The Ecology of the Riverine Rabbit

Bunolagus monticularis.

Thesis submitted in partial fulfilment of the degree

MSc (Zoology)

In the Faculty of Science
University of Pretoria
Pretoria, South Africa.

Andrew Graeme Duthie

March 1989.

To Dad and Mom

The Ecology of the Riverine Rabbit *Bunolagus monticularis*.

by

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ABSTRACT

Aspects of the ecology of *B. monticularis* were studied with a view to the species' conservation. This investigation indicates that the present distribution is half that of the past distribution and that only one third of the original habitat remains uncultivated. It is estimated that this area could, theoretically, support 1435 rabbits. The shrubs, *Pteronia erythrocaetha* and *Kochia pubescens* constitute the bulk of the species' diet; grasses are included in the diet whenever rainfall gives rise to new growth. Spatial use, social structure and activity pattern conform to the general leporid pattern of polygamy, solitary living and nocturnality. The breeding season extends from August to May and litters of one, possibly two, altricial young are produced after a gestation of 35 - 36 days.

ACKNOWLEDGEMENTS

I would like to express my sincere thanks and appreciation to the following people:

Professor T J Robinson for initiating this project and obtaining the funding for it. For his continued enthusiasm and interest in my progress and, as co-supervisor, his considered criticism of this thesis.

Professor J D Skinner for taking over the supervision of my research midway through the project and his advice and correction of this typescript.

Jan and Joan Human and their family for their generous hospitality and support. Especially Jan for making a house, his land and his labourers available to me during the field study. His personal involvement in the project ensured its success.

The Wildlife Society of Southern Africa and the S A Nature Foundation who so generously funded my research and publicised the project. Especially John Grieg, Erina Botha and Rob Soutter for their enthusiasm.

The Foundation for Research and Development, University of Pretoria, Rob Blundell and T B Spillane Bursary Trust from whom I received bursaries.

Consolidated Wire Industries for generously donating netting wire for an enclosure and the National Zoo in Pretoria for erecting it.

Miss Anne van Dyk for agreeing to establish a captive colony of rabbits at her Cheetah Research Station, De Wildt.

Martin Haupt and Mrs C Potgieter for their technical assistance.

Mrs J van Schalkwyk and Mrs N Brosnan for their secretarial help and love of THE bunny.

Alex and Aline for their kindness and friendship particularly during the difficult early stages of the study.

Anna, Ken, Brigitte, George, John, Chris and Andre for the many fun times.

Dad and Mom for their confidence in and support of my direction of study.

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CHAPTER 1

INTRODUCTION

The riverine rabbit, Bunolagus monticularis, first roused scientific interest in 1902 when two specimens were dispatched to the British Museum of Natural History from Deelfontein in the Cape Province by a British trooper, C.H.B. Grant. The taxonomist at the museum noted that these lagomorphs were "a completely unique species unlike anything else hitherto described" (Thomas 1903). He first named the species Lepus monticularis because of its hare-like morphology but, as a result of important dissimilarities, later changed this nomenclature to Bunolagus monticularis (Thomas 1929). Studies of the species' karyotype (Robinson & Skinner 1983) have confirmed this unique generic status.

Thomas believed that Bunolagus occurred in hilly terrain hence the specific name monticularis which is derived from "monticule" meaning small mountain (Robinson 1981). It was only in 1947 that Shortridge, after a protracted search, established the correct habitat type to be central Karoo riverine scrub. Between 1947 and 1948 he collected 26 specimens along the Renoster and Fish rivers near Calvinia (Robinson 1981).

In 1979 Robinson searched these rivers in the hope of obtaining specimens of Bunolagus for a systematic study. These efforts proved fruitless as the riverine scrub on both rivers had been destroyed resulting in the local disappearance of the species. A specimen was later captured near Victoria West (Robinson 1981).

In 1979 a survey of the present-day distribution of Bunolagus (Van Rensburg, Robinson & Skinner) established its rarity and its probable extinction in the absence of conservation action. Thus the species was listed as endangered in the Red Data Book of the International Union for the Conservation of Nature and Natural Resources (IUCN) in 1981 and a study of its biology proposed.

In keeping with the paucity of information on Bunolagus the objectives of the present investigation were broad. These were:

1. To acquire data pertinent to the basic biology of the species for use in the formulation of a conservation strategy. Particular emphasis was placed on space use, feeding and reproduction.

2. To provide a description of the species' typical habitat, its distribution and to estimate the extent of the remaining habitat.

3. To propose realistic management recommendations which, if implemented, would contribute to the conservation of the species.

4. Establish a captive breeding colony.

CHAPTER 2

STUDY AREA

Location

The study site was situated on the farm "Klipgat" (31°21S, 22°38E) and encompassed some 80 ha of Karoo riverine vegetation located along a four kilometre stretch of the seasonal Klein Brak river (Fig. 1). This particular locality was chosen since the riverine vegetation is undisturbed and because the species' presence was verified by several biologists prior to the initiation of the present investigation.

Topography

The study area at altitude 1320 m is bounded in the north by a ridge of low lying koppies which in turn are paralleled by a gravel track (Fig. 1A). From this track the flood plain and its associated riverine vegetation extends for 100-200m to the Klein Brak river which courses along its southern boundary. From here the ground rises slightly onto the plains of the Great Karoo.

Geology

Much of the surrounding geology comprises mudstone, a sedimentary rock. The weathering of this stone produces the alluvial soil deposited on the banks of the Klein Brak river which, in turn forms the substrate for the riverine vegetation. The horizon of this soil exceeds 1,5 m in places. Dolerite extrusions form the ridge of koppies in a "stacked boulder" type formation.

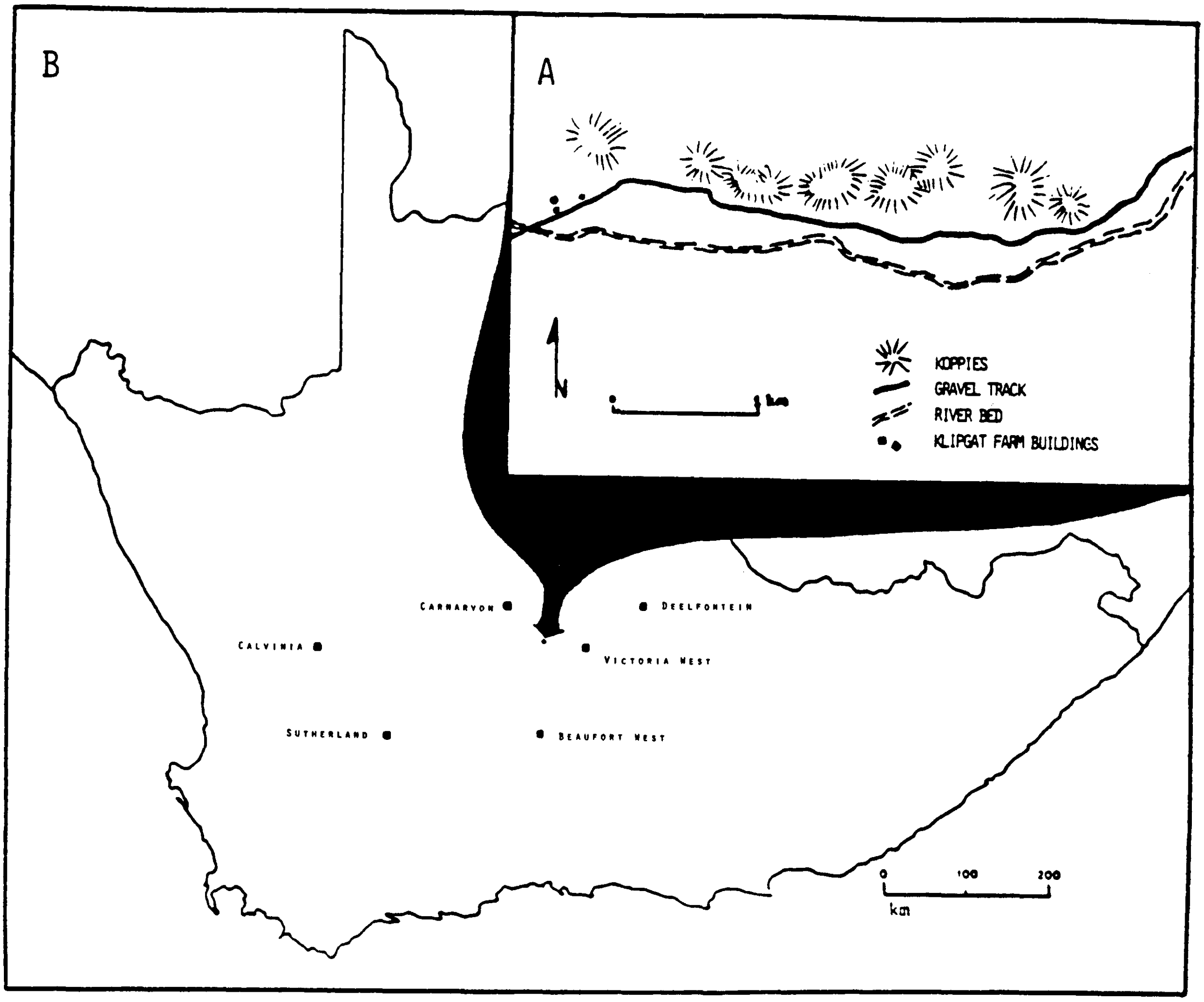

FIGURE 1 : (A) A SCHEMATIC AERIAL REPRESENTATION OF THE STUDY AREA AND (B) ITS RELATIVE GEOGRAPHIC POSITION IN THE CAPE PROVINCE, SOUTH AFRICA.

Climate

Noy-Meier (1973) defined a desert region as a water-controlled ecosystem with infrequent, discrete and unpredictable precipitation. This well describes the arid Karoo and the study site which receives a mean annual rainfall of 212 mm. More than 70% of the rain falls during the summer and ambient temperatures range between −10°C and 40°C with frost a common feature in winter. The salient points of the abiotic environment are summarised in Fig. 2 . During winter a strong northwesterly wind blows daily while an equally forceful southeaster prevails on summer nights.

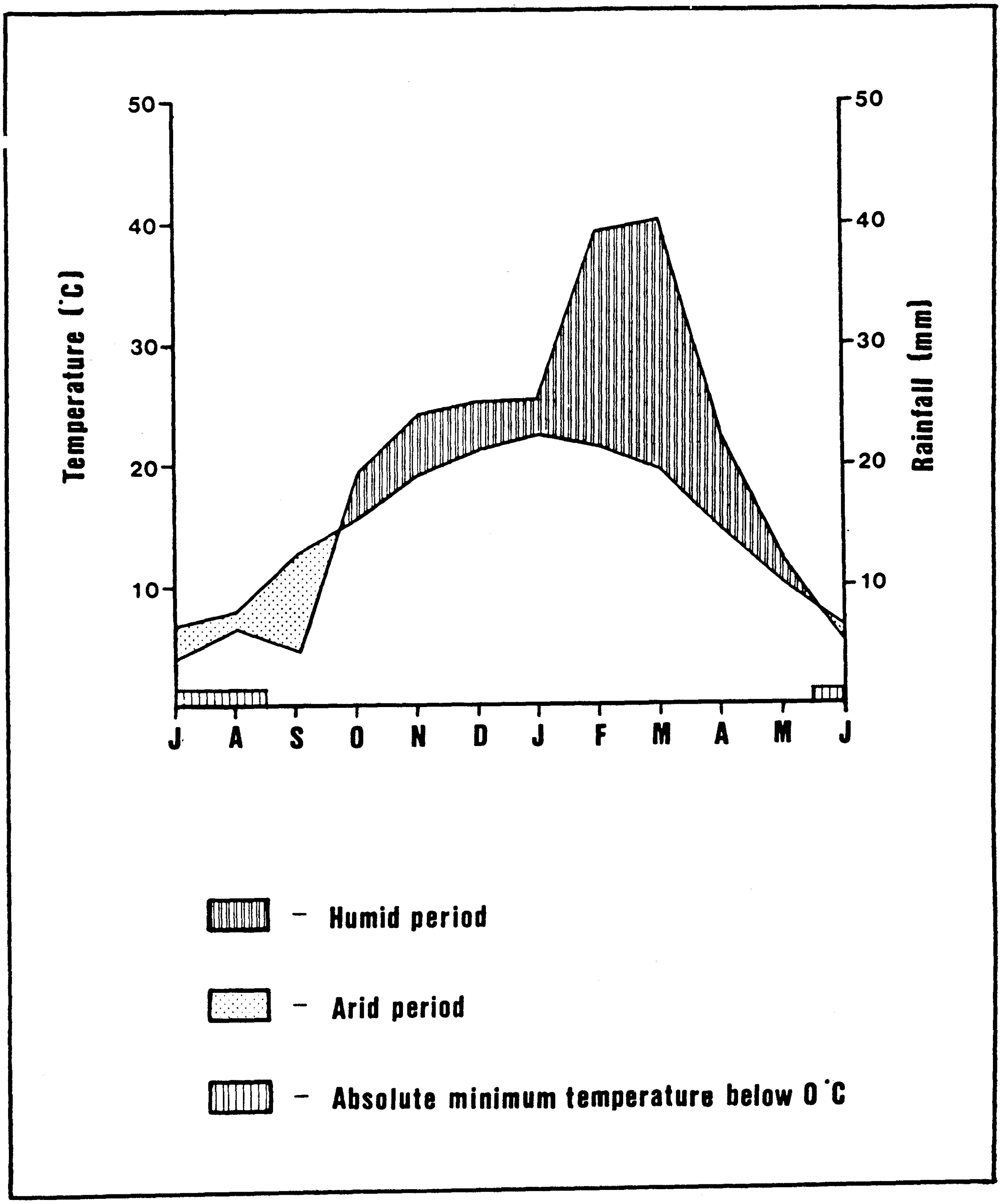

FIGURE 2 : CLIMATOLOGICAL DATA FOR THE STUDY AREA RECORDED FROM 1968 - 1988 ON THE FARM KLIPGAT (31°21'S, 22°38'E).

CHAPTER 3

DISTRIBUTION AND STATUS

INTRODUCTION

The designation of a species as endangered implies that a dramatic decrease in its numbers has occurred which, if left unchecked, will lead to its extinction within the foreseeable future. If the species in question is to be conserved, knowledge is required of the factors responsible for its decline. The present investigation thus sought to establish the magnitude of the difference in the past and present distribution of Bunolagus and to identify the reasons for this discrepancy.

MATERIALS AND METHODS

Distribution and Density

The distribution of the riverine rabbit was established by: (1) systematically working through 1/4 degree square grids on 1:250000 topo-cadastral maps of the central Karoo and (2) questioning, in detail, the occupants of suitably sited farms about the occurrence of the species (Survey 1, Van Rensburg, Robinson & Skinner 1979). Ambiguous records were discarded. The distributional limits of Bunolagus, obtained from these results, were then confirmed by searching riverine scrub on foot for rabbits. During the latter search the habitat adjoining major seasonal rivers abutting established distributional limits were covered by means of a 5 m width transect search (Survey 2).

The rivers associated with scrub typical of Bunolagus habitat (See Chap. 4) were recorded during the two surveys. The area of this riverine vegetation was then calculated from 1:50000 aerial photographs of the central Karoo obtained from the Geological Survey, Pretoria, South Africa, using a planimeter. The area of destroyed habitat was recorded by measuring the area of cultivated land abutting these rivers using the same technique.

Total counts of Bunolagus occupying two separate sections of riverine vegetation in the main study area were made on horseback during daylight hours. These areas (A and B) were 75 ha and 78 ha respectively, and were traversed along parallel transects 10m apart.

RESULTS

Distribution and Density

A comparison of the present distribution of Bunolagus (as determined by surveys 1 and 2; see Tables 1 & 2) with its known past distribution (Robinson 1981) shows that its range has decreased to about half of what it was forty to fifty years ago (Fig. 3). Population density was estimated at 0.166 and 0.064 Bunolagus per hectare, respectively, on site A and B (Table 3).

Habitat

The majority of riparian scrub, typical of Bunolagus habitat, is associated with the Sak/Klein Sak, Ongers, Brak, and the Riet/Klein Riet rivers (Table 4 & Fig. 3). In Table 4 the destruction of about two-thirds of the original habitat should be noted. An important anomaly in this table is the absence of Bunolagus from the riverine scrub along the Ongers river.

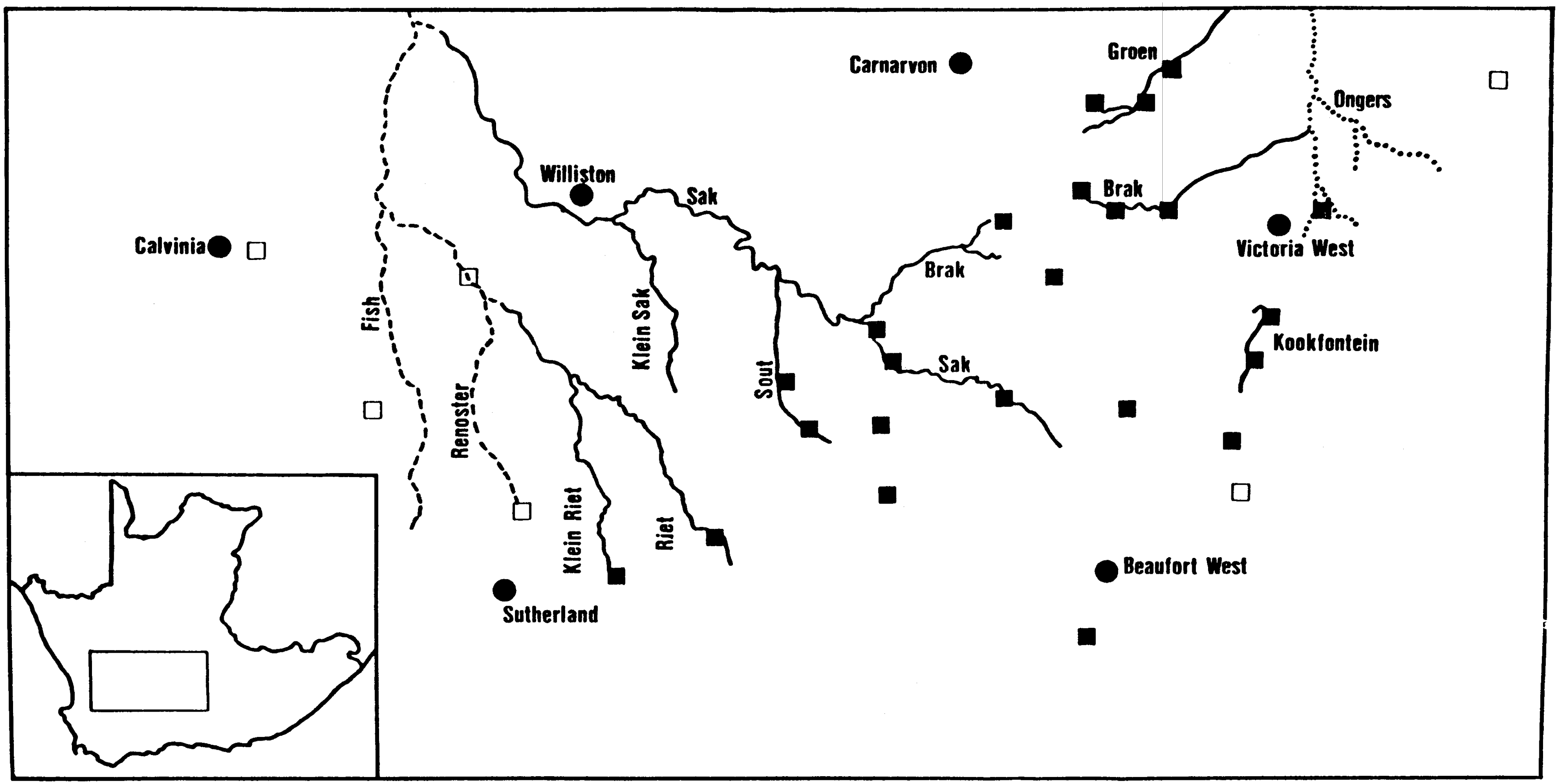

FIGURE 3 : MAP OF THE CENTRAL KAROO INDICATING THE RIVERS WHERE HABITAT HAS BEEN DESTROYED (---), WHERE SUITABLE UNOCCUPIED HABITAT IS FOUND (···). SOLID CIRCLES REPRESENT TOWNS AND SOLID SQUARES INDICATE THE PRESENT DISTRIBUTION OF <u>BUNOLAGUS</u> DETERMINED FROM SIGHT RECORDS. OPEN SQUARES INDICATE THOSE LOCALITIES WHERE MUSEUM SPECIMENS WERE PREVIOUSLY COLLECTED.

MAP REFERENCE (1:250 000)	FARM NAME	MAGISTERIAL DISTRICT
3123Cc	Kookfontein	Victoria West
3123Ca	Jakkalsfontein	" "
3123Ca	Pampoenfontein	" "
3122Bd	Adriaanskuil	" "
3122Bd	Elim	" "
3122Bc	Sandgat	" "
3122Bc	Klipgat	" "
3122Ba	Pampoenpoort	" "
3122Ba	Beyersfontein	" "
3123Ad	Content	Beaufort West
3122Ab	Prinshof	Loxton
3122Ad	Renosterfontein	"
3122Cc	Jakkalsfontein	Fraserburg
3121Db	Saaifontein	"
3121Db	De Kruis van Bloemfontein	" "
3121Dc	Rivierplaas	"
3121Dc	Goedverwachting	"
3022Cd	Rosenhof	Carnarvon
3220Ac	Kruisrivier	Sutherland
3220Ab	Geelhoek	"

Table 1: The farms from which sight records of *Bunolagus* were obtained during Survey 1.

MAP REFERENCE (1:250 000)	FARM	RIVER	LAGOMORPHS FOUND
Southern Rivers:			
3320Ba	Faberskraal	Geelbek	None
3220Ca	De List	Oubergs	One *L. saxatilis*
3220Bd	Waaikraal	Waaikraal	None
3222Ab	Bellevue	Gamka	One *L. saxatilis*
3222Ca	Letjiesbos	Gamka	None
3222Ad	Weltevrede	Gamka	None
3222Ad	Lombardskraal	Lombardskraal	One *B. monticularis*
Eastern Rivers:			
3222Ba	Montana	Sout	None
3122Bc	Biesiesfontein	Visgat	One *L. capensis*
3122Ba	Groot Boesmans-poort	Visgat	Two *L. capensis*
3122Ba	Klipkraal	Ongers	One *L. saxatilis*
3122Ba	Vlakkraal	Ongers	Four *L. capensis*
3122Ba	Kraanvoelvlei	Ongers	Two *L. capensis*
Northern Rivers:			
3020Bb	De Naaute	Carnarvonleegte	Three *L. capensis*
3020Bb	Leeukolk	Carnarvonleegte	None

Table 2: The various lagomorph species found associated with the rivers visited during Survey 2.

SITE	AREA (ha)	MONTH COUNTED	NUMBER OF RABBITS COUNTED	NUMBER OF HARES COUNTED	RABBIT DENSITY	MEAN LAGOMORPH DENSITY
A	75	April	12	0	0,160	0,166
A		May	13	0	0,173	0,166
B	78	May	5	9	0,064	0,179

Table 3. The numbers and densities of lagomorphs counted on sites A and B of the study are_.

RIVER	AREA OF ORIGINAL HABITAT (ha)	HABITAT REMAINING (%)	HABITAT DESTROYED (%)
Sak/Klein Sak	3298	14,8	
Riet/Klein Riet	878	3,9	
Brak	1582	7,1	
Sout	275	1,2	
Groen	653	2,9	
Kookfontein	137	0,5	
Ongers	1825	8,2	
Fish	7212		32,6
Renoster	6362		28,8
Total	22222	38,6	61,4

TABLE 4: The total area (ha) of the historic Bunolagus habitat. The percentage of this area remaining undisturbed and the percentage destroyed.

DISCUSSION

The difference between the past and present distribution of Bunolagus (Fig. 3) can be attributed to the destruction of suitable habitat on the seasonal Fish and Renoster rivers. This destruction which eliminated approximately 60% of the habitat (Table 4) was the result of extensive efforts to cultivate wheat on the banks of these rivers with the aim of turning them into the "bread basket of the Cape". This enterprise had failed by 1950 due largely to a shortage of irrigation water (Green 1955) and today sheep farming remains the mainstay of agriculture in the central Karoo.

It may be argued that the estimates of habitat destruction are flawed since it may not necessarily be reflected by the extent of cultivation along the rivers. However, it should be noted that only the alluvial soil next to rivers in the central Karoo is arable and that the vegetation typical of Bunolagus habitat is restricted to this substrate. Away from the riverine flood-plain the top soil is either too shallow, stony or too far from water for cultivation. Although cultivation does occur adjacent to farmsteads next to rivers in the remainder of the distribution area of Bunolagus, it is static and very limited in extent, and does not at present represent a significant threat to the species' habitat.

The reason for the absence of Bunolagus from the Ongers river vegetation (Table 4), which appears no different to the typical habitat, is not known. This absence is especially unusual since the Brak river, on which relatively large numbers of Bunolagus occur, is a tributary of the Ongers (Fig. 3). Robinson (1981) suggested that hunting with dogs may have contributed to the disappearance of Bunolagus from parts of its range. This does not appear to be so, since the density of the riverine scrub would negate the effective use of coursing dogs which rely on sight to maintain contact with their quarry.

Density estimates (0,064-0,166 rabbits per ha) for Bunolagus obtained during the present study are similar to those for the Cape hare, Lepus capensis (0,047-0,248 hares per hectare in the Orange Free State; Wessels 1978). While the methods employed in determining these values were unavoidably rough, double counting error was minimized by the species behaviour characteristics:

i) Bunolagus is solitary.

ii) It is also stationary diurnally when it lies-up in forms.

iii) Once a rabbit is flushed from a form it does not dig another immediately but lies-up under a bush. Thus, by checking form occupancy the possibility of recounting any particular rabbit was minimized.

iv) Bunolagus flushes from its form when a horse is five metres away which reduces miscounting.

In addition to five Bunolagus, nine Cape hares were also resident in the riverine scrub at site B. The vegetation of this area did not differ significantly from site A and the reason for the difference in species composition and Bunolagus densities is not readily apparent. However, it is possible that when

Bunolagus numbers are low as a result of mortality, L. capensis, which is normally an open plains species, extends its range into the riverine scrub which is marginal habitat for the species. Should this hold, it would parallel the interaction between the European rabbit, Oryctolagus cuniculus, and hare, L. europaeus (Flux 1981). Noteworthy from this observation is the fact that total lagomorph densities were similar on the two sites (Table 3).

Extrapolation of the higher Bunolagus density obtained in the present study to available habitat suggests that the habitat remaining could possibly support 1435 rabbits. However, the absence of Bunolagus from the vegetation of the Ongers river and the observation that densities may vary widely on the same river suggest that the actual total population size may be very much lower than this figure.

CHAPTER 4

DIET AND HABITAT CHARACTERISTICS

INTRODUCTION

Mammals generally spend a large proportion of their daily activity budget on food acquisition. This is not unusual since energy is required for all processes involved in the maintenance and reproduction of an animal. This important rôle of energy in a species' biology demands that some information be gained of its specific food requirements before steps can be taken to ensure its survival.

MATERIALS AND METHODS

Collection of Material

Monthly collections of fresh lagomorph faeces were made at three sites in the study area where only Bunolagus occurred. These samples were air dried and stored. Leaf material from each shrub and grass species in the study area was simultaneously collected as reference material for the identification of faecal fragments.

Vegetation Analysis

During October 1986 a point analysis of the riverine vegetation in the study area was undertaken by suspending a rope, marked at two metre intervals, across the vegetation on randomly (by using random numbers) assigned transects. The plant species rooted directly beneath each marker were noted and their width and height measured. A sample of 3000 points was taken. From these data the percentage vegetation cover, percentage occurrence, mean plant height and width were calculated.

Faecal Analysis

Faecal samples were homogenized in a coffee grinder and prepared for microhistological analysis following De Blase & Martin (1982). Using this method epidermal characters of faecal fragments were compared with those of reference material and identified to species level. Opaque fragments were classed as either monocotyledonous or dicotyledonous.

To facilitate identification, epidermi were cleared of palisade tissue by boiling in Hertwig's solution (De Blase & Martin 1982) until transparent. To randomise fragment sampling, faecal material was spread on a grid slide and only fragments touching intersections were counted. A hundred fragments from each sample were identified to species level.

Treatment of Data

The sample results were pooled for each month and correlated with the rainfall for that month. Preference ratings for each plant constituent of the diet were calculated by dividing its percentage composition of the diet by its percentage composition of the veld (Davies, Botha & Skinner 1986).

RESULTS

Vegetation Analysis

<u>Salsola glabrescens</u> (11,8%) and <u>Lycium spp.</u> (6,5%) constitute most of the vegetation cover (Table 5).

Other important components of vegetation cover were Osteospermum spinescens (3,4%), Pteronia erythrocaetha (3,3%), Galenia procumbens (1,6%) and Kochia pubescens (1,3%). Grasses were poorly represented and contributed only 5% of the vegetation cover compared to 30% contributed by dicotyledons.

Faecal Analysis

Unidentifiable epidermal fragments constituted 47 ± 0,89% (Mean ± SE) of monthly samples. Monocotyledons and dicotyledons comprised respectively 11 ± 1,45% and 88,3 ± 1,45% of identifiable fragments. The monthly percentage of grass in the diet correlated positively with rainfall ($r=0,88$; $P<0,05$; Fig. 4) but this did not apply to any of the dicotyledonous species. Of the latter, Pteronia erythrocaetha (Fig. 5) formed most of the diet followed by Kochia pubescens, Salsola glabrescens and Mesembryanthemaceae. Utilization of P. erythrocaetha increased in early autumn and late winter while peaks of feeding on K. pubescens and S. glabrescens corresponded with periods of low rainfall during winter and early summer.

Only 40% of the annual precipitation occurred from May to December (late autumn, winter, spring & early summer - Fig. 5). It was mainly during this relatively dry period that succulents, Lycium spp., Osteospermum spinescens, Pentzia incana, Rosenia humilis and Galenia procumbens were consumed. Eriocephalus ericoides was only taken in late winter and early spring. From January to March, the wet period, five

PLANT SPP.	OCCURRENCE (%)	VEGETATION COVER (%)	WIDTH (cm)	HEIGHT (cm)
SHRUBS:				
Salsola glabrescens	34,8	11,8	88,7 ± 38,0	56,2 ± 19,4
Lycium spp	11,2	6,5	104,6 ± 54,9	78,3 ± 30,0
Pteronia erythrocaetha	7,9	3,3	83,7 ± 27,8	46,9 ± 21,3
Osteospermum spinescens	5,3	3,4	130,0 ± 47,1	95,0 ± 27,5
Kochia pubescens	6,5	1,3	55,0 ± 53,1	34,9 ± 14,4
Galenia procumbens	4,0	1,6	70,0 ± 19,5	45,0 ± 10,0
Rosenia humilis	0,47	0,38	14,0 ± 4,8	9,3 ± 2,5
Pentzia incana	1,5	0,44	17,3 ± 14,1	15,8 ± 13,8
Mesembryanthemaceae	1,0	0,31	20,0 ± 5,0	10,0 ± 2,0
Helichrysum pentziodes	1,5	0,63	102,0 ± 65,6	65,6 ± 27,6
Eriocephalus ericoides	0,75	0,51	135,0 ± 47,9	91,2 ± 20,9
GRASSES:				
Eragrostis lehmania	17,1	3,1		
Eragrostis bergiana	4,3	1,9		
Stipagrostis obtusa	3,2	0,57		

TABLE 5: The percentage occurrence, percentage vegetation cover, width and height of the plants comprising *Bunolagus* habitat. (Plant identification by Grootfontein Agricultural College, Middelburg, RSA).

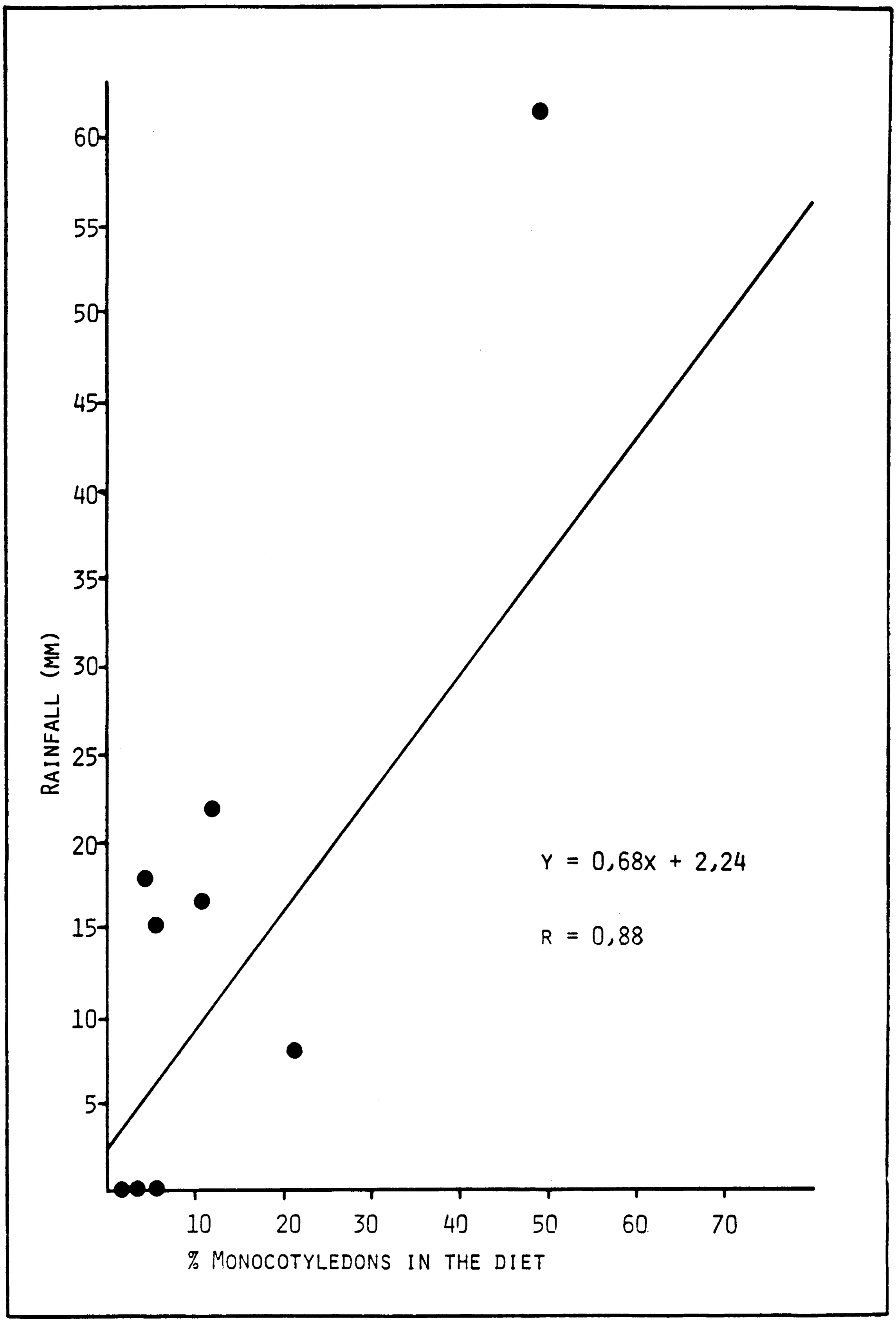

FIGURE 4 : A LINEAR REGRESSION OF THE % MONOCOTYLEDONS IN THE DIET OF <u>BUNOLAGUS</u> AND MONTHLY RAINFALL IN THE PERIOD JANUARY TO DECEMBER 1986.

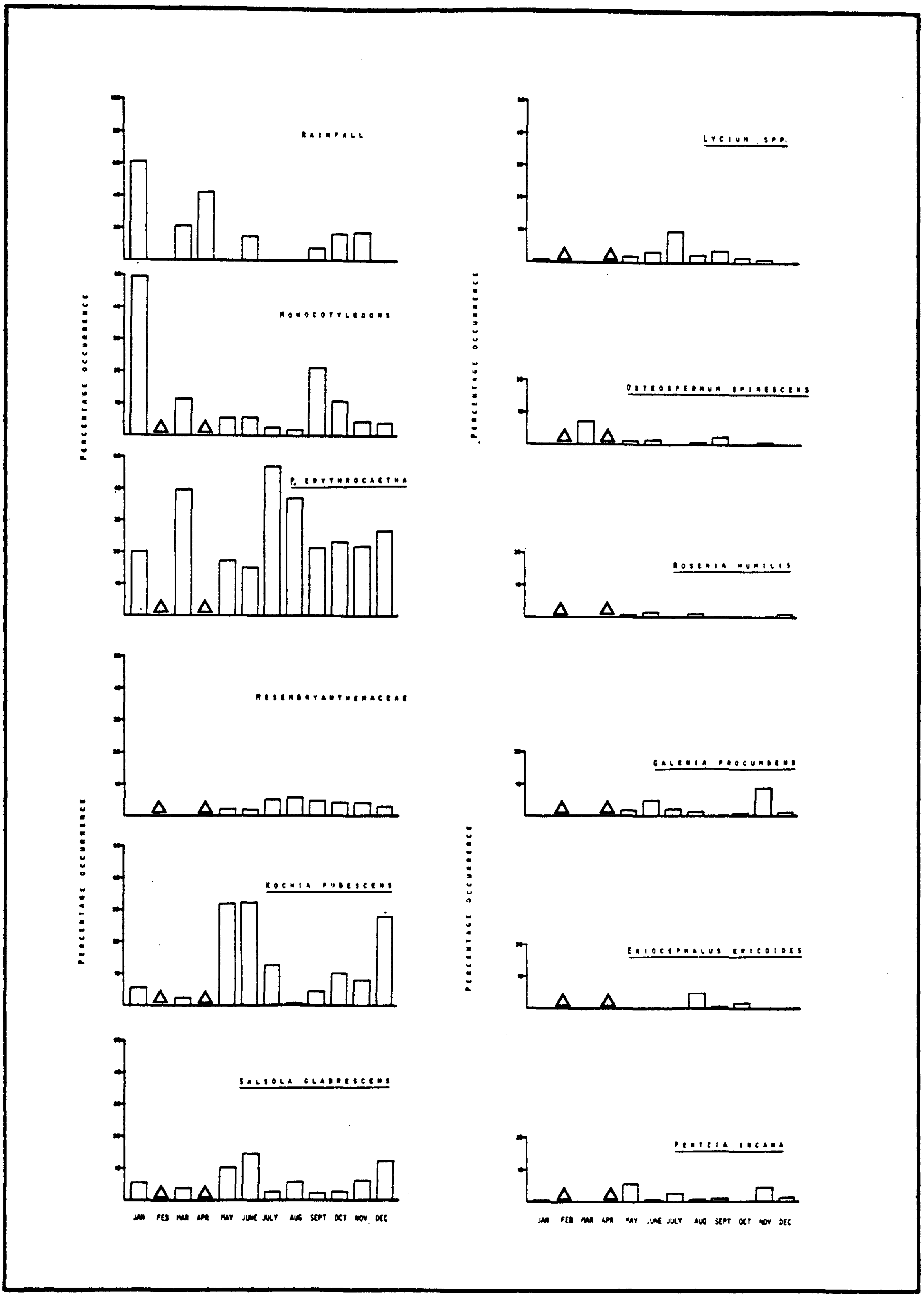

FIGURE 5 : SEASONAL VARIATION IN THE BOTANICAL COMPOSITION OF THE DIET OF <u>BUNOLAGUS</u> COMPARED TO RAINFALL. (△ SAMPLES DESTROYED BY FUNGAL GROWTH.)

plant species constituted the diet. This number increased to a mean of eight species from April to December, the dry period.

Preference Ratings

Bunolagus did not consume plants in relation to their availability. Instead succulents, P. erythrocaetha, R. incana, K. pubescens, G. procumbens and E. ericoides were specifically selected while grasses, S. glabrescens, Lycium spp. and O. spinescens were avoided (Table 6). These results apply only to late spring (October) the period for which these data are available.

DISCUSSION

The analysis of faecal samples as outlined in Materials and Methods tends to underestimate dietary dicotyledons (McInnis, Vavra & Krueger 1983). Contrary to this the Bunolagus diet was found to consist mostly of dicotyledons, suggesting that this herbage is consumed in relation to its availability (Table 5).

A shift between selecting predominantly grasses in the wet growing season (summer) to eating shrubs in winter has similarly been reported for Nuttall's cottontail, S. nuttallii, and blacktail jackrabbits, L. californicus (MacCracken & Hansen 1983). In Africa this has also been noted for the Cape hare, L. capensis, which consumes mainly grass but increases monocotyledon consumption in summer and dicotyledon consumption in winter (Stewart 1971).

PLANT SPP.	PREFERENCE RATING
PLANTS SELECTED:	
Mesembryanthemaceae	8,0
Pteronia erythrocaetha	5,0
Pentzia incana	2,66
Kochia pubescens	2,4
Galenia procumbens	2,05
PLANTS AVOIDED:	
Monocotyledons	0,55
Salsola glabrescens	0,22
Lycium spp.	0,20
Osteospermum spinescens	0,05

Table 6: The preference ratings of plants selected by *Bunolagus* during October 1986.

The flush of new growth after rain is no doubt as appealing to *Bunolagus* as it is to other African lagomorphs (Kingdon 1974) as is evidenced by the correlation in Fig. 4.

Response to Food Availability

Dietary preference for *P. erythrocaetha* over *S. glabrescens* and *Lycium spp.*, which were more abundant, may be related to both the greater succulence and accessibility of this plant. *Lycium spp.* are thorn covered which may be unattractive to browsers while *S. glabrescens* has very dry leaves. In the arid environment of the Karoo, with no surface water, *Bunolagus* must obtain all moisture from its forage. The correspondence of heavy reliance on *P. erythrocaetha* and *K. pubescens* in the dry period coupled to the high preference rating of Mesembryanthemaceae (Fig. 5 & Table 6) suggests that these more succulent plants were selected chiefly for their moisture content. Both the American desert cottontail, *S. audubonii*, and blacktail jackrabbit, *L. californicus*, when confronted with a water shortage also include large quantities of succulent material in their diet (Turkowski 1975; Westoby 1980). It is noteworthy however, that although *S. glabrescens*, *O. spinescens* and *Lycium spp.* are not important components of the *Bunolagus* diet they nonetheless play a significant rôle in providing it with cover (Table 5).

The expansion of the feeding niche during the dry season may be related to a drop in the productivity of preferred plants resulting in their inability to meet all the energy requirements of *Bunolagus*.

Furthermore, the cold dry season associated with winter and spring would further retard growth and contribute to the reduction in primary production.

Palatability

Davies, Botha & Skinner (1986) found that springbok ,Antidorcas marsupialis, preferred a number of plants regarded as unpalatable by sheep, Ovis aries. Thus, palatability ratings for domestic animals should be applied with caution to wild animals. Pteronia spp. and Pentzia spp. are plants which are unpalatable to O. aries but highly preferred by A. marsupialis and Bunolagus. G. procumbens and Salsola spp. which, respectively, are unpalatable to O. aries and highly palatable to A. marsupialis were the converse for Bunolagus. Avoidance of Lycium spp. by Bunolagus concurs with the pattern in A. marsupialis and O. aries. Eriocephalus ericoides is only eaten by Bunolagus in late winter and early spring at which time it becomes palatable as a result of new growth (Roux 1968).

CHAPTER 5

SPATIAL USE, SOCIAL STRUCTURE AND ACTIVITY.

INTRODUCTION

The manner in which mammals organise their utilization of space and time as individuals in a community reflects the distribution of the resources they require to survive (e.g. food, mates and refuges). Thus, by studying the space use patterns of these individuals, an insight can be gained of the area necessary to support a viable population of any particular species.

MATERIALS & METHODS

Capture

Bunolagus were captured by ascertaining their escape routes on foot or on horseback and subsequently driving them into nets. Following capture, rabbits were injected subcutaneously with 10 ml of a 10% glucose solution to allay the effects of capture induced hypoglycaemia (Keith, Meslow & Röngstadt 1968) and measured (Table 7).

Forms

The following measurements were made on forms found during the course of the study;

1. Length
2. Depth
3. Height(from the floor to the lower branches of the bush)
4. Width
5. Direction
6. Distance from the front of the form to the nearest bush.

Age Class	Sex	Mass (kg)	Ear Length (mm)	Hindfoot(cu) (mm)
Adult	Male	1,5	107	101
	Male	1,4	111	
Mean±SE		1,45±0,18	109±1,18	
	Female	1,6	112	101
	Female	1,5	104	100
	Female	1,8	107	102
	Female	1,7		
	Female	1,7	115	93
	Female	1,9	111	102
Mean±SE		1,7±0,15	109,8±1,47	99,6±1,37
Juvenile	Male	0,578	91	86
	Male	0,630	99	85
	Female	0,600	91	92

Table 7: Morphometric data for Bunolagus captured during the present study.

Radio Tracking

After weighing and measuring, each rabbit was fitted with a radio collar (AVM SB2 or Potch transmitter) and released. The battery life of these collars was three months. Radio-fixes were obtained by triangulation from base stations erected at 500 m intervals on the line of hills abutting the study area. Radio signals were perceived using an AVM LA-12 receiver connected to a four element Yagi antenna. The antenna was fixed to a pipe which slotted interchangeably into the base stations. Signal direction was read into a microcassette recorder from a protractor mounted on each base station. The zero point on all the protractors pointed south.

Radio-fixes were taken at 30 min intervals from dusk to dawn with a five minute lapse between readings as the researcher travelled by motorcycle between stations. The study animals were radio tracked simultaneously whenever this was possible.

Data Treatment

Estimation of Home Range Size

Radio-fixes were plotted on a 1:2500 map of the study area and home range size estimated by the restricted polygon method (Wolton 1985). The area of each polygon was determined by planimetry. To ascertain whether a rabbit had been tracked long enough to reveal the majority of its home range, the cumulative range area was plotted against the number of radio-fixes (Odum & Kuenzler 1955).

Intensity of Space Use

To discern the intensity of space use within the home range, radio-fixes were assigned to grid cells on the map according to the linked-cell method (Voight & Tinline 1980) and plotted as 3-D contour maps using the DISSPLA programme (Integrated Software Systems Corporation, San Diego, California).

Activity and Sociality Indices

Activity trends were determined by calculating the distance travelled per hour. The degree of sociality of simultaneously radio tracked rabbits was established by measuring the distance between simultaneous radio-fixes.

Social Structure

Group size, age class (adult or juvenile) and sex were recorded where possible.

Statistics

Student's t-test or the Mann-Whitney U-test were applied to data depending on whether or not they were normally distributed.

RESULTS

Capture

Two aspects of Bunolagus behaviour which facilitated its capture became apparent during early capture attempts. First, rabbits tend to return to the same small area (100 X 100 m) to lie-up each day and secondly, on each occasion when flushed, invariably use the same escape route.

Method	No of capture attempts		% successful
	Unsuccessful	Successful	
Foot	69	3	4,1
Horseback	3	9	75,0

Table 8: A comparison of the efficacy of two methods in establishing the movements of Bunolagus prior to capture attempts.

Capture success proved to be 75% when escape routes were ascertained on horseback as opposed to 4% for those determined on foot (Table 8). This is attributable to the improved visibility of the observer in the former situation.

Forms

Form dimensions and direction are given in Table 9.

Observation of a captive rabbit showed that forms are made by scraping the soil with the forelegs. In this process the latter are extended forward and then drawn backward together in a stroke which ends when the dislodged soil passes between the hindlegs.

Home Range Size

The mean (±SE) home range sizes of adult male and female Bunolagus were, respectively, 20,92 ± 1,44 ha and 12,88 ± 1,39 ha (Table 10). The difference between these means is not significant (Mann-Whitney U-test, U=0, P<0,05). The juvenile male (JM1) and female (JF2) studied in this investigation had home ranges of 3,67 ha and 4,2 ha and were estimated, respectively, to be two and three months old when tracking ceased.

The observation-area curves (Fig. 6) show that the increase in home range area had reached an asymptote in at least three females (F1,F2 & F4), the male M1 and the two juveniles (JM1 & JF1) and that these samples may thus be regarded as fairly accurate estimates of true home range size.

Spatial Organization

Radio tracking of the study animals was clustered temporally into three periods (Fig. 7). The home range of JF1 sampled in period 1 is presented in Figure 8 with those of F1, F2 and F3 sampled in period 2. Similarly, the home ranges of M1, M2, F4 and JM1, tracked simultaneously or serially during period 3, are shown together in Figure 9. No nonradio-collared rabbits were present in the area covered by the home ranges of F1, F2 and F3.

	Length (mm)	Depth (mm)	Width (mm)	Height (mm)	Direction (°)	Distance to front bush (mm)
	330	30	155	290	210	440
	520	25	120	170	291	440
	360	50	120	200	134	290
	415	35	130	190	100	1050
	420	35	105	180	90	1300
	330	10	105	180	277	640
	210	35	140	200	108	470
	270	0	110	180	341	500
	360	38	106	220	301	0
	270	28	160	150	109	0
	200	60	200	170	106	0
	200	20	110	150	226	500
	310	20	110	200	141	130
	220	20	100	230	147	100
	200	14	110	200	53	250
	240	10	110	190	17	170
	250	10	110	165	132	-
	260	10	105	155	141	-
	-	13	-	190	184	-
Mean±SE	299,7±2,0	24,9±0,83	124,2±1,2	190±1,3	163,5±2,16	369,4±4,66

Table 9: The measurements of 19 Bunolagus forms.

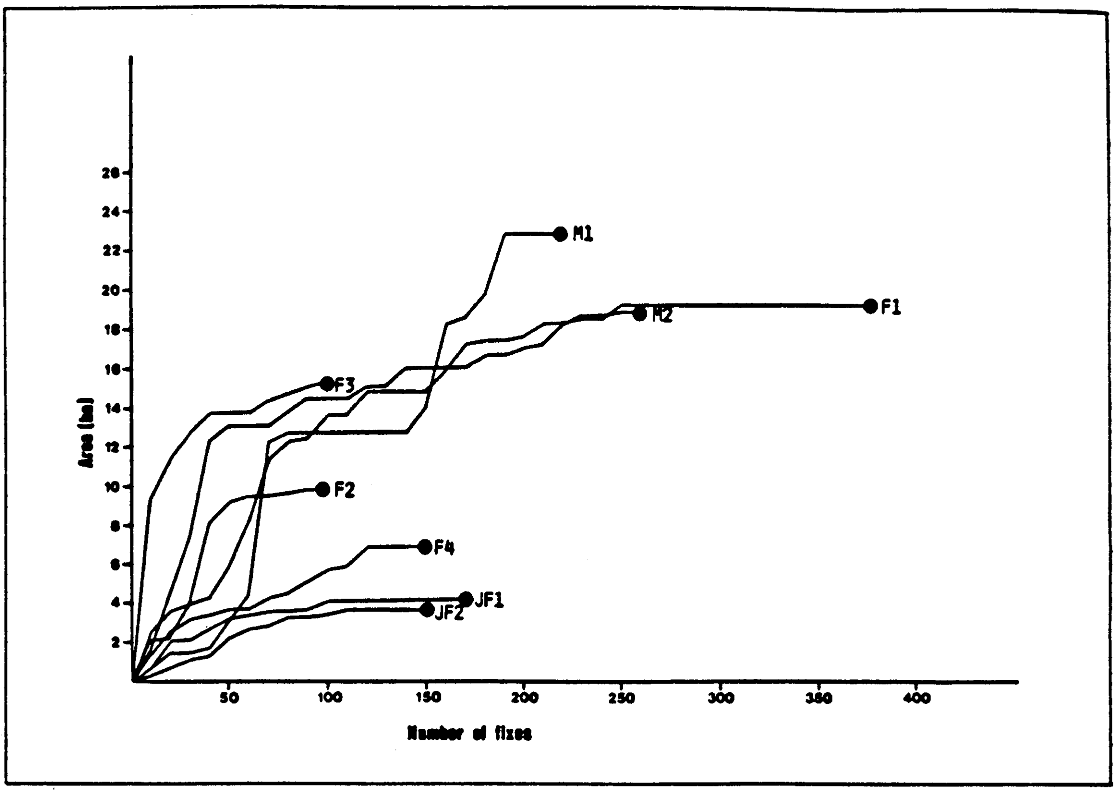

FIGURE 6 : THE OBSERVATION-AREA CURVES OF THE RESPECTIVE STUDY ANIMALS.

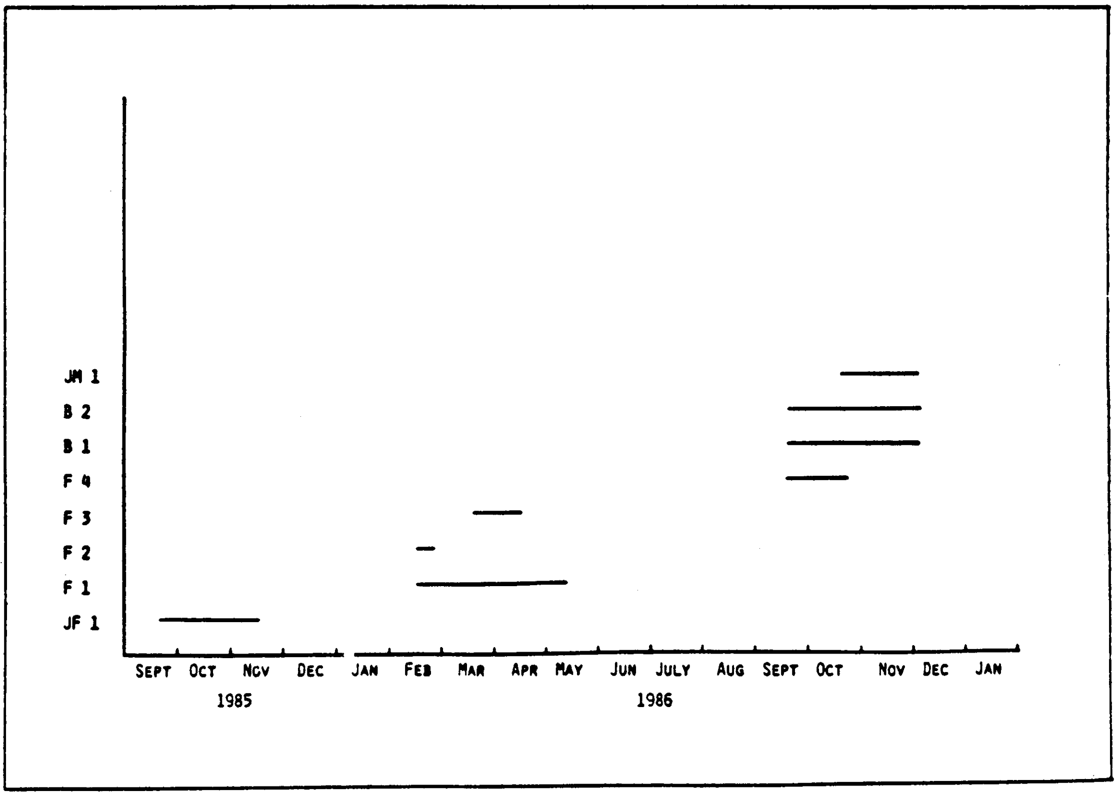

FIGURE 7 : THE PERIODS OVER WHICH THE RESPECTIVE STUDY ANIMALS WERE RADIO TRACKED.

Home range overlap between F1 and F2, F2 and F3 (Fig. 8) and M1 and M2 (Fig. 9) was 0,5 ha, 3,18 ha and 3,6 ha respectively. Expressed as a percentage of each home range this represents a mean (SE) of 3,8 ± 0,919, 26,4 ± 4,2 and 17,33 ± 1,22, respectively, for each of these dyads. Overlap between M2 and F4 was 28,7% of F4's home range and 8,7% of M2's home range. Sixty-one percent of M1's home range overlapped with F4's. In Figure 9, the digits one and two represent the capture localities of two females which were not radio tracked. The radio collar on the rabbit captured at point 2 failed soon after her release and another rabbit was captured at point 1 with M2 when the study animals were finally collected for captive breeding.

The intensity of home range use is presented in Figures 10,11,12 and 13. These show that although adult rabbits range widely, there are preferred core areas within the home range. In rabbits with overlapping home ranges these core areas are mutually exclusive (Fig. 10,11 & 12). By comparison, the juveniles intensively use the entire area of their small home ranges (Fig. 13).

Social Structure

Solitary rabbits constituted 97,3% of sightings while only five observations were made of adult pairs (Table 11). On four of these occasions one of the pair was radio collared (either the male or the female) and it was possible to capture the other animal to ascertain its sex. One radio collared male was seen in the presence of another rabbit for three days but it could not be determined if this was the

Rabbit Code	Home Range Size (ha)			
	Adult Males	Adult Females	Juvenile Males	Juvenile Females
M1	22,96			
M2	18,88			
F1		19,34		
F2		9,80		
F3		15,44		
F4		6,95		
JM1			3,67	
JF1				4,2
Mean±SE	20,92±1,44	12,88±1,39	3,67	4,2

Table 10: The home range sizes of adult and juvenile, male and female <u>Bunolagus</u>.

Group Size	1	2
No of Observations	213	6
% of Observations	97,3	2,7

Table 11: The frequency of <u>Bunolagus</u> groups sizes observed.

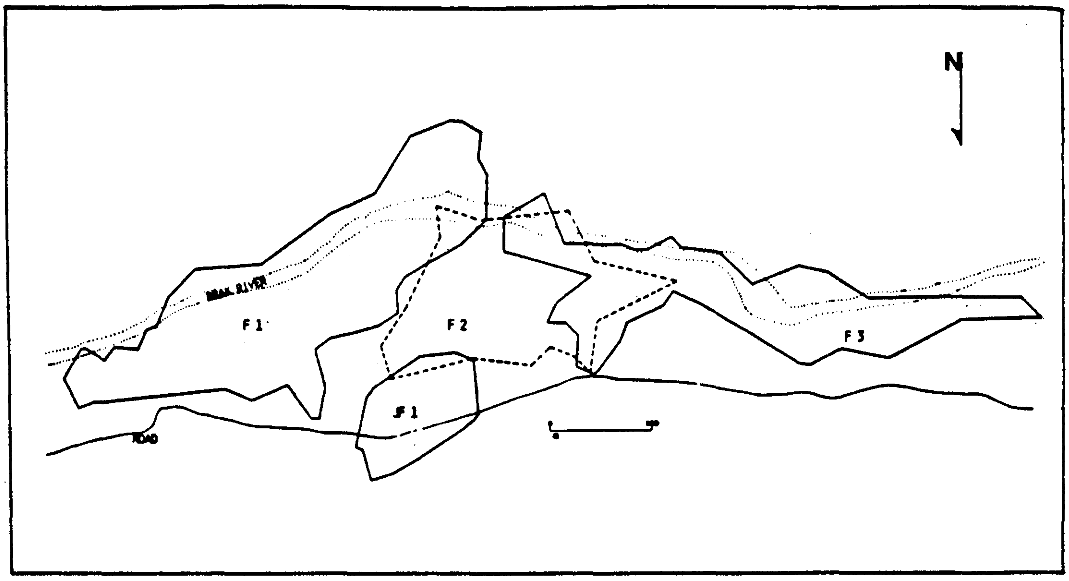

FIGURE 8 : THE SPATIAL ORGANIZATION OF THE HOME RANGES OF <u>BUNOLAGUS</u> TRACKED IN THE FIRST AND SECOND PERIOD.

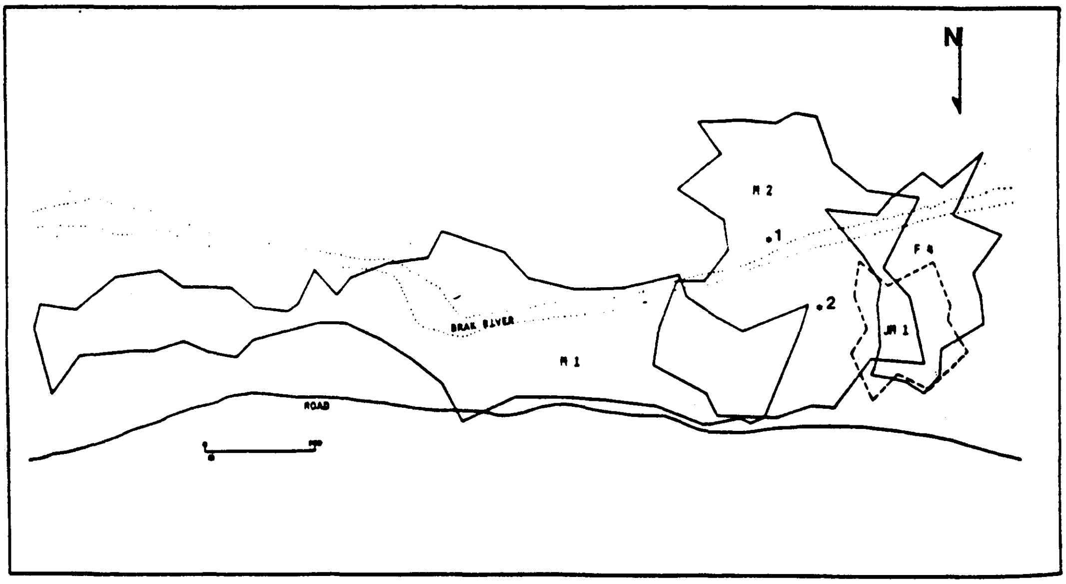

FIGURE 9 : THE SPATIAL ORGANIZATION OF THE HOME RANGES OF <u>BUNOLAGUS</u> RADIO TRACKED IN THE THIRD PERIOD.

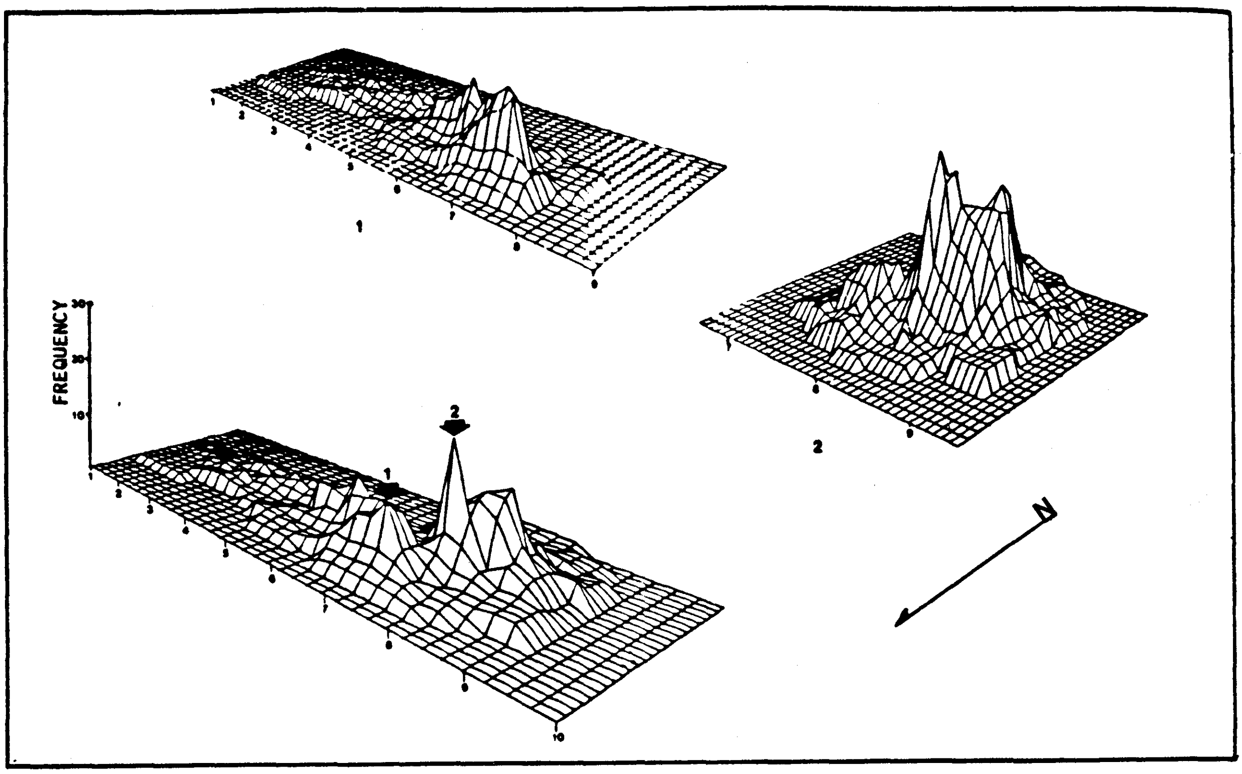

FIGURE 10 : THE INTENSITY OF HOME RANGE UTILIZATION BY M1 (NO 1) AND M2 (NO 2).

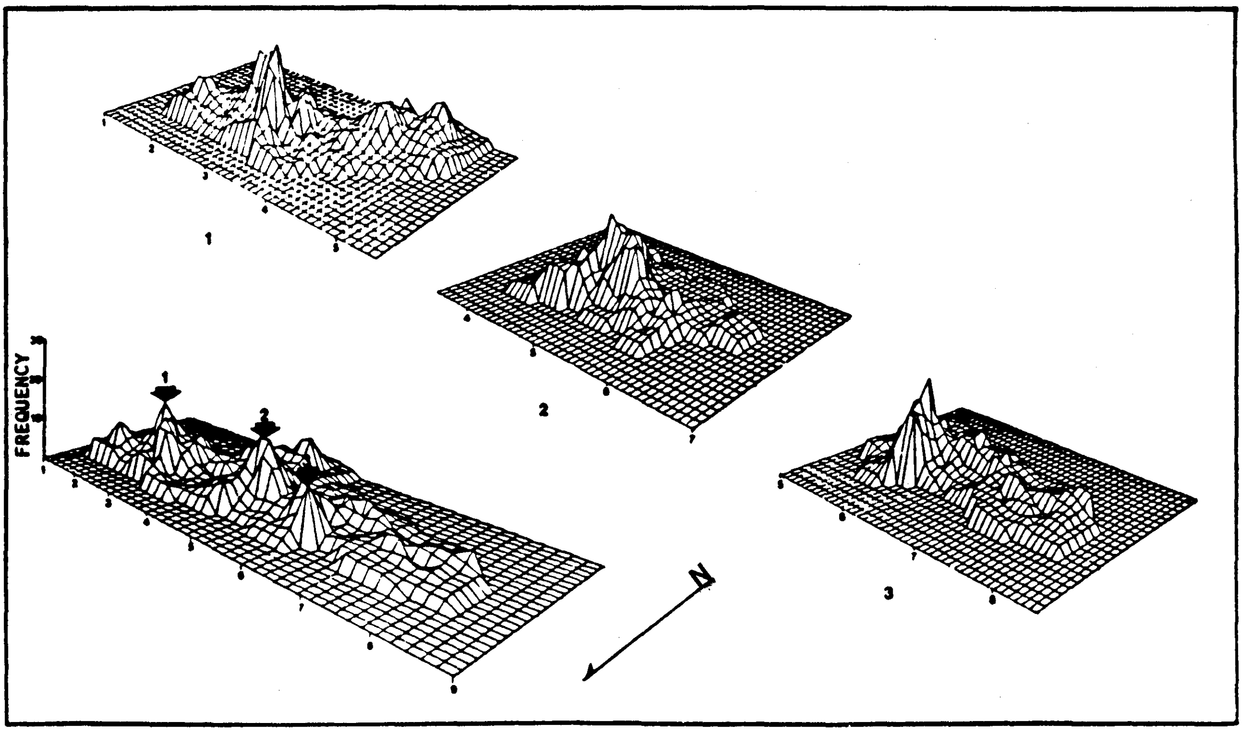

FIGURE 11 : THE INTENSITY OF HOME RANGE UTILIZATION BY F1 (NO 1), F2 (NO 2) AND F3 (NO 3).

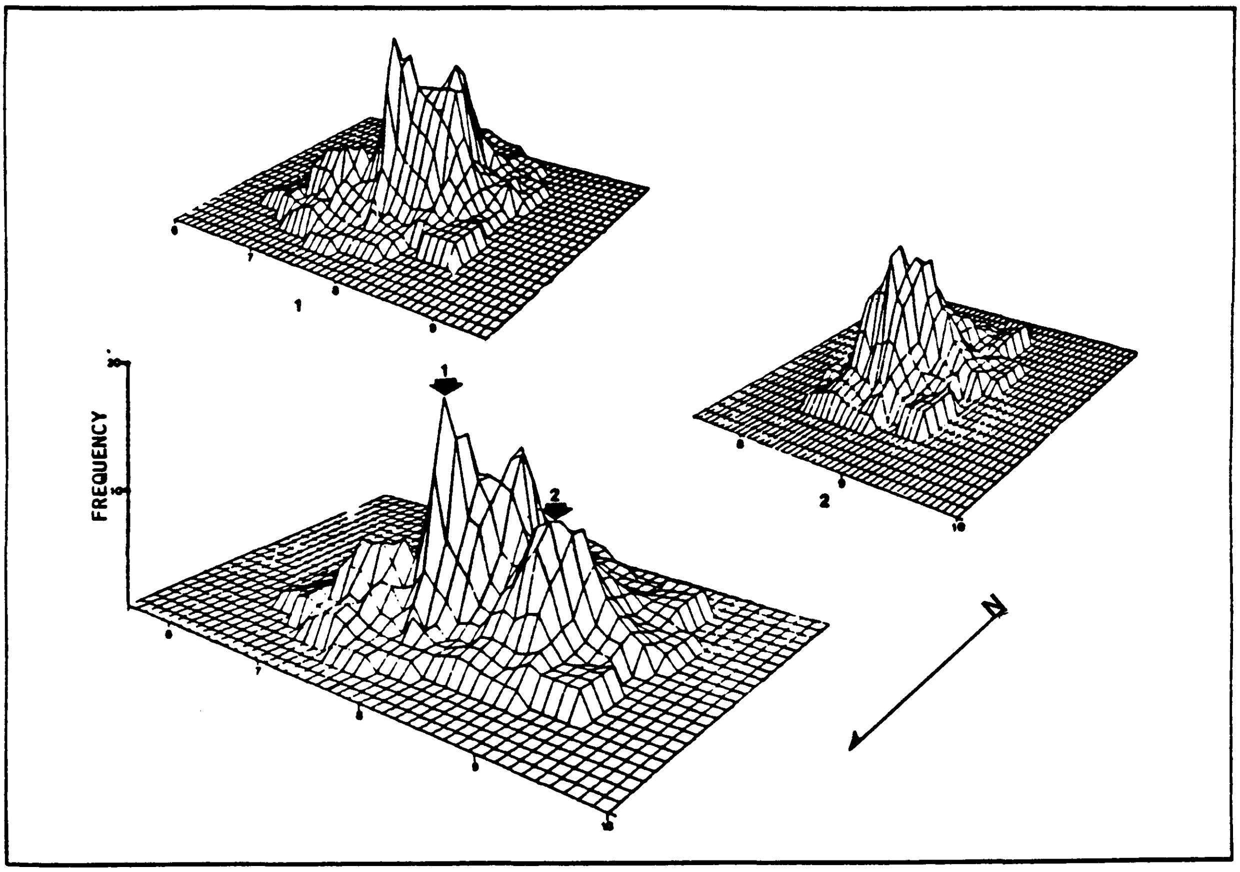

FIGURE 12 : THE INTENSITY OF HOME RANGE UTILIZATION BY M2 (No 1) AND F4 (No 2).

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same female each time. A couple, comprising a radio collared female and a juvenile weighing an estimated 300g, was also observed.

The frequencies of distances between simultaneous radio-fixes taken for M1 and M2, F1 and F2 and M2 and F4 are shown in Figure 14. Distances in the 0-50 m interval comprised 6,1%

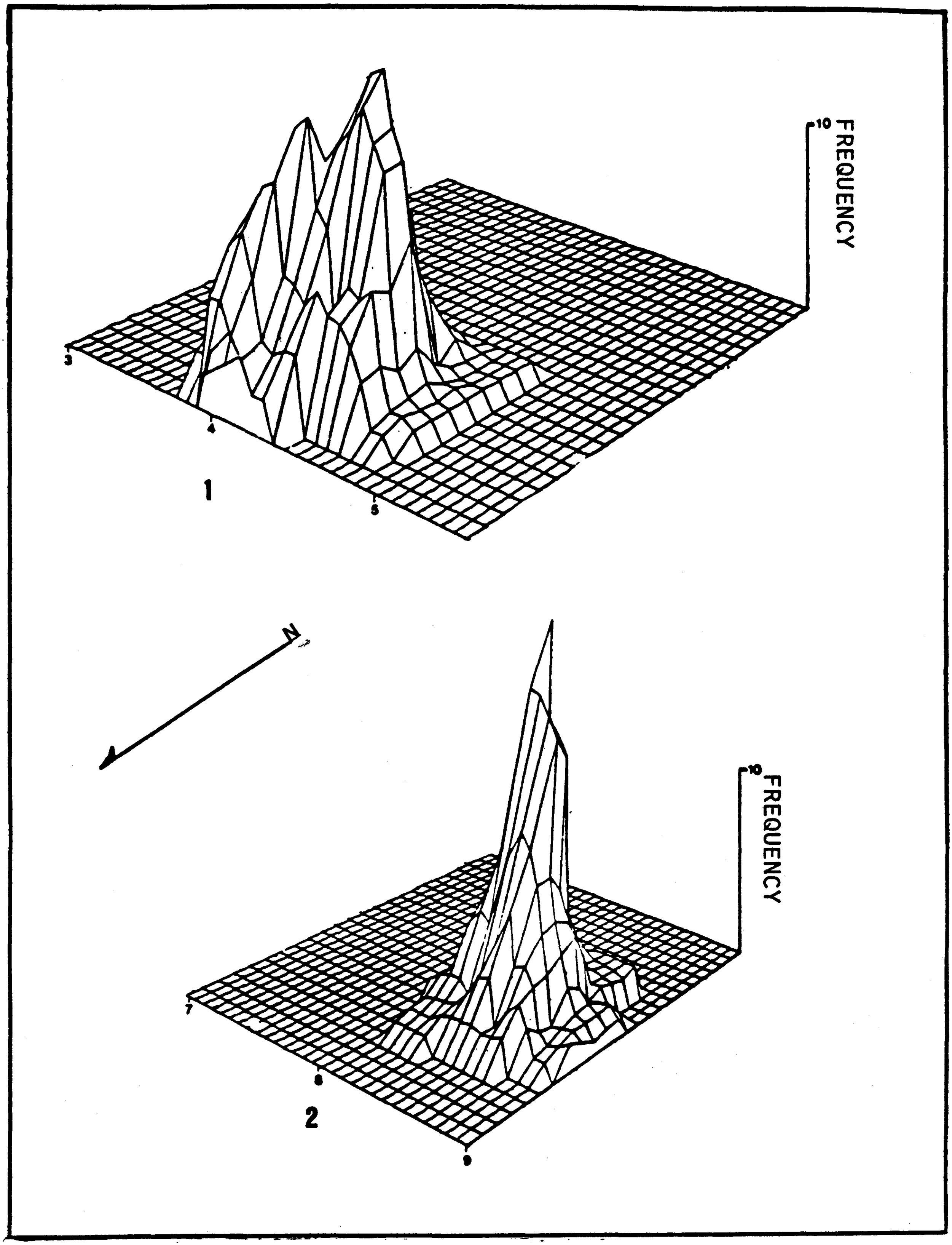

FIGURE 13 : THE INTENSITY OF HOME RANGE UTILIZATION BY JF1 (No 1) AND JM1 (No 2).

and 7,2%, in the like-sex groups, F1/F2 and M1/M2, respectively, and 10,6% in the mixed-sex group M2/F4. The mean inter-individual distances of F1/F2 and M1/M2 (t=53,8, df=313, P<0,05) F1/F2 and M2/F4 (t=56,27, df=235, P<0,05) and M1/M2 and M2/F4 (t=82,28, df=360, P<0,05) are not significantly different. Thus, there is no indication that the animals in the male-female dyad were more closely associated.

Activity

Indices of activity are presented for individual rabbits and summarized for the adult male, female and juvenile categories (Fig. 15). There is considerable inter-individual variation in the patterns of activity followed, and no trends are clearly discernable. The activity of some individuals (e.g. M1, M2, F1, F3 & JM1) is inclined toward a bimodal pattern while the patterns of others (F2, F4 & JF1) have a unimodal tendency. In the bimodal patterns, the difference between the mean of readings constituting the nadir and those constituting the peaks are not significant for any of the rabbits (F1: t=1,59, df=11; F3: t=1,05, df=11; M1: t=0,26, df=10; M2: t=2,16, df=11; JM1: t=1,25, df=10). Likewise, in those rabbits with a unimodal activity pattern the difference between the mean of readings before 01h00 and those thereafter is not significant (F2: t=1,43, df=10; F4: t=0,26, df=10; JF1: t=0,92, df=10).

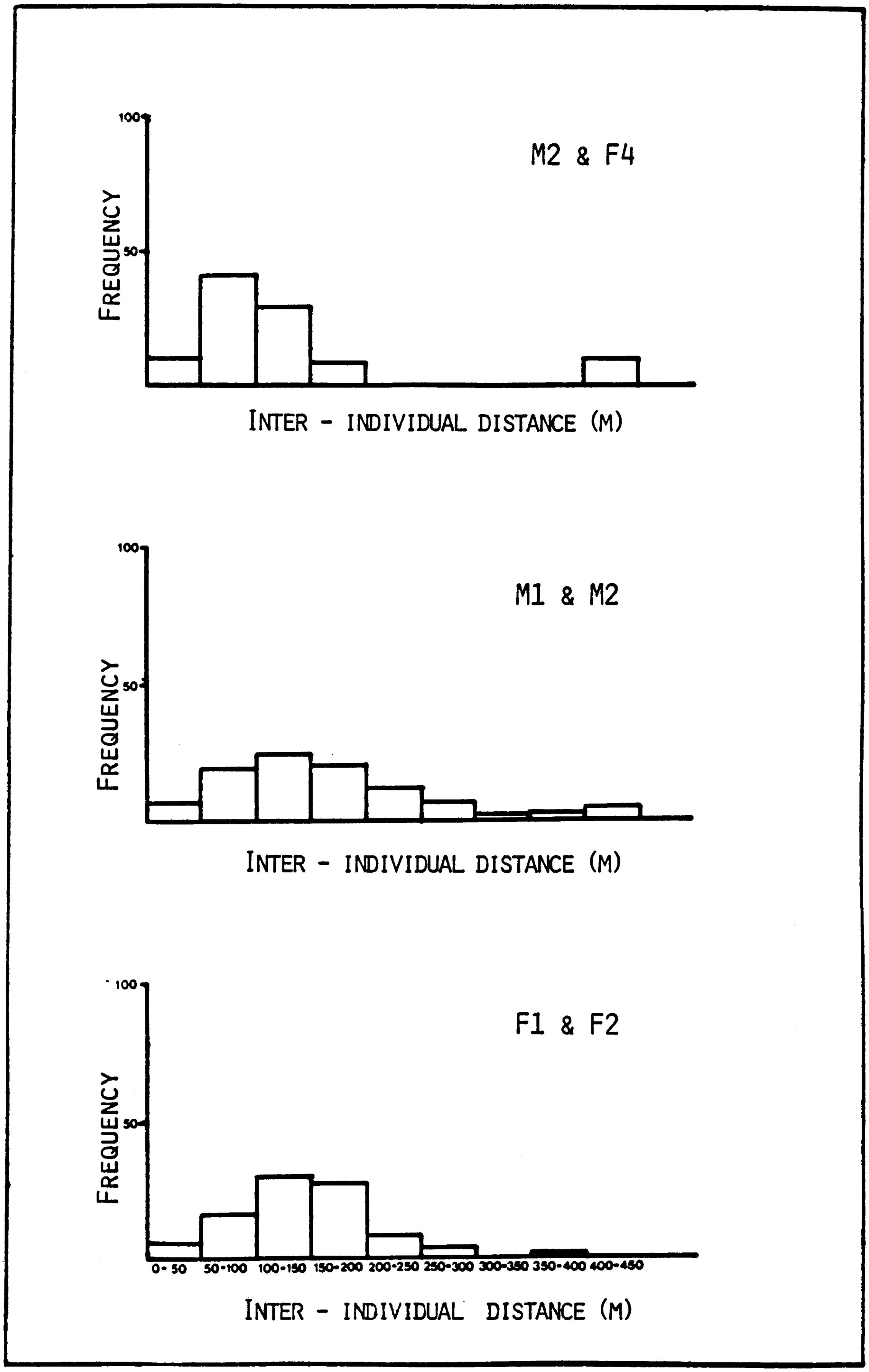

FIGURE 14 : THE FREQUENCY OF INTER - INDIVIDUAL DISTANCES OF SIMULTANEOUSLY RADIO TRACKED RABBITS.

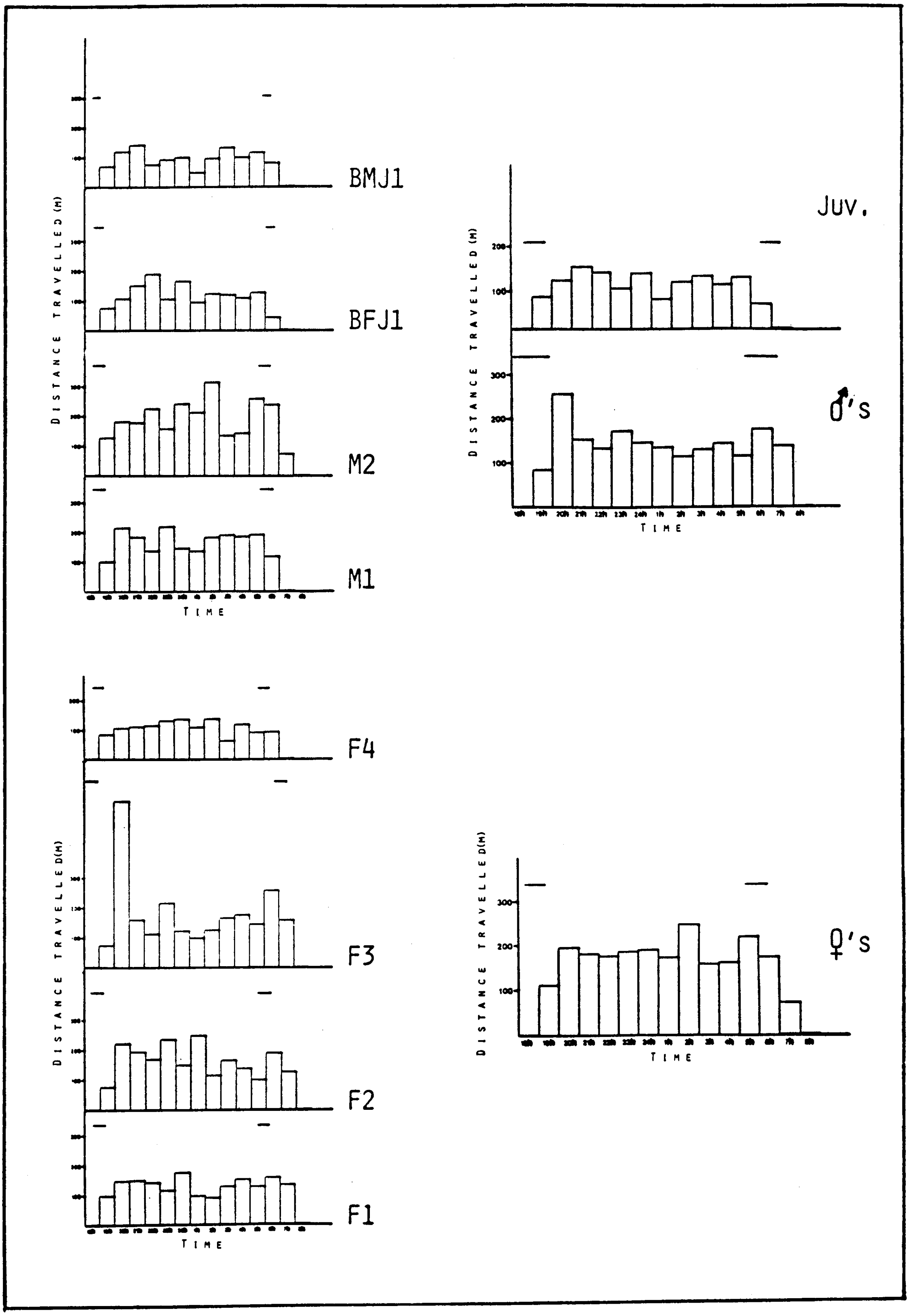

FIGURE 15: THE ACTIVITY PATTERNS OF THE INDIVIDUAL STUDY ANIMALS AND SUMMARIES OF EACH SEX AND AGE CLASS. (——— DENOTES SUNRISE AND SUNSET.)

DISCUSSION

Capture

The sedentary behaviour of <u>Bunolagus</u> greatly facilitated their location on successive days and their habitual use of an escape route meant nets could be placed with a high degree of certainty that a rabbit would be ensnared. On average, rabbits flushed from cover when the researcher was between 5-10 m away on horseback and 1-5 m on foot. However, the elevated position of the former resulted in a higher capture success rate because rabbit escape routes could be more accurately observed.

Forms

The European hare, <u>L. europaeus</u>, constructs its forms to obtain maximum protection from the sun and prevailing wind (De Vos & Dean 1965). <u>Bunolagus</u> forms meet similar requirements. It is possible that <u>Bunolagus</u> select sites for forms such that a bush will obscure the entrance. However, it is likely that this observation is just an artifact of the dense habitat and needs testing.

Home Range Size

The convex polygon method, which is conventionally used in studies of home range size, was not applied in this investigation since it resulted in gross overestimates by including habitat which <u>Bunolagus</u> does not use (i.e. the hills and plains adjacent to the riverine vegetation).

Interspecific comparisons of home range size should only be made between studies employing the same techniques (Sanderson 1966). Consequently, only home ranges determined by radio telemetry are utilized in comparisons that follow. Compared to the 15,56 ± 1,40 ha of the Bunolagus mean home range that of the European hare, Lepus europaeus, was 29 ± 20,9 ha (Netherlands; Broekhuizen & Maaskamp 1982) and 53 ± 13 ha (New Zealand; Parkes 1984); that of the snowshoe hare, L. americanus, was 2,5 ± 0,8 ha to 6,9 ± 3,7 ha (Alaska; Boutin 1984) and that of female cottontail rabbits, Sylvilagus floridanus, 3,1 ha (Wisconsin; Jurewicz, Cary & Röngstadt 1981).

Leporid home range size scales allometrically with body size (Swihart 1986) which explains the larger home range of L. europaeus. Home range may, however, vary intraspecifically both annually and seasonally in relation to: primary productivity (Haugen 1942; Jurewicz, Cary & Röngstadt 1981; Trent & Röngstadt 1974), the reproductive cycle (Trent & Röngstadt 1974) and population density (Boutin 1984; Lowe 1958; Toll, Baskett & Conaway 1960).

In S. aquaticus a twelvefold increase in density resulted in a threefold decrease in home range size (Lowe 1958; Toll, Baskett & Conaway 1960). Similarly, a threefold increase in L. americanus density caused a threefold decrease in mean home range size (Boutin 1984). Both L. americanus and Bunolagus have similar body weights consequently the differences in their home ranges might be explained by the density effect. The density of L. americanus was

0,393 hares/ha in Boutin's study compared to the 0,166 rabbits/ha in the present investigation. The disparate habitats of the two species no doubt also contributed to the observed differences in home range size.

Mammalian home range size and metabolic rate scale to body size with the same exponent. McNab (1963) thus suggested that home range size is determined by metabolic rate. Swihart (1986), however, found that leporid home ranges differ substantially from sizes predicted by body size energetics alone. Furthermore, the allometric relationship between body and home range size does not apply intersexually in leporids. Males are generally smaller than females but usually have significantly larger home ranges (Cowan & Bell 1986). In this respect Bunolagus tends toward the general leporid pattern.

Spatial Organization

This sex difference in leporid home range size arises because different resources influence the movements of each sex. The size of the female's home range is determined largely by the availability of food resources as well as the requirements of parental care and, in the promiscuous polygamous mating system of leporids, the dispersion of females in turn determines male home range size (Cowan & Bell 1986). In S. floridanus the male home range increased 1,5 times up to the peak of the breeding season and then decreased concomitantly with testes regression. In contrast, female home ranges halved in size following the first litter and the appearance of new vegetative growth (Trent & Röngstadt 1974). Bunolagus was not tracked sufficiently long to determine such

However, home range size could be expected to remain stable for most of the year because of the long breeding season (Chapter 6) and the stable arid environment with only sporadic rain to stimulate vegetative growth.

Territoriality is a rare feature of leporid biology (Cowan & Bell 1986). The low degree of intrasexual home range overlap in Bunolagus is thus more likely to be a result of the low density which characterised this population. In swamp rabbits, S. aquaticus, intrasexual overlap of less than 25% in home ranges occurred at densities of 0,137 rabbits/ha but at densities of 1,65 rabbits/ha this changed to between 25-75% (Lowe 1958; Toll et al. 1960).

The more intensively used exclusive core areas within Bunolagus home ranges probably arose because rabbits tended to position themselves as far as possible from their neighbours. L. americanus females similarly prefer those sections of the home range furthest from the borders with their neighbours (Boutin 1980).

Social Structure

Mammalian societies are the combined result of the life history of the species concerned, its predator avoidance strategy, resource exploitation strategy and its strategies for mating and rearing of young to maturity (Crook, Ellis & Goss-Custard 1976).

The majority of mammalian species are solitary (Linn 1984) and group living is generally a consequence of some limiting resource (e.g. food, females or refuge sites) or predation pressure which concentrates individuals and results in cooperation or conflict (Alexander 1974). Bunolagus is essentially a solitary species only deviating for mating purposes and in the development of mother-infant bonds for the raising of offspring (Table 11).

The only wild leporid known to form stable, structured groups is the European rabbit, Oryctolagus cuniculus, (Cowan & Bell 1986). Group size and social structure in this species varies in relation to the availability of refuges (i.e. burrows) which are a limiting factor. Since Bunolagus uses forms for refuge, and these can be constructed anywhere within its habitat, there is no resultant pressure to aggregate.

Temporary feeding associations occur in a number of leporid species (Cowan & Bell 1986) when feeding on a restricted food source or in the open with little cover. A dominance hierarchy may prevail (Monaghan & Metcalfe 1985) which gives dominant animals access to the most food. However, these associations have advantages for all individuals in the group as corporate vigilance results in each individual spending less time vigilant and relatively more time feeding (Monaghan & Metcalfe 1985).

The food resources of Bunolagus are relatively abundant and evenly distributed throughout its habitat and individuals are not therefore forced into close proximity to each other.

Predator avoidance comprises two aspects. First, it is necessary to avoid detection and then once detected, a prey animal should be able to flee or defend itself. For many big or plains-dwelling herbivores the former requirement is difficult to achieve and they may survive more successfully by forming groups to utilize the selfish-herd effect (Hamilton 1971) or corporate vigilance effect (Pulliam 1973). However, for smaller mammals such as Bunolagus living in thick vegetation, the possibility of detection is greatly reduced, and may be further enhanced, by spacing out (Tinbergen, Impekoven & Franck 1967). In addition, it is easier for a solitary, fleetfooted rabbit to escape a predator, once detected, by dashing out of sight and concealing itself in the dense scrub than would a cohesive group. Cowan & Bell (1986) suggest that the development of cryptic colouration and the absence of the white tail flag found in many leporids, including Bunolagus, may have resulted from this strategy.

Leporid females nurse their young for a period of 5-20 minutes each night and provide no other parental care (Broekhuizen & Maaskamp 1980; Röngstadt & Tester 1971; Sorenson, Rogers & Baskett 1972). With this form of post natal care a paternal component is not required and males maximize their reproductive success by mating with as many females as possible. Pairbonds are thus expected to form only around periods of oestrus in the females.

In nonpregnant S. floridanus (Marsden & Holler 1964) and O. cuniculus (Myers & Poole 1962) oestrous behaviour occurs in cycles of seven days while S. aquaticus (Marsden & Holler 1964) exhibits this behaviour every 12 days. Only at the peaks of these cycles and during postpartum oestrus do the males associate with females for any length of time. During postpartum oestrus S. aquaticus and S. floridanus males may stay with a female for up to three days. The observation of a pair of Bunolagus in association for the same period suggests that their oestrous period may be similar to that of S. floridanus. Further evidence of little intersexual contact in Bunolagus is the nonsignificant difference between the mean inter-individual distance of like-sex and mixed-sex dyads (Fig. 14).

In the colonial O. cuniculus the frequency of adult-juvenile interactions is relatively high with most aggression directed intrasexually (Cowan 1987). However, little is known of these social relationships in solitary leporids. Tefft & Chapman (1987) mention that adult-juvenile interactions in captive S. transitionalis, are few. The juvenile male in the present study was tolerated by both sexes until it was at least two months old. In juvenile L. americanus home range size is half that of the doe when they are six weeks old and attains the same size at two months (Röngstadt & Tester 1971). This relatively rapid development compared to Bunolagus may be a result of the precociality of hare neonates.

Activity

Mammalian activity patterns vary in relation to food availability, predation pressure, weather and reproductive status (Ashby 1972). Leporids are nocturnal but extend their activity diurnally in summer when nights are short (Holler & Marsden 1970, Lemnell & Lindlöf 1981, Kolb 1986). *Bunolagus* is clearly nocturnal but it was not ascertained whether activity patterns vary seasonally. Lemnell & Lindlöf (1981) found great inter-individual variation in activity in mountain hares, *L. timidus*, with a general trend toward bimodality with peaks at sunset and sunrise. These patterns were only followed by some animals in the present study.

CHAPTER 6

REPRODUCTION AND MORTALITY

INTRODUCTION

The survival of a species in an undisturbed ecosystem depends upon its ability to maintain a balance between natural mortality and reproduction. In a species declining numerically it is assumed that this balance has been disturbed. Conservation management seeks to maintain or increase the numbers of such a species to a level at which it can, theoretically be viable in evolutionary time. Thus, an insight into the parameters which operate in the dynamic interplay between reproduction and mortality are essential to this end.

MATERIALS AND METHODS

The endangered status of Bunolagus precluded the use of a shot sample as a means of gathering reproductive data. Consequently, information could only be obtained from incidental observations of wild and captive rabbits. The latter consisted of a colony of two males and two females established in an enclosure within the riverine scrub of the study area. In the field old breeding stops were distinguished from other holes of similar size by the presence of caked rabbit fur on the floor. Length, entrance diameter and nest cavity diameter were measured.

RESULTS

Breeding Season

Evidence of breeding was found in all months except June, July, October, November, December and January (Table 12).

Litter Size and Breeding Synchrony

Three observations of singleton litters were obtained from the captive rabbits . Apart from these births a further four juveniles were produced in this colony between January 1987 and May 1987 (Table 13). One pair of these juveniles were about twice the size of the other pair suggesting synchronous births if these were singleton litters. Further evidence of synchronous reproduction in the species was forthcoming from two adult females (from the captive colony) who gave birth in transit to Pretoria on the 31 May 1987. They produced a kitten each on the same night. That these kittens were not the result of a twin birth was indicated by the fact that both females had bloodied hair periferal to the vagina.

Gestation Period

The evidence for a gestation period of 35-36 days is indirect. Twenty four hours prior to the completion of the enclosure in August 1986 a single male was captured within its confines, subsequently radio collared and released. Following its final construction the next day, an adult female was observed to be trapped within the enclosure. Eleven days thereafter a second, subadult, female was introduced into the enclosure. A further 19 days later a juvenile rabbit was seen with the adult female.

DATE			OBSERVATION	ESTIMATED MONTH OF PARTURITION
24	August	1985	Lactating female	August
17	September	1985	Juvenile female	August
29	September	1986	Juvenile male	August
14	September	1986	Pregnant female	September
22	September	1986	Dead neonate	September
14	October	1986	Juvenile male	September
3	March	1986	Juvenile male	February
25	May	1987	Juvenile males(encl.)	March
25	May	1987	Juvenile males(encl.)	April
26	May	1986	Juvenile seen	April
28	May	1986	Newly evacuated nest	April
5	June	1986	Juvenile seen	May
18	June	1986	Juvenile seen	May
27	June	1987	2 kittens born in transit	May

Table 12: Observations of *Bunolagus* breeding patterns obtained during the study.

DATE	EVENT
16 August 1986	Adult male caught in enclosure radio collared and released.
17 August 1986	Enclosure completed and adult female weighting 1800g found in enclosure.
28 August 1986	Sub-adult female weighing 1500g caught and transferred to enclosure.
3 September 1986	Adult male weighing 1500g caught and transferred to enclosure.
16 September 1986	A juvenile seen in the enclosure with the adult female.
22 September 1986	Dead neonate found in the enclosure.
21 January 1987	Radio collared male returned to enclosure.
22 January 1987 to 27 May 1987	Four young produced. All males.
31 May 1987	Two captive females give birth to a kitten each while in transit to Pretoria.

Table 13: The sequence of events leading to the establishment of a captive colony of <u>Bunolagus</u> in the study area and the production of young.

Assuming that the adult female gave birth to this juvenile and was inseminated immediately afterwards by the male (day 1) during her post partum oestrus, she would have produced the dead neonate found in the enclosure 36 days later. This neonate may have been born one or two nights earlier since the enclosure was checked every two days, hence a gestation of 35-36 days. Although the other female was present in the enclosure it is unlikely that she gave birth to the dead neonate because of her subadult status. Furthermore, the kitten was found on the side of the cage frequented by the adult female.

Development and Growth.

Standard measurements, recorded post partum, from two of the three neonates born during the study are presented in Table 14. These individuals died one and four days, respectively, after birth. The third neonate also perished but was too badly trampled for measurement.

All three kittens were altricial at birth; they had closed eyes and a sparse pelage consisting of 1 mm long black hair except under the chin, belly and inner pinnae. The latter parts were pink and bare at birth but developed a covering of cream fur within 48 h. In the kitten which survived for four days the eyes remained closed and locomotion did not develop beyond a wobbly belly-crawl.

Growth data were recorded sporadically from a single wild-caught juvenile over a period of approximately one month

Mass (g)	Hindfoot (mm)	Ear (mm)	Tail (mm)	Total Length (mm)
40	26	20	7	130
42	27	17	8	132
41±1,0	26,5±0,5	18,5±1,5	7,5±0,5	131±1,0

Table 14: Standard measurements recorded for two *Bunolagus* neonates (Mean±SD).

DATE	MASS (g)	GROWTH RATE (g/day)
17 October 1986	570	
2 November 1986	770	12,5
7 November 1986	1020	13,1

Table 15: The mass and growth rate of a single free-living juvenile *Bunolagus* male.

before its transmitter failed (Table 15). During this time the mean growth rate was 12,8 ± 0,46(SD)g/day.

Breeding Stops

All breeding stops were dug into the hummock of soil held by the roots of shrubs in the study area (Fig. 16). The mean depth of stops was 265,7±2,32(SE) mm and they extended into the soil at an angle of about 30° below horizontal. From the entrance, 100,7±1,09 mm in diameter, the stop broadened into a chamber 137,1±1,51 mm wide (Table 16). The latter was lined with dry grass and then fur. Two stops were found sealed with tamped down soil and a few twigs.

Mortality

Two radio collared females (F2 & F3) were taken by African wildcats (Felis lybica). A pair of spotted eagle owls, Bubo africanus, which nested 200m away from the enclosure, did not capture lagomorphs of any description. The majority of prey brought to their nest were birds.

DISCUSSION

Breeding

The discontinuity of records in the present study merely reflects the disruption caused by commitments to other aspects of this investigation. Breeding probably occurs throughout most of the year as it is unlikely that rabbits will breed during the cold, dry August and September months but not during the warm, moist October to January period.

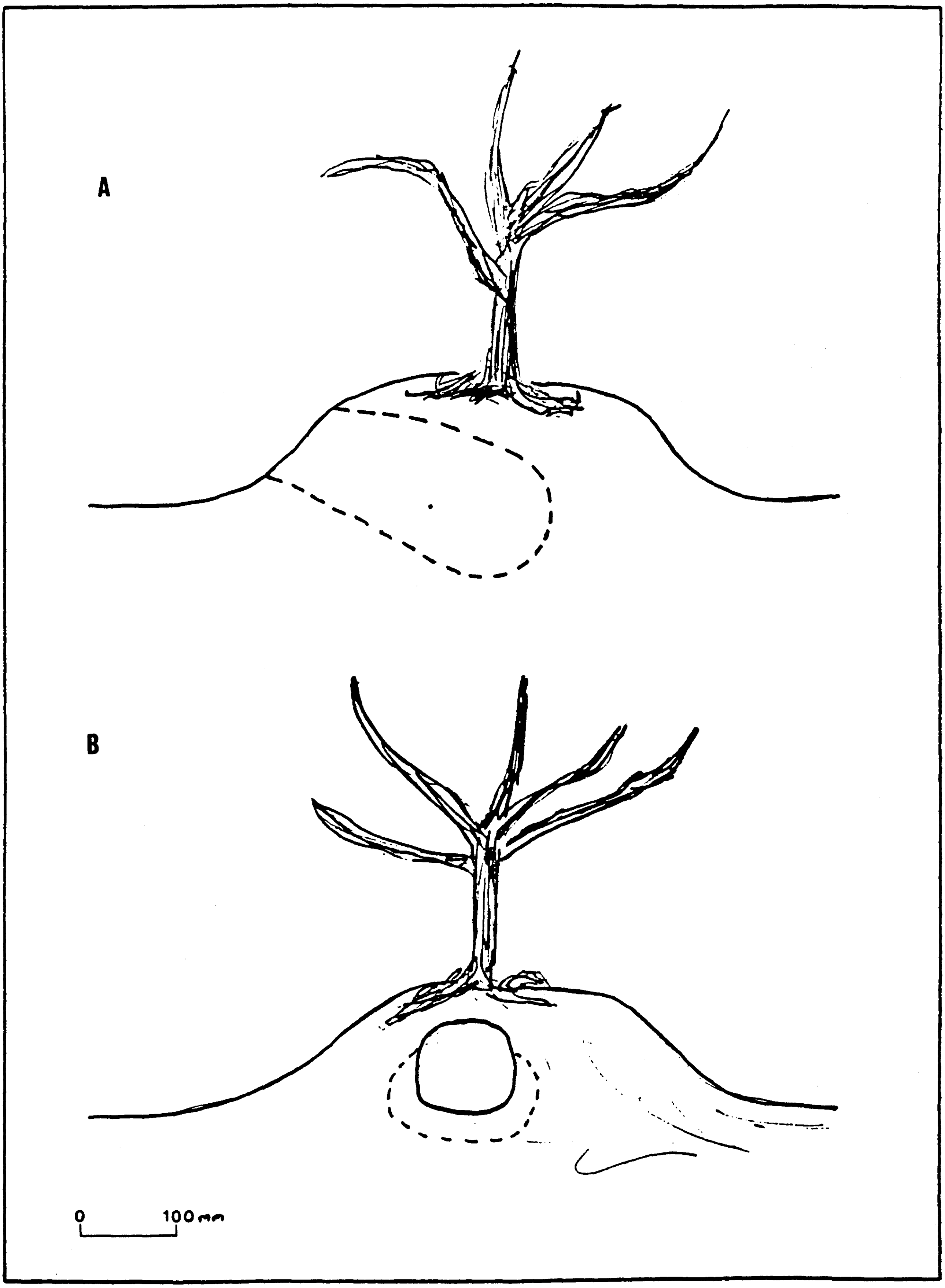

FIGURE 16 : THE BREEDING STOP OF <u>BUNOLAGUS</u>. A. SIDE VIEW IN CROSS-SECTION
B. FRONTAL VIEW.

In lagomorphs the length of the breeding season is inversely correlated with latitude while, conversely, litter size is directly correlated (Bothma & Teer 1977; Conaway, Sadler & Hazelwood 1974; Flux 1981; Lord 1960). The Bunolagus breeding season and litter size are similar to those of other lagomorphs occurring at or below the same latitude (Bothma & Teer 1977; Cervantes & Lopez-Forment 1981; Durant 1981; Hayashi 1981; Kingdon 1974; Smithers 1983; Verheyen & Verschuren 1966).

Light, vegetation and temperature are implicated as factors which determine the length of lagomorph breeding seasons. Poole (1960) showed that, in Australia, O. cuniculus' breeding season coincides with periods of abundant green vegetation irrespective of the light regime. Flux's (1965) research supported this finding but showed that, in contrast, the proximate cue in the timing of breeding in L. europaeus was photoperiod. In the male pygmy rabbit, S. idahoensis, breeding is controlled by light while that of the female depends on the condition of the vegetation (Wilde 1981). With the erratic rainfall regime of the Karoo the condition of vegetation is most likely to play the dominant role in stimulating reproduction in Bunolagus.

In life history theory first order "strategies" are those that arise as a consequence of body size while second order "strategies" vary between populations according to environmental circumstances (Western 1979).

Length (mm)	Entrance Diameter (mm)	Nest Cavity Diameter (mm)
200	100	140
310	90	130
250	105	120
300	95	170
260	105	130
290	115	140
250	95	130
265,7±2,32	100,7±1,09	137,1±1,51 (Mean±SE)

Table 16: The length, entrance diameter and nest cavity diameter of seven _Bunolagus_ breeding stops (Mean±SE).

A short breeding season forces a female to concentrate her resources in a few large litters while a long breeding season allows the production of a number of young spread out over many small litters (Stearns 1976). The small litter size of _Bunolagus_ has thus evolved in response to its long breeding season - a second order "strategy". Chapman (1984) showed a significant negative correlation of gestation period with latitude in New World rabbits. In contrast Swihart (1984) found that gestation time was a first order "strategy" in lagomorphs in general. However, Swihart's (1984) data for body weight in New World rabbits support Chapman. In this respect the gestation period of _Bunolagus_ compares favourably with that of _S. aquaticus_ which occurs in similar latitudes.

Chapman (1984) suggests that the longer gestation period produces more precocial rabbit young which are better equipped to counter predation and competition. In support of this hypothesis Chapman (1984) cites data involving a comparison of S. transitionalis (Tefft & Chapman 1983) with S. brasiliensis neonates (Durant 1981). It ,however, appears that measurements of S. transitionalis extrapolated to birth were compared with measurements of S. brasiliensis 1-3 days old. Measurements of the two species between 1-4 days do not appear to differ significantly (Durant 1981; Tefft & Chapman 1983).

Inherent in a comparison of body measurements, as an index of precociality, is the assumption that heavier rabbit neonates have more highly developed motor and sensory functions, for it is really these aspects that will determine an animal's ability to avoid predators and cope with competition. Altricial young are essentially helpless irrespective of their size and if larger neonates are to be shown to be more successful at avoiding predation, it will be necessary to establish a correlation between neonate size, motor and sensory capabilities at birth and their rate of development before Chapman's (1984) hypothesis can be proven.

Synchronized Breeding

Synchronized breeding has also been reported in S. floridanus (Conaway & Wight 1962; Marsden & Conaway 1963) and in S. bachmanii (Chapman & Harman 1972). This phenomenon has very clear reproductive advantages in swamping predators with prey; a similar advantage would hold for *Bunolagus* if, as the limited data suggest, the species is characterised by synchronous breeding.

Breeding Stops

The structure of *Bunolagus'* breeding stops most closely resembles that of *O. cuniculus* (Lloyd & McCowan 1968) and *S. transitionalis* (Tefft & Chapman 1987). In *S. transitionalis* the nest is excavated a few hours before parturition using the teeth and forefeet (Casteel 1966). Unfortunately active construction of breeding stops by *Bunolagus* was never observed and consequently, whether a similar situation prevails cannot be confirmed.

Growth and Development

The growth rate of *Bunolagus* (Table 15) in the linear phase is similar to that of *L. capensis* (Flux 1970), which has only a slightly heavier adult mass, and *L. americanus* (Severaid 1942), which has a similar mass. Except for a sparse covering at birth, development of the *Bunolagus* neonate to four days follows the pattern found in *S. transitionalis* and *S. floridanus*. Neonates of the latter are born pink and hairless but develop pelage within a day. Their eyes only open at seven days and locomotion develops at ten days. At fourteen days juveniles leave the nest (Beule & Studholme 1942; Tefft & Chapman 1983). The production of an altricial neonate confirms the rabbit status of *Bunolagus* which was originally placed in the Genus *Lepus* by Thomas (1903), the members of which are characterized by precocial young.

Mortality

All avian and terrestrial predators in the Karoo are hunted as vermin by the sheep farmers of the area. While ecologically unsound, this practice must undoubtedly benefit Bunolagus. Robinson (1981) noted that hunting of rabbits with dogs might be a major mortality factor. However, despite Shortridge's remark (in Robinson 1981) that it runs so slowly and clumsily that any dog can catch it, Bunolagus is in fact as fleetfooted as L. capensis. Furthermore (as noted in Chapter 3) the density of the riverine scrub negates the effective use of hunting dogs.

CHAPTER 7

CONSERVATION RECOMMENDATIONS

The survival of a species in perpetuity will depend on the conservation of its habitat and the maintenance of sufficient genetic diversity, within the species, to enable it to adapt to environmental change. In practical terms this includes the protection of the species' habitat from gross man-induced changes and the conservation of an effective population size and a number of heterogenous gene pools (Schaffer 1981).

Endangered status for Bunolagus appears justified since its distribution has halved in only fifty years representing a loss of approximately two-thirds of its original habitat as a result of cultivation. Although habitat destruction is static at present, its resumption at past rates will result in the rapid extinction of the species in the wild. If the continued survival of Bunolagus is to be assured then the first step to its conservation is the elimination of this pressure through legislation or the setting aside of protected areas.

On the strength of very basic genetic principles Franklin (1980) recommended an effective minimum population size (Ne) of 500 to maintain sufficient genetic variation for adaptation to environmental change. Soule (1980) pointed out that the conservation of long-term evolutionary potential may, however, require larger populations. The present state of our knowledge of Bunolagus' biology does not allow the fixing of a minimum population size to survive demographic, environmental and genetic stochastic events.

In the light of this state of uncertainty it will be prudent to conserve as much of the remaining habitat as possible, especially since its estimated carrying capacity (1400) is close to Franklin's (1980) minimum effective population size of 500.

The fragmented, linear nature of Bunolagus habitat makes it impractical to conserve a single area large enough to maintain a viable Bunolagus population. More effective coverage of this habitat can be achieved by several smaller reserves (Simberloff & Abele 1982) distributed across as many rivers as is possible to counter the effects of sporadic flooding.

With a view to conserving as much habitat as possible, conservation action should include all forms of land use, from pristine natural areas to sheep farms. Consequently, it is suggested that conservation priorities be set for the protection of Bunolagus habitat:

1. Primary Zone

This area is centred on the Karoo National Park at Beaufort West and includes possible additions to it. The riparian vegetation of this park is unsuitable for Bunolagus but riverine vegetation on recently purchased adjacent land may prove suitable for reintroduction once it has recovered from the effects of overgrazing.

Furthermore, in future all planned additions to the park should take Bunolagus into account. Even if land is purchased which does not abut the park it can still benefit from the high level of protection a park offers. Connecting land can be purchased at a later stage. With this strategy in mind the Sak river, approximately 30 km northwest of the park's current boundaries, offers suitable habitat with Bunolagus present in it.

2. Secondary Zone

Envisaged here is a system of conservancies where the cooperation of farmers is formally contracted. The South African Natural Heritage Programme is a good vehicle for its promotion. Participants will be expected to prevent hunting of the species and will have to maintain its habitat. The unsuitability of the Karoo for the development of cultivation and the high cost of tapping underground water resources, may ensure that these farmers continue to leave their riverine vegetation uncultivated while benefiting from it as natural grazing.

In addition, the establishment of conservancies on the Brak, Sak and Riet rivers (Fig. 3) will maximize the geographic distribution of the conserved population. This will, in turn, contribute to the conservation of genetic variation and reduce the effects of local flooding, disease and other catastrophes on the total population.

3. Tertiary Zone

The tertiary zone includes all residual habitat not protected by the other zones. In this area little more can be done than make farmers aware of the existence of the species, its endangered status and the contribution they can make to its conservation. Furthermore, the existence of legislation which protects the riverine vegetation and the associated ecological benefits to the farmer of conserving it can be pointed out.

Overshadowing the viability of small isolated populations is the spectre of inbreeding depression (Ralls, Brugger & Ballou 1979) and no discussion on the conservation of Bunolagus would be complete without reference to it. While it seems likely that the species has been subjected to some degree of inbreeding in the past, given the nature of its habitat, the potential for this has been exacerbated by the fragmentary nature of its current distribution. In general, the effects of inbreeding depression can be mitigated by migration between adjacent demes (Allendorf 1983) but whether this has been severely compromised by the recent habitat destruction is moot and awaits more detailed investigation.

The initiation of the captive colony of Bunolagus at the De Wildt Cheetah farm is a direct consequence of the present study. Attempts are currently underway to provide a genetically sound captive breeding programme with the stated intention of reintroducing the species into areas of its former range.

Reintroduction of captive rabbits should only take place to areas of suitable unoccupied habitat in order to prevent the transfer of the genetic load resulting from these bottle-neck populations. Likewise, to maximise the effective size of these founder populations care should be taken to maintain a balanced sex ratio with introductions. Finally, the suitability of the habitat in which reintroductions are to occur must be critically established.

To start with a point analysis of the vegetation should be performed following the method described in Chapter 4 and the results compared with those in Table 5. The percentage vegetation cover and structure should be of the same order to provide enough cover for Bunolagus. The species composition of the vegetation need not be exactly the same but shrubs should be palatable and provide enough moisture for Bunolagus during the dry season.

SUMMARY

The present distribution of Bunolagus was determined in two surveys and compared with its past distribution obtained from the literature. The extent of habitat destruction through cultivation and the area of habitat remaining were estimated from aerial photographs. Densities of rabbits were determined at one locality by counts on horseback.

Results showed that the species' distribution has halved in only fifty years which represents a loss of two-thirds of its original habitat through cultivation. Extrapolation of densities to the area of habitat remaining, suggest that this habitat could, theoretically, support 1435 rabbits.

Diet was determined by faecal analysis and compared to the results of a vegetation analysis of the habitat. The shrubs, Pteronia erythrocaetha and Kochia pubescens constitute the bulk of the diet although these species are , respectively, the third and fifth most abundant plants in the environment. Bunolagus is essentially a browser, grazing only when rain results in new growth.

Movement patterns, social structure and activity were studied using radio telemetry. By this means it was ascertained that Bunolagus makes use of forms to rest up diurnally, and is active nocturnally. The species is solitary; sexes associate temporarily for mating. Males have a home range of 20,92 ± 1,44(SE) ha and females 12,88 ± 1,39(SE) ha.

OPSOMMING

Die huidige verspreiding van *Bunolagus* is deur twee opnames bepaal en met die spesie se historiese verspreiding (verkry uit die literatuur) vergelyk. Die hoeveelheid habitat omskep in landerye en dié hoeveelheid wat ongerep is, is van lugfotos bepaal. Digthede van *Bunolagus* is op een lokaliteit bepaal deur tellings te perd.

Resultate dui op 'n halvering van *Bunolagus* se verspreidingsgebied in die afgelope vyftig jaar met 'n verlies van byna twee-derdes van sy oorspronklike habitat. Na beraming kan die oorblywende habitat 1435 konyne onderhou.

Diëet is deur misanalise bepaal en met die resultate van 'n plantegroei-analise van die habitat vergelyk. *Bunolagus* vreet hoofsaaklik die struike *Pteronia erythrocaetha* en *Kochia pubescens*. Grasse word slegs by die diëet ingesluit kort na somer reënval wanneer nuwe groei 'n aanvang neem.

Bewegingspatrone, sosiale struktuur en aktiwiteit is deur radiotelemetrie bepaal. *Bunolagus* lê onaktief in 'n kooi gedurende die dag en is aktief snags. Die spesie is alleenlopend en kom slegs bymekaar tydens paring. Mannetjies het 'n loopgebied van 20,92 ± 1,44(SE) ha en wyfies 12,88 ± 1,39(SE) ha.

Data oor die voortplanting van <u>Bunolagus</u> is uit waarnemings in die natuur en van 'n kolonie in gevangenskap ingewin. Die teelseisoen strek van Augustus tot Mei en werpsels van een, moontlik twee, swak ontwikkelde kleintjies word na 'n dratydperk van 35-36 dae gebore. Pasgebore kleintjies word in ondergrondse neste versorg. Tekens van teelsinkronie is in die kolonie waargeneem. Die groeitempo in die liniëre fase van 'n jong konyn was 12,8 ± 0,46(SD) g/dag.

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