. Carnegie Mus. Nat. Hist. 17, 1-71.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen, London.

Lancaster, D.A. 1964. Life History of the Boucard tinamou in British Honduras: II, breeding biology. Condor 66, 235-276.

LeBoeuf, B.J. 1972. Sexual behaviour in the Northern elephant seal, *Mirounga angustirostris*. Behaviour, 41, 1-26.

LeBoeuf, B.J. 1974. Male-male competition and reproductive success in elephant seals. Amer. Zool. 14, 163-176.

Lechleitner, R.R. 1958. Certain aspects of behavior of the black-tailed jack rabbit. Amer. Midl. Nat. 60, 145-155.

Leuthold, W. 1977. African Ungulates: A Comparative Review of their Ecology and Behavioural Ecology. Springer, New York.

Leyhausen, P. 1965. The communal organisation of solitary mammals. Symp. Zool. Soc. Lond. 14, 249-263.

MacArthur, R.H. and Pianka, E.R. 1966. On the optimal use of a patchy environment. Am. Nat. 100, 603-609.

MacArthur, R.H. and Wilson, E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Macdonald, D.W. 1981. Dwindling resources and the social behaviour of capybaras (*Hydrochoerus hydrochaeris*) (Mammalia). J. Zool. (Lond.) 194, 371-391.

Macdonald, D.W. 1983. The ecology of carnivore social behaviour. Nature (Lond.) 301, 379-384.

Macdonald, D.W. and Amlaner, C.J. 1980. A practical guide to radio tracking. In: C.J. Amlaner and D.W. Macdonald (eds), A Handbook on Biotelemetry and Radio Telemetry. Pergamon Press, Oxford. Pp 143-159.

Macdonald, D.W., Ball, F.G., and Hough, N.G. 1980. The evaluation of home range size and configuration using radio tracking data. In: C.J. Amlaner and D.W. Macdonald (eds), A Handbook on Biotelemetry and Radio Tracking. Pergamon Press, Oxford. Pp 405-424.

Martindal, S. 1982. Nest defence and central place foraging: a model and experiment. Behav. Ecol. Sociobiol. 10, 85-90.

Maynard Smith, J. 1964. Group selection and kin selection. Nature (Lond.) 201, 1145-1147.

Maynard Smith, J. and Price, G.R. 1973. The logic of animals conflict. Nature (Lond.) 246, 15-18.

McNaughton, S.J. 1979. Grassland-herbivore dynamics. In: A.R.E. Sinclair and M. Norton-Griffiths (eds), Serengeti: Dynamics of an Ecosystem. University Chicago Press. Pp 46-81.

Mech, L.D. 1970. The Wolf: The Ecology and Behaviour of an Endangered Species. Natural History Press, Garden City, New Jersey.

Mendoza, S.P. and Mason, W.A. 1986. Parental division of labour and differentiation of attachments in a monogamous primate (*Callicebus moloch*). Anim. Behav. 34, 1336-1347.

Moehlman, P.D. 1979. Jackal helpers and pup survival. Nature (Lond.) 277, 382-383.

Mohr, E. 1949. Einiges vom grossen und vom kleinen Mara (*Dolichotis patagonum* Z. und *Salinicola* Burm.). Zool. Gart. Lpz. 16, 111-133.

Monaghan, P. and Metcalfe, N. 1985. Group foraging in wild brown hares: effects of resource distribution and social status. Anim. Behav. 33, 993-999.

Monfort, A. and Monfort, N. 1974. Notes sur l'ecologie et le comportement des oribis (*Ourebia ourebi* Zimmermann 1783). Terre Vie 28, 169-208.

Montgomery, G.G. and Lubin, Y.D. 1978. Movement of *Coendu prehensilis* in the Venezuelan llanos. J. Mammal. 59, 887-888.

Musters, G.C. 1897. At Home With The Patagonians. John Murray, London.

Neill, S.R. St.J. and Cullen, J.M. 1974. Experiments on whether schooling by their prey affects the hunting behaviour of cephalopds and fish predators. J. Zool. (Lond.) 172, 549-569.

Newdick, M.T. 1983. The behavioural ecology of urban foxes, *Vulpes vulpes*, in Oxford. D.Phil. thesis, Oxford.

Nowak, R.M. and Paradiso, L. 1983. Walker's Mammals of the World, 4th Edition. Johns Hopkins University Press, Baltimore.

Olrog, C.C. and Lucero, M.M. 1981. Guiá de los mamiferos Argentinos. Fundación Miguel Lillo, Tucuman, Argentina.

Osgood, W.H. 1943. The mammals of Chile. Publs. Field Mus. Natur. Hist. Publ. Zool. Ser. 30, 1-268.

Pearson, O.P. 1948. Life history of mountain viscachas in Peru. J. Mammal. 29, 245-274.

Pearson, O.P. 1951. Mammals in the highlands of southern Peru. Bull. Mus. Comp. Zool. Harv. Univ. 106, 117-174.

Pielowski, Z. 1972. Home ranges and degree of residence of the european hare. Acta Theriol. 17, 93-103.

Ralls, K. 1976. Mammals in which females are larger than males. Q. Rev. Biol. 51, 245-276.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. Am. Nat. 111, 177-201.

Rathbun, G.B. 1979. The social structure and ecology of elephant-shrews. Z. Tierpsychol., Adv. Ethol. Suppl. 20, 1-80

Rood, J.P. 1970. Ecology and social behaviour of the desert cavy (*Microcavia australis*). Amer. Midl. Nat. 83, 415-454.

Rood, J.P. 1972. Ecological and behavioural comparisons of three genera of Argentine cavies. Anim. Behav. Monogr. 5, 1-83.

Rostagno, C.M. 1981. Reconocimiento de suelos de Peninsula Valdes. Publicaciones del Centro Nacional Patagonico, Chubut, Argentina. Contribution 44.

Rowland, I.W. 1974. Mountain Vizcacha. Symp. Zool. Soc. Lond. 34, 131-141.

Schaller, G.B. 1972. The Serengeti Lion: A study of predator-prey relations. University Chicago Press, Chicago.

Siegel, S. 1956. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill, New York.

Simpson, G.G. 1950. History of the fauna of Latin America. Am. Sci. 38, 361-389.

Smythe, N. 1970. On the existence of "pursuit invitation" signals in mammals. Am. Nat. 104, 491-494.

Smythe, N. 1978. The natural history of the Central American Agouti (*Dasyprocta punctata*). Smithson. Contrib. Zool. 257, 1-52.

Sokal, R.R. and Rohlf, F.J. 1969. Biometry. W.H. Freeman and Company, San Francisco.

Taber, A.B. and Macdonald, D.W. 1984. Scent dispensing papillae and associated behaviour of the Mara, *Dolichotis patagonum*, (Rodentia: Caviomorpha). Notes from the Mammal Society No. 48. J. Zool. (Lond.) 203, 298-301.

Tenaza, R.R. 1975. Territory and monogamy among Kloss' gibbons (*Hylobates klossi*) in Siberut Island, Indonesia. Folia Primatol. 24, 60-80.

Tilson, R.L. 1980. Klipspringer (*Oreotragus oreotragus*) social structure and predator avoidance in a desert canyon. Madoqua 11, 303-314.

Tilson, R.L. and Tilson, J.W. 1986. Population turnover in a monogamous antelope (*Madoqua kirkii*) in Namibia. J. Mammal. 67, 610-613.

Tinbergen, N. 1953. The Herring Gulls' World. New Naturalist Series, Collins, London.

Treisman, M. 1975. Predation and the evolution of gregariousness. I. Models for concealment and evasion. Anim. Behav. 23, 779-800.

Trivers, R.L. 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35-57.

Trivers, R.L. 1972. Parental investment and sexual selection. In B. Campbell (ed), Sexual Selection and the Descent of Man. Aldine, Chicago. Pp 139-179.

Trivers, R.L. 1974. Parent-offspring conflict. Am. Zool. 14, 249-265.

Vehrencamp, S.L. 1977. Relative fecundity and parental effort in groove-billed anis, *Crotophaga sulcirostris*. Science (Wash., D.C.) 197, 403-405.

Vehrencamp, S.L. 1978. The adaptive significance of communal nesting in groove-billed anis, *Crotophaga sulcirostris*. Behav. Ecol. Sociobiol. 4, 1-33.

Vine, I. 1973. Detection of prey flocks by predators. J. Theor. Biol. 40, 207-210.

Voight, D.R. and Tinline, R.R. 1980. Strategies for analysing radio tracking data. In: C.J. Amlaner and D.W. Macdonald (eds), A Handbook on Biotelemetry and Radio Tracking. Pergamon Press, Oxford. Pp 387-404.

Weir, B.J. 1970. Chinchilla. In: E.S.E. Hafez (ed), Reproduction and Breeding Techniques for Laboratory Animals. Lea and Febiger, Philadelphia. Pp 209-223.

Weir, B.J. 1974. Reproductive characteristics of Hystricomorph rodents. Symp. Zool. Soc. Lond. 34, 265-301.

Weir, B.J. 1974. The tuco-tuco and plains vizcacha. Symp. Zool. Soc. Lond. 34, 113-130.
Wickler, W. and Seibt, U. 1981. Monogamy in crustacea and man. Z. Tierpsychol. 57, 215-234.
Wickler, W. and Seibt, U. 1983. Monogamy: an ambiguous concept. In: P. Bateson (ed), Mate Choice. Cambridge University Press, Cambridge. Pp 33-50.
Williams, G.C. 1966. Adaptation and Natural Selection: A critique of some current evolutionary thought. Princeton University Press, Princeton.
Wilson, E.O. 1975. Sociobiology: The New Synthesis. Belknap Press, Harvard.
Wilson, S. and Kleiman, D.G. 1974. Eliciting play: a comparative study (*Octodon, Pediolagus, Phoca, Choeropsis, Ailuropoda*). Am. Zool. 14, 341-370.
Wittenberger, J.F. 1981. Animal Social Behaviour. Duxbury Press, Boston.
Wittenberger, J.F. and Tilson, R.L. 1980. The evolution of monogamy: hypotheses and evidence. Annu. Rev. Ecol. Syst. 11, 197-232.
Yoffe, A.E., 1983. La Mara. Fauna Argentina 13, Buenos Aires.
Zeveloff, S.I. and Boyce, M.S. 1980. Parental investment and mating systems in mammals. Evolution 34, 973-982.
Zimmerman, E. 1778. Geographische Geschichte des Menschen und der vierfubigen Thiere. Bd. 2, Leipzig.