SEASONAL VARIATION IN THE DIET OF *Rhabdomys pumilio* AND *Otomys irroratus* IN EASTERN THORN BUSHVELD: WITH SPECIAL REFERENCE TO BARK CONSUMPTION.

By

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DECLARATION

This thesis, unless specifically indicated to the contrary in the text, is my own original work.

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CONTENTS

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1. ABSTRACT

Seasonal variation in the diets of two sympatric rodents, *Rhabdomys pumilio* and *Otomys irroratus* was investigated over a period of twelve months. The annual diet of the former included 34 plant species while that of the latter had 31 species. Twenty-seven of the plant food species were common while *R. pumilio* had seven, and *O. irroratus* five unique food items. Seasonal variation in the quantity and diversity of food plants utilized, however, ensured that the actual overlap of the diet was minimal. Species richness of the diet reflected the heterogeneity of the habitat and plant food formed the largest proportions of the stomach contents of both species.

The diet of *R. pumilio* was dominated by the utilization (>40%) of ephemeral, high quality foods (insects, fruit and seeds) from spring to early autumn. This resulted in significant variation in the major components of their seasonal diets. In contrast, the diet of *O. irroratus* was dominated by consistency with monocots contributing between 64% and 72% seasonally and dicots contributing around 20%. There was little overlap in diet and *R. pumilio* ate significantly less monocots. Significant variation in the composition of the diets would have reduced competition and allowed coexistence. Reproduction in *R. pumilio* appeared to be linked to the presence of high quality food in their diet while the consistency of diet in *O. irroratus* was reflected in their being permanently in reproductive condition.

The most important components in terms of abundance and frequency of occurrence in the diet of *R. pumilio* were insects, grass seeds, dicot seeds and fruit while in *O. irroratus*, the four most important components were monocots of which the top three were grasses. Of the latter, *Sporobolus fimbriatus* and *Melica decumbens* were not only the most important components by far, but were also the most abundant in the habitat. These results confirmed *R. pumilio* as an opportunistic omnivore and *O. irroratus* as a specialist herbivore utilizing the most commonly occurring plants.

An increase in bark consumption during dry winter months was evident in both *R. pumilio* and *O. irroratus*. Bark consumption peaked with increased density of *R. pumilio* juveniles which tended to eat more bark than adults and similarly *R. pumilio* tended to eat more bark than *O. irroratus*. The onset of bark consumption appeared to be linked to a marked reduction in the water content of the monocots, which constituted the major food category for both species in winter.

2. INTRODUCTION

Romer (1971) stated that rodents, which include rats and mice, are the most successful of all living mammals. Vaughan *et al.* (2000) listed 34 Families, 354 genera and about 1685 species of rodents. Among rodents, Muridae and Cricetidae form the two major families (Misonne 1974). Muridae have radiated widely around the world and are only absent from Antarctica and some oceanic islands (Vaughan *et al.* 2000). Muridae appear fairly late in the fossil record (middle Miocene), but the subfamily has been remarkably plastic from an evolutionary point of view (Carleton & Musser 1984). Murinae feed on a variety of plant material and on invertebrate and vertebrate animals (Vaughan *et al.* 2000). Murinae is the largest subfamily under Muridae and it contains about 529 known species. The majority of southern African rodents are murids with *Rhabdomys* belonging to the Murinae while *Otomys* belongs to the Otomyinae (Meester *et al.* 1986).

The transition of woodland to savanna in Africa resulted in an expanded grassland ecosystem (Kurten 1971) and the abundant supply of grass leaves, stems and seeds as food, may have promoted the invasion of murids into Africa from southeast Asia (Perrin & Curtis 1980). Herbivory arose from the omnivorous habit of the ancestral murid stock (Vorontsov 1962; Landry 1970). In response to various environmental changes, some grassland murids of Africa modified their diet to that of herbivory thereby exploiting fully the abundant food supply and increasing species diversity (Perrin & Curtis 1980). *Otomys* is one such murid that has become a specialized herbivore and shows the necessary digestive adaptations for this habit (Curtis & Perrin 1979). *Rhabdomys*, on the other hand, has retained dietary versatility and shows adaptations indicating an omnivorous habit (Curtis & Perrin 1979). The omnivorous habit confers greater ecological plasticity on *Rhabdomys* and thus one finds that they have a more extensive distribution than *Otomys*.

The striped mouse, *Rhabdomys pumilio* (Sparrman, 1784), and the vlei rat, *Otomys irroratus* (Brants, 1827), are prominent sympatric rodents found in many parts of southern Africa. They have been studied from various habitats in and around South

Africa. Their ubiquitous presence and often numerical dominance together with their ability to share the natural resources available in their habitat with apparently minimal conflict, make them ideal candidates for a study on small mammal diets in the Eastern Cape.

Rhabdomys pumilio is monotypic and, although herbivorous, is closer to an omnivorous line of murid radiation (Misonne 1969; Perrin & Curtis 1980). Differences are reported in feeding habit of *R. pumilio* living in different habitats. It is a versatile species that has variously been described as a granivore (Davis 1942; Choate 1971; Smithers 1971; Brooks 1974; Fuller & Perrin 2001) or herbivore (Hanney 1965 ; Roberts 1951; Rosevear 1969; Kingdon 1974; Delany 1975) or an omnivore (Field 1975; Perrin & Curtis 1980; Perrin 1980a; Rautenbach 1982; Smithers 1983; Churchfield 1985), preferring fruits and seeds in the laboratory (Curtis & Perrin, 1979). It has a wide distribution extending to almost all parts of southern Africa (Davis 1974) and is regarded as a broad niche species which has been recorded from arid Kalahari dunes to moist grassland habitats (Brooks, 1974).

R. pumilio is an r-selected species producing a few large litters during a restricted summertime breeding season when abundant but ephemeral high quality food resources are available (Davis 1973; Brooks 1974; Perrin 1980a). Taylor & Green (1976) showed that breeding in three granivorous species including *Rhabdomys* was restricted to the time of year when weed seeds and/or cereals formed a major part of the diet. Stein (1953: In Taylor & Green 1976) found that *Microtus arvalis* bred in winter amongst high quality food crops such as rye and rape, but failed to breed in a nearby uncultivated land which had an abundance of green food; implicating diet quality rather than availability of resources, as critical in reproduction.

The vlei rat, *O. irroratus*, belongs to the small African subfamily, Otomyinae, which contains two genera, *Otomys* and *Parotomys*, with five species belonging to the former and two to the latter genus (Meester *et al.* 1986) and they are specialized herbivores (Misonne 1974). Insects and seed materials, which are typical components of the diet of many rodents, are conspicuously absent from the diet of the Otomyinae. Together with the mole rats, these are probably the only truly herbivorous rodents occurring in southern Africa (Perrin & Curtis 1980). *O. irroratus* is the most widespread species of this subfamily, and it has a limited distribution within the southern African sub-region. The restricted distribution of this species may be a reflection of their dietary habit.

O. irroratus is often associated with damp vleis and wet grasslands on the fringes of streams and swamps. Absence of this species in the arid regions of southern Africa such as the northwestern, north and northern parts of the central region including Botswana (Misonne 1974), could be related to their feeding habit. *O. irroratus* is a specialist herbivore feeding entirely on green plant material with the exclusion of decaying vegetation (Perrin 1980a) and his finding are corroborated by several studies (Shortridge 1934; Dieterlen 1968; Smithers 1971; Davis 1973). Herbivorus rodents like *Microtus agrestis*, breed exclusively on a diet of green plants (Gorecki & Gebczynska 1962; Drozdz 1966; Watts 1969) and they resemble *Otomys* in this respect.

In contrast to *R. pumilio*, regional differences are less apparent in *O. irroratus* diet as they remained strictly herbivorous over a wide range of habitats (see *inter alia* Davis 1973; Rowe-Rowe 1986; Kerley 1989; Monadjem 1996; Jackson & Spinks 1998). They tend to select the most abundant and often most stable plant resources which includes the succulent stems of grasses, grass seeds, young shoots of reeds, forbs, and even non-indigenous plants such as the thistle (*Cirsium vulgara*), as well as fruits and seeds of a great many of shrub and tree species (Davis 1973; Curtis & Perrin 1979; Perrin 1980a). Davis (1973) found that they did eat nearly all of the plant species that occurred in their habitat and Curtis & Perrin (1979) recorded that they ate grass in preference to other plant material or seeds.

Consistent feeding habit is often associated with stable fat reserves and regular breeding and is common in K-selected species (Perrin 1980a). *O. irroratus* does not exploit ephemeral food resources (contrast *R. pumilio*) and this is considered as one of the reasons why they have a constant level of body fat (Perrin 1980b). A similar consistency in the level of body fat or in diet choice is not obvious in equatorial (Field 1975), boreal non-hibernating (McNab 1968), hibernating (Jameson & Mead 1964), deserticolous, or temperate species (Sawicka-Kapusta 1968). The body fat reserve in *R. pumilio* was both higher and more variable than that of *O. irroratus* in Fish River Valley population and Perrin (1980a) suggested their fluctuating energy and nutrient intake together with seasonal breeding as the reason for such difference. Although the body fat reserve was not determined in this project, two of the aspects that directly influence body fat levels, namely diet and breeding, are investigated.

The study of the diets of animals is crucial for understanding relationships between species (Zimmerman 1965; Bar *et al.* 1984) and between an animal and its environment. These relationships may determine community structure, species diversity, relative abundance, and resource partitioning among species and individuals (Connell 1975).

Both food and microhabitat partitioning are important for the co-existence of grassland rodents (Jenkins 1993). Rusterholz (1981) observed that an important element in the relationship between niche overlap and competition was the availability of environmental resources especially food resources. Resource scarcity prevalent in winter seasons often leads to dietary overlap characterized by increased competition and possible population decline (Perrin 1980a). It was found that during winter, diet breadth was reduced with an increase in dietary overlap among common rodents inhabiting in an agroecosystem in Argentina (Ellis *et al.* 1998).

Rhabdomys and *Otomys* are sympatric over the entire range of *Otomys* and utilize the same spatial and temporal habitat. This suggests that potentially, they are competitors. Consequently, the primary aim of this study was to examine, on a seasonal basis, the dietary separation and / or overlap of *Rhabdomys* and *Otomys*.

One component of diet among many species of rodent, is bark. In the northern hemisphere, bark consumption has been reported mainly during winter and even under snow cover (Hansson 1986). However, bark of deciduous trees was attacked even during summer-autumn under grass cover (MacVicker & Trout 1994). The extent of bark damage varied between various peak years (Larsson 1975; Myllymäki 1977; Hansson 1992; 1999). Very few omnivorous rodents are implicated in bark consumption in the northern hemisphere but herbivores belonging to genera *Microtus*, *Arvicola* and *Clethrionomys* have been widely reported to be bark eaters (Baxter & Hansson, 2001).

The explanation for bark consumption in the northern hemisphere varies between lack of mineral availability, especially calcium and sodium (Hansson 1990; 1991) or nutritional content (Pitelka & Schultz 1964; Acuman 1965; Auman & Emlen 1965). On the other hand increase in the concentration of phenols and turpentines have been negatively correlated with bark attack by voles (Hansson *et al.* 1986).

In the southern hemisphere, bark consumption has been reported from the montane deserts in Argentina, where *Ctenomys eremophilus* and *Microcavia australis* consume the bark of the Creosote Bush, *Larrea cuneifolia* (Borruel *et al.*1998). In Australia, *Rattus fuscipes* and *Mastocomys fuscus* include bark in their diet (Carron *et al.* 1990). McNally (1955) reported that bark-eating of exotic pine trees in Victoria State occurred during dry winter months.

Similarly to Australia, bark consumption in South Africa occurred mainly during dry winter months in the summer rainfall areas (Davis 1942; Hechter-Schulz 1962; Willan 1984) and the need to secure moisture has been considered as one of the major reasons why rodents include bark in their winter diet (Atkinson 1993; Baxter & Hansson 2001). In the winter rainfall areas of the south-western Cape, bark-eating is reported to occur during the dry summers (see Baxter & Hansson 2001). *R. pumilio*, *M. natalensis* and *O. irroratus* are the three species known to eat bark within commercial pine plantations (Davis 1942; Hechter-Schulz 1962; Atkinson 1993; Taylor & Perrin 1996). They have also been reported to include the bark of indigenous trees and shrubs in their diet under natural conditions (Perrin 1980a; Rowe-Rowe 1986; Wirminghaus & Perrin 1992; Baxter *et al.* 1999). Hechter-Schulz (1962) suggested that *R. pumilio* was the chief bark-eater while Wirminghaus (in Atkinson 1993) suggested that in certain areas it is *O. irroratus* that does the most damage.

Rhabdomys and *Otomys* have been implicated in damage in commercial pine plantations due to their bark-eating habit (Taylor & Perrin 1996). Baxter *et al.* (1999) and Baxter & Hansson (2001) have indicated that this habit extends to indigenous trees and shrubs. Consequently, as the second component of this project, it was decided to make special note of the presence of bark in the natural diet of these two rodents in an attempt to find reasons for seasonal bark-eating.

The onset of reproduction in rodents is often linked to environmental factors, especially food. Breeding is often reported to reach a peak during the latter parts of the rainy season, when food availability is high, and declines during the dry season as the food resources become exhausted. Numerous studies have confirmed an increase in rodent populations following good rainfall (*inter alia* Nel 1978; Perrin & Swanepoel 1987; Bronner *et al.* 1988). Neal (1986) reported peak reproductive activity in many rodent species, especially those found in arid or semi-arid regions, during the rainy season. Increased food availability has been associated with population increase resulting from unseasonal reproduction in *Apodemus sylvaticus* (Smyth 1966; Watts 1970; Hansson 1971) and *Rattus norvegicus* (Taylor 1968) or from an improved survival or increased immigration as in *Apodemus sylvaticus* (Flowerdew 1972) and *Mus musculus* (Newsome, 1970). *Rhabdomys*, with its opportunistic omnivory and dietary plasticity is regarded as a seasonal breeder while *Otomys*, with its conservative specialist herbivory, is thought to breed throughout the year (Skinner & Smithers 1990). This aspect of the biology of the two rodents constituted the third component of this study aimed at correlating the changes in diet with changes in reproductive condition.

3. MATERIALS AND METHODS

3.1 STUDY SITE

The research took place on the Honeydale section of the University of Fort Hare's Research farm ($30^0 46'$ S, 26^0 54' E). The area falls under southern savanna biotic zone and the habitat type is Eastern Thorn Bushveld (Lubke & Bredenkamp 1996). The region receives summer rainfall with an annual mean of 575mm and is affected by the El Niño Southern Oscillation resulting in regular drought periods. Both temporal and spatial distribution of the rainfall is highly variable (ARDRI, 1989). Monthly rainfall figures for the study period were obtained from the livestock section of Fort Hare Research farm. Seasons were defined as: winter = May–August; spring = September-October; summer = November-February; Autumn = March-April (see Attwell 1982).

The soil at the site is a silty loam of the Glenorsa series, which is shallow with a stony surface (Soil Classification Working Group 1991). The study area is subdivided into 12 plots each measuring 100m x 50m and separated from other plots by buffer strips at least 5m wide. The plots are subjected to six different burning regimes as part of a long term fire ecology project and have burning intervals of one, two, three, four and six years and two control plots where no burning takes place. Research specimens were obtained almost exclusively from the four year, six year and control plots as their plant species composition was most similar (Trollope pers. comm.). Furthermore these plots had higher rodent densities and thus yielded better trap success.

3.2 PLANTS

3.2.1 Relative abundance of plants for food and cover

The percentage cover of abundant plant species was estimated from a point quadrat grass survey carried out by the UFH Agricultural Faculty during April 1999. The grass and forbs were clumped under one category while the shrubs and tree species were treated as a separate category. This was to include those with similar distribution and cover in one group. Most prominent grass and shrub species were allocated a rank order according to their relative importance.

3.2.2 Reference plant collection

In order to provide a comprehensive survey of potential food plants, a representative sample of all abundant plants found on the sites during all seasons, was collected and pressed. Species identification was done by comparison with specimens in the Albany Museum Herbarium at Grahamstown. The collection of plant reference material is lodged at the University of Fort Hare Herbarium. The entire list of plant species collected is taxonomically arranged in Appendix 1.

3.2.3 Moisture content of common plants

A similar but separate collection (see 3.2.2) was made to determine the moisture content of the plants. This collection included grass stem and leaves, stem and leaves of herbs and bark from all the trees and shrubs found in the habitat. These samples were placed in beakers and their wet mass was recorded. They were then oven-dried at 45^{0}C for a period of three weeks and their mass loss was taken to indicate their moisture content. As most forbs are annuals it was not possible to determine full seasonal variation in their moisture content.

3.2.4 Histological preparation

Plant species, which were a potential food source for the rodents, were identified from the literature and from field observations of food leftovers and signs of feeding. These plants were identified, processed as explained under Microhistology section (3.2.4.1) and mounted on glass slides to form part the reference slide collection for identification of the diet content (after Storr 1961). This collection was later extended to include all the common species found at the study site. This method has been widely used for species identification of the stomach contents of mammals (Stewart 1967; Scotcher 1977; Monro 1982; Everett *et al.*1992).

3.2.4.1 Microhistology

Fresh samples of the aerial parts of plants were collected at the study site and brought to the laboratory. They were soaked in FAA solution for twelve to fifteen hours to arrest their metabolism and to soften the tissue. Next, four or five leaves of each species were cut into fragments 10-15mm in length and rinsed in water to remove FAA. They were then placed in separate 300ml round bottom ("kjeldahl") flasks and immersed in 7-10 ml concentrated nitric acid. The amount of the acid used varied depending on the size and thickness of the leaf material. The mixture was agitated and heated for five minutes in a water bath set at boiling point, 200ml boiling water was added and the contents were allowed to boil another 3-10 minutes, depending on the thickness and lignification of the leaf, until the green colour was lost. The fragmented plant material was then transferred into a beaker with 200ml hot water and rinsed for 5 minutes. This process was repeated before the loose epidermal tissue was removed from the rest of the leaf material using a light paintbrush. The plant fragments were then passed through an alcohol series of 30%, 50%, 70% and 2X 100%, before being stained with aniline blue in lactophenol and mounted in euparal on a slide. For each species a minimum of two reference slides were made with each one containing both abaxial and adaxial epidermal tissue. The slides were examined using a compound microscope at 100X and 400X magnification.

The various treatments to which fresh plant tissues were subjected during the extraction and the mounting process caused certain degree of distortion in shape and colour of these tissues. The dietary content had also undergone some structural change due to chewing and grinding, maceration and chemical digestion by enzymes in the stomach. Such distortions made species identification difficult when comparison was made between the slides of freshly prepared tissue and the slides of tissue made from the unidentified stomach contents because they diverged from one another not because of their origin but because of the different conditions to which they had been exposed. In addition to this, the amplified effect of minor differences when using microanalysis made the reliability of reference material limited to certain part of a specimen rather than the whole specimen. Some plant species had considerable anatomical differences between various parts and also between different age groups. To accommodate for such differences, the reference collection had to be made even bigger and often more overlapping.

Some partially digested dietary materials such as easily digestible young plant stems or leaves or those with overlapping structural features such as internal tissues of stem, fruit and roots were very difficult to identify using light microscopy. Scanning electron microscopy (SEM) was used for identification of such dietary material. When using SEM, both reference and unidentified dietary materials had to be scanned to generate their digital images. Reference species were processed by critical point drying while the unidentified food material was isolated from the rest of the dietary material and put through the alcohol series before preparing them for SEM. As these procedures are costly, they were kept to a minimum.

3.2.5 Critical point drying preparation and electron microscopy

The leaves and stems of likely food-plants were cut with a sharp scalpel into 2 to 3mm pieces across the longitudinal plane. These pieces were then soaked in 6% glutaraldehyde overnight for fixation. After draining, the specimen was soaked in 0.05m sodium cacodylate for up to 4 hours and then washed and run through an alcohol series (20%, 30%, 50%, 70%, 80%, 90% & 2X 100%) with a duration of 20 minutes in each. The alcohol treated specimen was then transferred into an Hitachi HCP-2 critical point dryer and dehydrated for about 6 hours to preserve the structure and shape of all its tissues. The dehydrated material was then mounted on an aluminium stub using conducting carbon cement (LEIT-C), which provides conductivity and also serves as a mounting medium. The specimens were then gold coated before being examined under the scanning electron microscope. Images of important features such as structure, shape, size, and arrangement of cells, hairs, trichomes and stomata were digitally recorded from these specimens. Differences in magnification were taken into account when recording the image.

3.2.6 Preparation of dietary material for SEM imagery

Dietary material that could not be identified even under a light microscope was separated from he rest and placed in a glass vial for scanning electron microscopy. Unlike the reference material these dietary items were already exposed to various conditions, which altered the shape and structure of their cells. With this in mind it was decided not to proceed with critical point drying which is a preserving rather than restoring process and therefore irrelevant to those specimens which may not have their original structure intact to start with. Dehydration of the diet content was carried out by running them through an alcohol series (70%, 80%, 90% & 2X 100%) for 20 minutes each. The dehydrated specimens were then mounted on aluminium stubs with conducting carbon cement (LEIT-C), and gold coated before being examined under the scanning electron microscope.

3.3 RODENTS

3.3.1 Trapping

In order to optimize trap-success, snap traps were placed at right angles to runways that showed evidence of frequent use (e.g. foot marks, discarded plant cuttings, adjacent plants with gnawed stems and leaves, fresh droppings). This allowed access from both directions and prevented accidental triggering of traps by rodents approaching from the hind side of the trap. A peanut butter and rolled-oats mixture was used as bait. Live traps were not used since digestion of stomach content carries on with animals trapped in live traps and this would in effect not only obscure the identifiable features but also the quantity of the stomach contents.

A total of 46 small wooden and 48 large metal snap-traps were used for each trapping session. Trapping occurred monthly between March 1998 and February 1999. The traps were set in pairs with a combination of one large and one small trap at 10 metre intervals along a transect. Five parallel transects set at 10 metre distance from each other covered the whole area selected for trapping in a month. The traps were usually set in the afternoon and checked every 8 to 12 hrs until a minimum of six *R. pumilio*, the principal species investigated, was captured. One trapping session usually took two to three consecutive days to conclude.

As trapping progressed it became obvious that even with additional trapping effort it was not possible to maintain the sample size at or above the minimum level in all sessions as planned initially. On no occasion did the numbers drop below four *R. pumilio* per session.

3.3.2 Processing of trapped animals

Trapped animals were removed from the trap, placed in a polythene bag before they were transported to the laboratory for removal of the stomach. Each animal was weighed before standard museum measurements (head and body, tail, hind foot and ear length) were taken using a plastic ruler.

The stomach was removed and its wet weight measured before being preserved in 70% alcohol for later analysis. All the skulls were removed from the carcasses, dried and labeled with a tag containing all the field data. The skulls have been lodged as voucher specimens at the Amathole Museum in King Williams Town.

3.3.3 Classification into castes based on sexual and reproductive condition

All specimens trapped were initially assigned to castes using the criteria of Willan (1982) (Table 1). Reproductive males were distinguished from non-reproductive males on the basis of whether the testes could be palpated into the scrotal sac, if this was the case then the animal was classified as reproductive (Brooks 1974).

Females were classified as juvenile, perforate (reproductively active adult) and imperforate (non-reproductive adult). This classification was based on body mass, body size and condition of reproductive system. The condition of the vaginal orifice was the key feature for classifying adult females into breeding individuals and non-breeding individuals.

The sub-adult category, which was decided solely on the basis of mass, was discontinued in the present study as the mass of an animal can vary by 5 to 8g depending on the state of their stomach. It is quite possible for a well-fed sub-adult to be identified as an adult or an ill-fed adult as a sub-adult. Though the same limitation is applied to the threshold between adult and juveniles, consideration of other distinctive features such as body size and condition of the reproductive organ as described earlier, is expected to reduce any mass related bias.

Table 1. The summary of physical determinants used by Willan (1982) to ascertain sex and reproductive castes in two rodent species. (Asterisks indicate those categories that were adopted in this study.)

Caste	Reproductive Condition	Mass of *O. irroratus*	Mass of *R. pumilio*
Scrotal Male*	Testes fully developed and descended	≥ 90g	≥ 35g
Non Scrotal Male*	Testes undescended, not fully developed	≥ 90g	≥ 35g
Perforate Female*	Vaginal orifice open	≥ 90g	≥ 35g
Imperforate Female*	Vaginal orifice sealed	≥ 90g	≥ 35g
Sub-adult	Either sex: below sexual mass and above juvenile mass	50-89.9g	25- 34.9g
Juvenile*	Either sex: below sub-adult mass	<50g	< 25g

3.3.4 Stomach content analysis

The stomach was cut open and the contents placed in a petri-dish. Freshly ingested bait was easily separated from the natural food items and discarded. The stomach contents were then rinsed with water through a 159 µm sieve to remove small particles and discard stomach enzymes and fat molecules. Material left in the sieve was preserved in 70% alcohol in a vial for identification using light microscopy. The importance of each food type was expressed in two ways a) frequency of occurrence and b) proportional contribution expressed as a percentage. Frequency of occurrence was calculated as the number of stomachs in which a particular food type was observed.

Percentage contribution was determined as follows: the content of each stomach was mixed thoroughly, a small sample was then placed in a gridded petri-dish and examined under a dissection microscope at 40X magnification (see Hansson 1970; Kerley 1989). An estimate of the relative cover of each food category in the microscope field was made for five random fields. The relative cover of each food type was then averaged over the five fields and expressed as a percentage. The combined contribution of all food types adds up to 100%. Due to the high heterogeneity of stomach content it was necessary to combine similar dietary items into nine categories for statistical analysis. The dietary categories allocated to the stomach contents were: 1. monocots 2. dicots 3. insects 4. grass seeds 5. dicot seeds 6. fruits 7. flowers 8. tubers and 9. bark (Table 2).

Table 2. The criteria used to select dietary material, which constitute each of the nine major food categories (see text).

Dietary category	**Identification features**
Monocotyledon	Includes stems and leaves of monocots especially grasses
Dicotyledon	leaves of bushes and trees and herbs, stem of herbs that are not lignified to wood.
Insect	Mainly exoskeleton, partially digested muscles
Grass seed	Both outer cover and endosperm of seeds
Dicot seed	Endosperm and outer shell/nut of seeds
Fruit	Fleshy part of fruits
Flower	Flowers of all types of plants
Root	Root and any underground storage part
Bark	Lignified material from both trunk and branches irrespective of age.

3.4 DATA ANALYSIS

3.4.1 Physical parameters

The mean values of standard museum measurements of the four population cohorts (adult males, adult females, pregnant females and juveniles) of *R. pumilio,* were calculated and compared using ANOVA and Tukey's HSD tests. No analysis of the *O. irroratus* data was attempted on account of small sample sizes.

3.4.2. Dietary analysis

Comparison of stomach contents using Spearman's rank correlation was carried out to determine:

a) seasonal association between the diet of *R. pumilio* and *O. irroratus*. Here the monthly averages estimated for all the categories of food taken in a month by the two species were compared between identical months.

b) seasonal association between the diet of *R. pumilio* only . Here the average values determined for all the dietary items found in the diet of *R. pumilio* in a season were compared with those of all the other seasons.

All the data pertaining to "percentage contribution to the diet" were arcsine transformed before they were statistically analysed. As many samples were relatively small, months were combined to give larger sample sizes. The combinations were March and April (MA) (MA = autumn), May and June (MJ), July and August (JA) (MJ & JA = winter), September and October (SO) (SO = spring), November and December (ND) and January and February (JF) (ND & JF = summer). Monthly, bimonthly and seasonal variation in the proportion of the individual dietary categories was tested using ANOVA and Tukey's HSD tests. ANOVA tested the overall dietary variation while bimonthly and seasonal variation was determined using Tukey's HSD tests.

The contribution of fruit to the monthly stomach contents exhibited a pattern different from that of the other food types. When months were combined as above, obvious differences became obscured. Consequently, the monthly combinations for fruit were FM, AM, JJ, AS, ON & DJ.

3.4.3 Frequency estimates of dietary content

The relative importance of each food type over the entire study period was expressed as frequency of occurrence. Frequency of occurrence was calculated from the number of stomachs in which a particular food type was observed as a fraction of the total number of stomachs. Frequency of occurrence values were converted to percentages for annual dietary comparison.

3.4.4 Annual mean percentages of dietary items and dietary categories

The mean annual percentage of each food item and each dietary category was calculated by averaging the monthly percentage contribution of each dietary item or each dietary category over the entire study period. The mean annual percentages of the dietary contents of the two coexisting rodents were compared using t-tests.

4. RESULTS

4.1 PLANTS

4.1.1 Plant cover

Eight species of grasses formed the dominant monocots in the habitat (Table 3a). *Sporobolus fimbriatus* was the dominant grass species with a percentage cover of 31.5% followed by *Melica decumbens* with 16.7% cover. Under the shrubs and trees category, six species were identified as dominant in the study area (Table3b). *Acacia karroo* with 37% cover dominated followed by *Lippia javanica* with 18% cover.

Table 3a. Relative percentage cover of grass and herbaceous vegetation at the study site obtained from an annual point quadrat survey. The rank allocated to each species indicates its relative importance in the habitat as a potential food source. Only those plants that have a percentage cover above 2 % are listed.

Grasses and Herbaceous vegetation	% cover	Rank
Sporobolus fimbriatus	31.5	1
Melica decumbens	16.7	2
Themeda triandra	14.9	3
Herbaceous vegetation (forbs)	9.8	4
Cymbopogon plurinodis	8.6	5
Digitaria eriantha	7.2	6
Cynodon dactylon	3.7	7
Panicum maximum	2.0	8

Table 3b. Relative percentage cover of shrubs and tree (woody vegetation) at the study site obtained from an annual point quadrat survey. The rank allocated to each species indicates its relative importance in the habitat as a potential food source. Only those plants that have a percentage cover above 2% are listed.

Woody vegetation (trees and shrubs)	% cover	Rank
Acacia karroo	37.0	1
Lippia javanica	18.0	2
Lycium sp	13.2	3
Diospyros lycoides	12.0	4
Ehretia rigida	11.3	5
Maytenus heterophylla	2.3	6

4.1.2 Moisture Content

The percentage moisture lost (g) in the bark of five major tree species, and collective moisture percentage loss in five dominant grass species and five dominant herb (forbs) are given in Table 4.

Table 4. Seasonal change in moisture content of grass, forbs and bark of major bush/tree species, is expressed in % dry mass

Species	**Autumn**	**Winter**	**Spring**	**Summer**
*Ehretia**	57.5	53.8	57.2	60.7
*Diospyros**	42.0	40.1	44.4	47.3
*Grewia**	61.6	53.9	55.0	59.5
*Buddleja**	27.5	24.7	24.6	27.2
*Acacia**	52.2	52.0	52.1	52.2
Grasses +	41.6	14.2	39.3	49.6
Forbs #	71.8	....	68.6	69.8

* The values for bark are adopted from Ntshebe (1997)

\+ The values for grasses are means for common grass species *Sporobolus fimbriatus, Melica decumbens, Themeda triandra, Cymbopogon plurinodis* and *Cynodon dactylon* collected during 1999 - 2000.

\# The values for Forbs are the means for prominent herbs *Asparagus* sp., *Berkheya* sp., *Teucrium capense, Pelargonium* sp., *Oxalis* sp., *Senecio* sp. and *Drimiopsis* sp. collected during 1999 - 2000. No value is available for winter during which the annuals had died back.

4.2 HISTOLOGY

4.2.1 Microhistology

Approximately 80 plant species were identified as potential food sources. The reference collection contained 25 species of monocots belonging to five families and 56 species of dicots belonging to 29 families (see Appendix 1 for a species list). This reflected the high heterogeneity of the habitat. For each species a minimum of four reference slides were made and the entire collection totalled over 350 slides. When stomach contents with various parts of the same plants were encountered, species identification based on the reference slides alone was difficult. Scanning electron microscopy was used for identification of such dietary material.

Roughly 50% of the total available plant species was present in the entire stomach contents of the two rodent species. The stomach content of *R. pumilio* contained 34 plant species while that of *O. irroratus* contained 31 species of plants. This shows that both species exercise some degree of selection among the available food resource.

4.2.2 Scanning Electron Microscopy (SEM)

As explained in the Materials and Methods section, SEM images were of high quality and were highly effective in teasing out the distinctive features of cells, trichomes or stomata to make species identification a little easier. The high cost and the time involved with this exercise, however, did not allow the entire unidentified materials to be subjected to this process. A selection of the images generated by SEM is included in Appendix 2. Using this method in future research, which involves stomach content identification, is highly recommended.

4.3 RODENTS

As the trapping progressed it became obvious that even with the additional trapping effort it was not possible to maintain the desired sample size at or above the minimum level of six animals per species per session as planned initially. It must be noted that on no occasion did the sample size for *Rhabdomys* drop below four animals. *Otomys* on the other hand, proved more difficult to trap and only one specimen was trapped in spring.

During the twelve months, 82 *R. pumilio*, 37 *O. irroratus* and 17 *M. natalensis* were trapped. Two *Myosorex varius* constituted the only insectivores trapped .

4.3.1 Physical parameters

The mean values of standard museum measurements for the four population cohorts of *R. pumilio* were calculated and are summarized in Table 5a. No significant differences were evident when the field measurements of three population cohorts (adult males, adult females, gravid females) were compared: mass (F=1.011), HB (F=0.3696), T (F=0.9301), HF (F=2.780) and E (F=1.825). A comparison of standard museum measurement of juveniles and the above three cohorts indicated significant differences in all the five measurements (ANOVA: F values between 4.065 and 36.92). In all measurements excepting tail (T), the juveniles were significantly smaller than the adult cohorts (Tukey: q values between 3.779 and 13.45). The tail measurement of the juvenile cohort resembled that of the adult cohorts except with respect to males which had significantly longer tails ($q=4.901$; $p<0.01$).

Table 5a. Mean and ratio values of the standard museum measurements of four population cohorts of *R. pumilio* captured from Fort Hare Research Farm, Alice.

Physical parameter	Adult male	n	Adult female	n	Pregnant	n	Juvenile	n
Mass (g)	47.1	47	46.0	24	58.0	11	32.2	13
H/Body (mm)	111.1	47	111.8	24	126.0	11	100.2	13
Tail (mm)	93.4	47	89.2	24	98.2	11	88.2	13
Tail:Body	1:1.2	47	1:1.3	24	1:1.3	11	1:1.1	13
Hind foot (mm)	21.3	47	21.7	24	22.5	11	20.6	13
Ear (mm)	12.8	47	13.0	24	15.1	11	11.8	13

A similar comparison for *O. irroratus* (Table 5b) showed no significant differences for HB ($F=2.523$), T ($F=1.256$) and E ($F=2.116$). There were significant differences in Mass ($F=6.327$; $p=0.0046$) where pregnant females were predictably heavier than non-pregnant females ($q=4.638$; $p<0.01$) and males were significantly heavier than non-pregnant females ($q=4.462$; $p<0.01$). Males had significantly larger feet than females ($q=4.113$; $p<0.05$). It must be noted that no juveniles were trapped.

Table 5b. Mean and ratio values of the standard museum measurements of three population cohorts of *O. irroratus* captured on Fort Hare Research Farm, Alice.

Physical parameter	Adult male	n	Adult female	n	Pregnant	n
Mass (g)	142.6	17	129.3	8	146.8	12
H/Body (mm)	171.0	17	166.7	8	172.2	12
Tail (mm)	94.9	17	90.3	8	91.3	12
Tail:Body (mm)	1:1.8	17	1:1.84	8	1:1.89	12
Hind foot (mm)	28.4	17	26.7	8	26.5	12
Ear (mm)	23.7	17	22.3	8	22.4	12

4.4 DIET

4.4.1 Stomach contents

Approximately 8% of the dietary material was unidentifiable and the rest was identified to specific or generic level.

Thirty-four plant species were found in the stomach contents of *R. pumilio* trapped during the study period. The total stomach contents of *O. irroratus* contained thirty-one plant species (Table 6). An additional eleven items of food, which could not be distinguished to species level were also separated from the diet of *R. pumilio* while the stomach contents of *O. irroratus* contained eight items of unidentifiable food. These were included in broad categories such as fruits, dicot and monocot seeds, roots, unidentified dicots or monocots, flowers, bark and insects. Twenty-six species of plant were common to the stomach contents of both rodent species. The dietary spectrum of *R. pumilio* contained seven unique food materials, which could be identified to species level. The entire stomach contents of *O. irroratus* contained only five unique food materials that were identifiable to species level.

Table 6. Total number of plant species identified in the stomach contents of *R. pumilio* (n = 82) and *O. irroratus* (n = 37).

Plants	*R. pumilio*	*O. irroratus*
Number of identified species	34	31
Number of families	19	17
Number of unique species	7	5

4.4.2 Seasonal Variation

Seasonal variation was tested both on intra- and inter-specific level for *R. pumilio* and *O. irroratus*.

4.4.3 *Rhabdomys pumilio*

Spearman's Rank Correlation analysis between the eight major categories of food (root which formed the ninth category was left out as it was consumed in very small quantities by *R. pumilio* alone) found in the stomach of *R. pumilio* for the four seasons indicates no significant association between any of the seasons (Table 7a). When a similar comparison was made between the dietary content of *R. pumilio* with that of *O. irroratus* no significant association was evident (Table 7b).

Table 7a. Results of Spearman's Rank Correlation analysis for intraspecific seasonal association of diet in the stomach contents of *R. pumilio*. Rho >0.64 ($P<0.05$) indicates significant association when N=8.

	Spring	**Summer**	**Autumn**
Winter	$r_S = 0.31$ $p = 0.25$ N.S	$r_S = 0.41$ $0.10<p<0.25$ N.S	$r_S = 0.63$ $0.05<p<0.10$ N.S
Autumn	$r_S = 0.02$ $p>0.25$ N.S	$r_S = 0.56$ $0.05<p<0.10$ N.S	------------
Summer	$r_S = 0.41$ $0.10<p<0.25$ N.S	------------	------------

The lowest overlap of dietary items for *R. pumilio* in the various seasons was observed between spring and autumn ($r_s = 0.02$; $p>0.25$), while summer and autumn and autumn and winter had relatively higher overlap ($r_s = 0.56$& 0.63; $0.05<p<0.10$) but at no point was the overlap significant.

ANOVAs performed on the average consumption of the nine food categories showed highly significant monthly differences for all categories except Grass Seed where the variation was not significant ($F=1.70$; $p=0.081$). A similar result was found for consumption on a bimonthly basis except that in this instance Dicots did not show significant variation ($F=1.64$; $p=0.154$).

4.4.4 *Otomys irroratus*

A similar statistical analysis using Spearman's Rank Correlation could not be performed for *O. irroratus* since the test could not accommodate the high number of zero values obtained for the monthly diets. Only two food items (monocots and dicots) were eaten in more than four months of the year.

ANOVAs were performed on the monocot and dicot monthly and bimonthly means. No significant monthly (F=1.599; p=0.131) or bimonthly (F=1.701; p=0.166) variation was found. Monocot consumption was consistently high and this item constituted 67.9% of the annual diet.

In contrast, dicots did vary significantly on a monthly (F=3.599; p=0.0011) and bimonthly (F=5.165; p=0.002) basis. Dicots were consumed in relatively large amounts during January, February, March and June but were not consumed at all in April and May.

4.4.5 Comparison of diets of *R. pumilio* and *O. irroratus*

Inter-specific diet comparisons of the eight major food categories present in the stomachs of *R. pumilio* and *O. irroratus* for the four seasons shows no significant association between the dietary contents (Table 7b). The least overlap was in spring (r=0.12; p>0.25) while autumn and winter show relatively greater overlap in dietary contents (r=0.62 & r=0.59; p<0.10).

Table 7b. Results of Spearman's Rank Correlation analysis for interspecific seasonal association of diet between *R. pumilio* and *O. irroratus* stomach contents. Rho > 0.64 ($p<0.05$) indicates significant association when N=8

Rhabdomys* vs. *Otomys	Rho p
Autumn	$r_{s} = 0.62$ $0.05<p<0.10$ N.S
Winter	$r_{s} = 0.59$ $0.05<p<0.10$ N.S
Spring	$r_{s}=0.12$ $p>0.25$ N.S
Summer	$r_{s}=0.49$ $0.10<p<0.25$ N.S

4.5 AUTUMN

4.5.1 Climate and flora

The monthly rainfall peaked at 114mm in March (early autumn) (Fig.1). The mean rainfall for autumn was 72.8mm. The average monthly temperature dropped from 19.2^{0}C in March to 17.8^{0}C in April (Fig. 2). The mean temperature of 18.5^{0}C recorded during autumn was the second highest when compared with the other seasons.

The moisture content of the forbs was at its peak while that of bark and grasses reached their second highest during this period (Table 3). *Grewia* sp., *Lycium* sp., *Solanum* sp. and *Ziziphus* sp. were the four plant species that bore flowers and fruits during autumn.

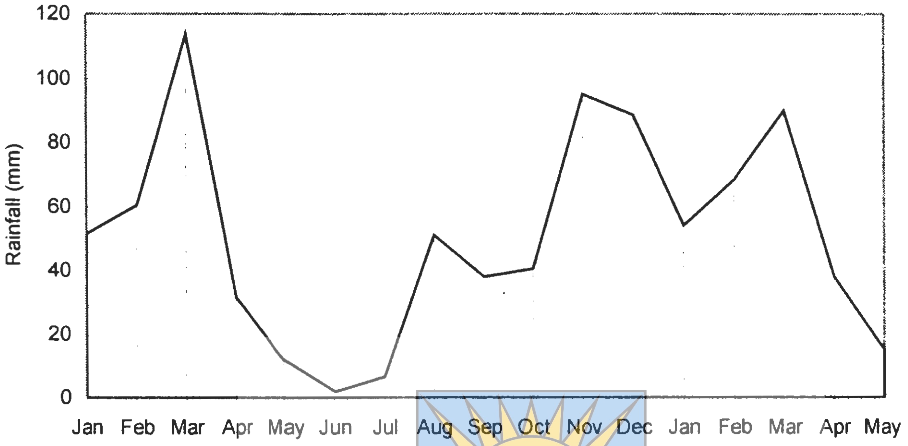

Fig. 1. Average monthly rain figures recorded at the Fort Hare Research Farm during the study period (1998-1999).

Fig. 2. Maximum, minimum and mean temperatures recorded at the Fort Hare Research Farm, Alice (1998-1999).

4.5.2 Population structure

More *R. pumilio* were caught during autumn than *O. irroratus* (Fig. 3) although in April they were caught in equal proportions. The sex ratio was 1:0.63 (n=13) for *Rhabdomys* and 1:2 (n=6) for *Otomys* (Fig. 4a & 4b). All the animals caught were in reproductive condition (n=19) and no juveniles were present for either species. Half of *R. pumilio* caught in March (n=4) were gravid while none were pregnant in April, probably indicating the end of the breeding season. All of the *O. irroratus* females (n=4) caught during autumn were gravid.

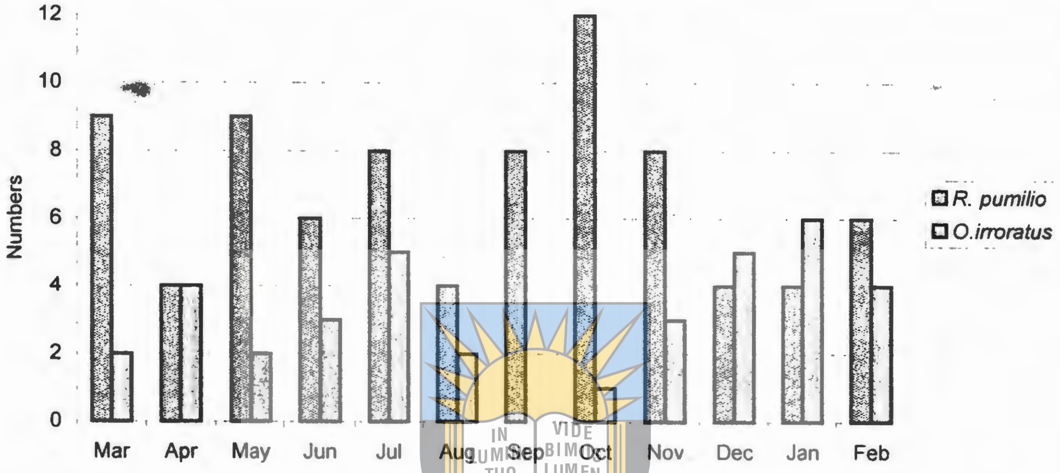

Fig. 3. Seasonal changes in the proportion of *R. pumilio* and *O. irroratus* captured from Alice (1998-1999).

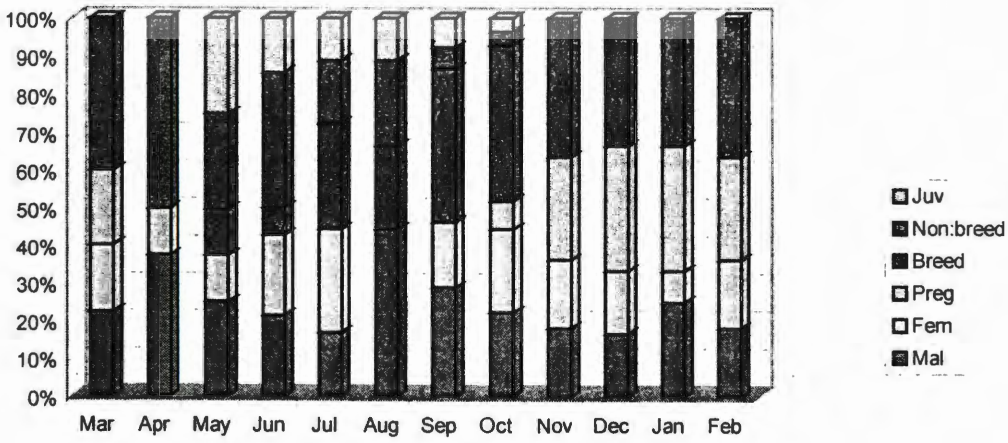

Fig. 4a. Seasonal variations in six life stages of *R. pumilio* .

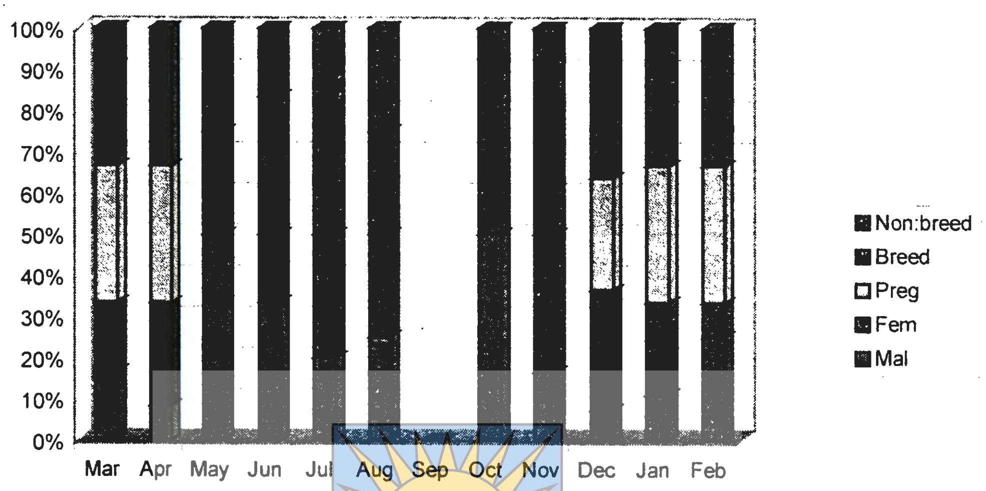

Fig. 4b. Seasonal variations in five life stages of *O. irroratus*.

4.5.3 *R. pumilio* diet

Fruits (27.8%) followed by dicots (20.9%) dominated the diet in autumn. These categories were followed by insects, dicot seeds and monocots (all above 10%) (Table 8). There is a significant increase in the consumption of fruit ($q=8.114$; $p< 0.001$) and dicot seeds ($q=8.962$; $p< 0.001$) between summer and late autumn while there is a significant decline in the consumption of grass seeds ($q=4.422$; $p< 0.05$) between late summer and autumn. Consumption of insect, flower, root and bark in autumn months did not vary significantly from that of the summer (Fig. 5a). No flowers were present in the diet during autumn.

Table 8. The seasonal change in the mean frequency of occurrence (%) of nine major diet categories in the stomach content of *R. pumilio* caught from Fort Hare Research Farm, Alice

Diet	Autumn	Winter	Spring	Summer	ANOVA	p
Bark	0.8	7.4	0.1	0.5	F=6.384	0.0006
Dicots	20.9	23.9	15.6	35.9	F=2.105	NS
Dicot seed	14.8	1.6	25.1	1	F=41.17	<0.0001
Flower	0	0.1	0.9	1.3	F=2.912	0.0396
Fruit	27.8	8.5	0.4	5.4	F=4.577	0.0053
Grass seed	7.5	0.8	0.6	14.9	F=6.177	0.0008
Insects	16.7	7.1	34.3	19.9	F=12.00	<0.0001
Monocots	10.3	32.9	9.4	17.1	F=10.84	<0.0001
Root	0	0	4.1	1.5	F=1.823	NS
TOTAL	98.8	82.3	91.5	97.4		

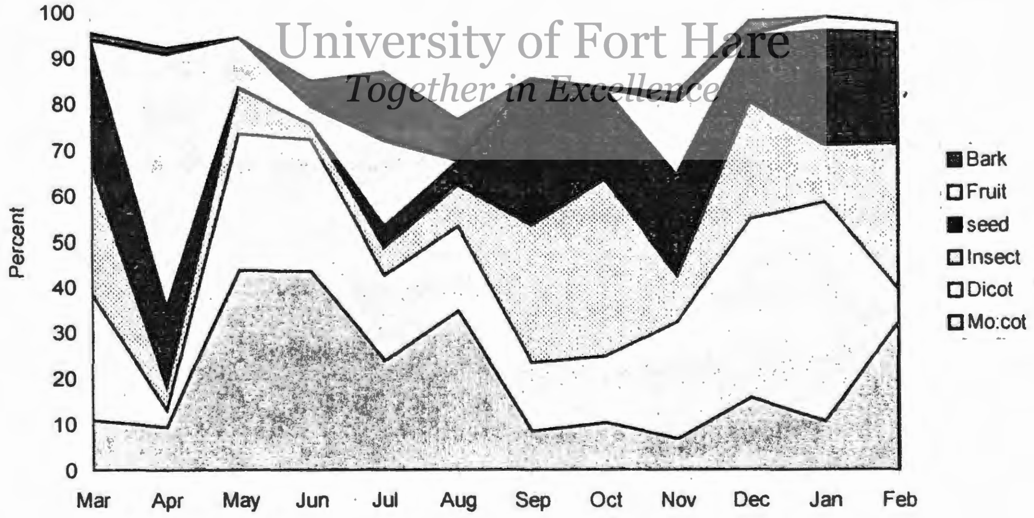

Fig. 5a. Seasonal variation in the consumption of six major food categories by *R. pumilio* captured from Fort Hare Reseaιch Farm, Alice (1998-1999). (Unshaded part indicates the unidentified portion of the diet).

The broad categories in Table 8 can be further subdivided (see Table 9) to reveal the degree of dietary overlap at the species level in certain instances. *Asparagus*, a monocot, was the most eaten plant species during autumn (Table 9). The bulk of the fruit and dicot seed content in the stomachs was from *Lycium* sp.

Table 9. Seasonal comparison of the percentage contribution of major food items found in *R. pumilio* stomach contents. Only those, which constituted more than 2% of the diet were considered.

Autumn	%	Winter	%	Spring	%	Summer	%
Fruit	27.8	Monocot. unid.	28.6	Insects	34.3	Insects	19.9
Insects	16.7	Fruit	8.5	Dicot seeds	25.1	Grass seeds	14.9
Dicot seeds	14.8	*Oxalis*	7.9	*Oxalis*	6.6	*Berkheya*	10.1
Grass seeds	7.5	Bark	7.4	Root	4.1	Monoc unid.	6.8
Monoc. unid.	4.3	Insects	7.1	Monoc.unid.	4.0	*Oxalis*	6.5
		Pelargonium	4.1	*Asparagus*	2.1	Dicot unid.	6.5
Asparagus	4.0	*Solanum*	4.1			Fruit	5.4
Solanum	3.5	*Pseudognaphalium*	3.4			*Pelargonium*	3.4
Pelargonium	2.7	*Asparagus*	2.5			*Senecio*	3.3
Falkia	2.5					*Sporobolus*	2.4
Delosperma	2.4					*Themeda*	2.4
						Asparagus	2.3
						Delosperma	2.3

4.5.4 *O. irroratus* diet

During autumn the largest dietary item for *O. irroratus* was monocots 67% (Table 10), *Sporobolus* (20%) and *Trachyandra* (15 %) constituted more than half of the monocots present in the diet (Table 11). Dicots, which formed 25.4% of the diet, were the second largest constituent of the diet. During autumn the consumption of fruits peaked at 3.9%. Relatively more dicot seeds than grass seeds were consumed while no bark was consumed during autumn (Fig. 5b).

Table 10. The seasonal change in the mean percentage contribution of seven major dietary categories in the stomach contents of *O. irroratus* caught from Fort Hare Research farm, Alice

Diet category	Autumn	Winter	Spring	Summer
Monocots	67.0	68.3	64.0	72.0
Dicots	25.4	24.8	6.5	20.0
Grass seed	0.2	1.7	0	2.7
Dicot seed	1.3	0	1.5	3.3
Fruit	3.9	0	1.1	2.0
Bark	0	1.3	0	0
Flower	1.7	0.3	0	0
TOTAL	99.5	96.4	73	100

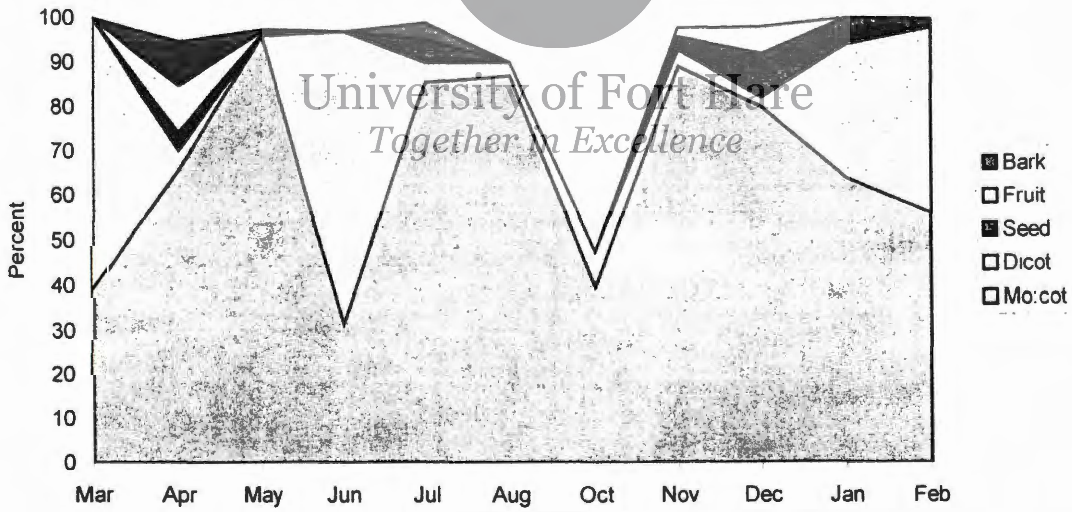

Fig. 5b Seasonal variations in the consumption of five major food categories by *O. irroratus* captured from Fort Hare Research farm, Alice. 1998-1999. (The unshaded part indicates unidentified diet content).

Table 11. Seasonal comparison of the percentage contribution of major food items found in *O. irroratus* stomach contents. Only those, which constituted more than 2% of the diet were considered.

Autumn	**%**	**Winter**	**%**	**Spring**	**%**	**Summer**	**%**
Sporobolus	20.0	*Sporobolus*	42.6	*Sporobolus*	26.5	*Sporobolus*	19.6
Trachyandra	15.0	*Berkheya*	17.3	*Asparagus*	15.0	*Trachyandra*	19.0
Cymbopogon	13.6	*Melica*	8.0	*Melica*	12.5	*Melica*	14.8
Melica	10.0	*Trachyandra*	7.5	*Themeda*	4.0	*Hermannia*	5.3
Pseudognaphalium	6.0	*Eragrostis*	4.1	*Hibiscus*	3.5	*Teucrium*	4.5
Fruit	3.8	*Panicum*	2.6	*Panicum*	3.0	*Cymbopogon*	4.3
Senecio	3.6	*Delosperma*	2.0	*Cymbopogon*	2.5	*Grewia*	4.1
Berkheya	3.5	*Oxalis*	2.0	*Pelargonium*	2.5	*Asparagus*	4.0
Sutera	3.3					*Themeda*	3.6
Panicum	3.0					Dicot seeds	3.3
Selago	2.6					*Cynodon*	3.0
Solanum	2.3					*Oxalis*	3.0
						Grass seeds	2.6
						Solanum	2.3

4.5.5 Interspecific comparison of rodent diets in autumn

The high quality food items (insects, seeds, fruit) in the stomach contents of *Rhabdomys* accounted for 66.8% of the entire diet in autumn (Table 8). The *O. irroratus* stomachs contained only 5.4% high quality items (Table 10).

The combined percentage of dicots and monocots in the diet of *R. pumilio* accounted for 31.2% (Table 8) while that in *O. irroratus* accounted for 92.4% (Table 10). The approximately 30% overlap in diet indicates a possible area of competition. *Otomys* ate significantly more monocots than *Rhabdomys* ($t=4.752$; $p<0.001$) but there was no significant difference ($t=-0.689$; $p=0.26$) between the proportion of dicots in the diet.

Tables 9 and 11 show that the possible dietary overlap is in fact minimal with respect to monocots and dicots with the two rodents tending to feed on different species. This leaves fruit, which constituted only 3.8% of the diet of *Otomys*, as a possible source of competition.

4.6 WINTER

4.6.1 Climate and flora.

The mean winter rainfall was 6.7mm. The lowest monthly rainfall was 2mm June (Fig.1). The lowest monthly mean temperature (12.8^{0}C) for the year was also recorded in June (Fig. 2). Moisture content of the forbs and the grasses declined to their lowest during winter (see Table 4). Compared with autumn, the reduction in moisture content of grasses was 27.4% while the moisture reduction in bark was slight at only 1.34%. *Lycium* sp continued to bear fruits in winter. Drought resistant plants such as karroid shrubs or hypophytes such as *Albuca* sp, *Bulbine* sp, *Drimiopsis* sp or those with rhizomes such as *Trachyandra* sp, *Teucrium* sp, and *Asparagus* sp or succulents such as *Delosperma* sp were the only species present in the habitat with any green vegetative parts.

4.6.2 Population structure

As with autumn, more *R. pumilio* than *O. irroratus* were caught during winter. The sex ratio was 1:0.69 (n=27) for *R. pumilio* while the sample of *O. irroratus* contained no females in May and the sex ratio for winter (1:0.71) was biased towards males (n=12). In winter, 75% of *Rhabdomys* were considered non-reproductive adults while only 25% of *Otomys* were non-reproductive. With the onset of winter, the first juvenile *R. pumilio* were trapped and they constituted 41% of the population. No gravid females of either species were caught during winter.

4.6.3 *R. pumilio* diet

Monocot (32.9%), with significantly higher consumption than in autumn, ($q=6.259$; $p<0.0001$), and dicots (23.9%) dominated the diet in winter (Table 8). Compared with autumn, the consumption of bark increased with it being significantly higher ($q=7.137$; $p<0.001$) in late winter. Consumption of insects declined significantly ($q=3.959$; $p<0.05$) as well as that of dicot seed ($q=8.561$; $p<0.001$). Significantly less fruit ($q=8.114$; $p<0.001$) was taken by mid-winter. Dicot consumption was slightly higher (20.9 vs. 23.9%) and grass seed consumption slightly lower.

A comparison between the diets of juvenile and adult animals revealed that juveniles consumed slightly more bark than adults as well as more fruit, dicot and monocot seeds (see Fig. 6). When comparing males and females, females tended to eat more bark than males.

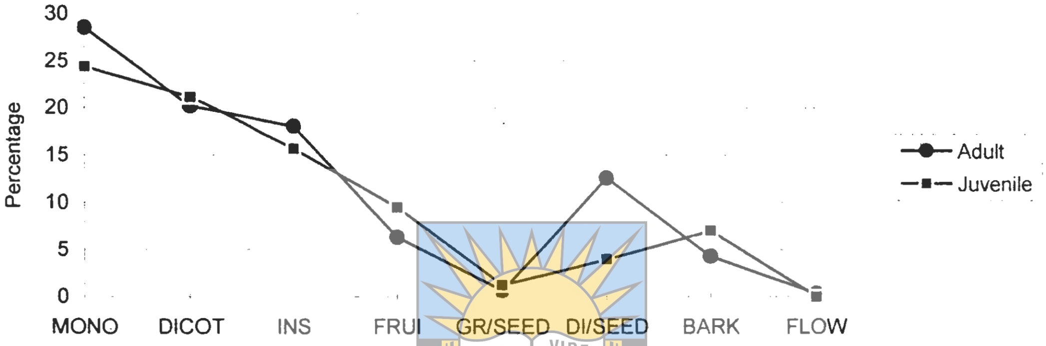

Fig. 6. Annual average of eight categories of food eaten by adult and juvenile individuals of *R. pumilio* caught from Fort Hare Research Farm, Alice (1998-

4.6.4 *O. irroratus* diet

O. irroratus stomach contents in winter did not show any significant change in the composition of the major food categories. Monocots constituted 68.3% of the diet and by far remained the major dietary category. Dicots constituted 24.8% of the diet and this proportion was similar to that found in the autumn diet (Table 10). The remaining food items constituted only 3.3% of the total. Winter was the only season during which bark was present in the diet of *Otomys*.

4.6.5 Interspecific comparison of rodent diets in winter

Insects, seeds and fruit in the diet of *Rhabdomys* dropped to 18% while in *Otomys* they constituted a mere 1.7% and this consisted entirely of grass seeds. Monocots and dicots eaten by *Rhabdomys* in winter increased significantly ($q=5.888$; $p<0.001$) to 56.8% while the increase for *Otomys* was marginal (0.7%) to 93.1%.

Once again *Otomys* ate significantly more monocots than *Rhabdomys* ($t=-4.682$; $p<0.001$) and there was no significant difference ($t=1.173$; $p=0.129$) between the proportion of dicots in their diet.

The dietary overlap of approximately 56% can be examined in more detail in Tables 9 and 11. In reality, the overlap is little more than 2% (see also Discussion: Diets in Winter).

4.6.6 Bark

Bark consumption peaked during winter. In *R. pumilio* it reached 7.4% of the diet whereas for the rest of the year it constituted less than 1%. In *O. irroratus* bark constituted 1.3% of their winter diet and did not appear in stomach contents in the other seasons.

4.7 SPRING

4.7.1 Climate and flora.

Moderate rainfall fell during spring. The average rainfall was 43.2mm and mean temperature for the season was14.9^{0}C. Active growth, flowering and seeding was observed in a number of plants, which includes grasses, forbs, shrubs and trees. *Rhus* sp in early spring and *Ehretia* in mid-spring were the two major fruit bearing trees present at this time. *Trachyandra* , *Albuca, Bulbine* sp and *Drimiopsis* sp were some of the monocotyledon hypophytes, which bore flowers and seeds during spring.

4.7.2 Population structure

More males than females (1:0.82) were trapped at the beginning of spring for *R. pumilio* (n=20). The mean proportion of *R. pumilio* juveniles present during spring was 5%, considerably lower than in winter. The first gravid female was trapped in October while 90% of the animals were regarded as being in reproductive condition.

Only one *O. irroratus* was trapped during spring.

4.7.3 *R. pumilio* diet

Insects and dicot seeds dominated the diet. A significantly higher proportion (34.3%) of insects were consumed in spring (q=8.418; p<0.001) and this contrasted with a significant drop in both monocot (q=6.654; p<0.001) and bark consumption (q=5.405; p<0.01) (see Table 8). Dicot seed consumption (q=12.52; p<0.001) was significantly higher. Flowers, fruit, grass seed and roots constituted only 6% of the total diet while the combination of monocots and dicots constituted 25%.

4.7.4 *O. irroratus* diet

Monocots constituted 64% of the stomach contents of the single *O. irroratus* in spring and again dominated the diet. The proportion of dicot material was markedly lower at 6.5% and fruit constituted 1%. The remainder (27%) was not identifiable (see Table 10).

4.7.5 Interspecific comparison of rodent diets in spring

The fact that only one specimen of *Otomys* was trapped makes meaningful comparison impossible. The monocot proportion of the diet was similar to the other seasons as were the contributions of all other food categories with the exception of dicots and the large unidentifiable component.

There was some dietary overlap with *Asparagus* constituting 2.1% of *Rhabdomys*' diet and 15% of *Otomys*' diet. Once again *Sporobolus* dominated (26.5%) the diet of *Otomys* and contributed less than 2% to that of *Rhabdomys* (see Tables 9 and 11).

4.8 SUMMER

4.8.1 Climate and flora

The study site received the second highest and most consistent monthly rainfall during summer. The mean monthly rainfall figure was 65.5mm and the mean monthly temperature, 20^{0}C, was the highest of all four seasons. Increased plant cover and insect activity was observed in the habitat during summer. Two abundant grass species that were in full bloom during summer period were *Melica* sp and *Sporobolus* sp. The mean percentage of moisture in bark, forbs and grasses was the highest during summer period (see Table 4).

4.8.2 Population structure

December and January were the only months during which a slightly higher proportion of *Otomys* were trapped. The sex ratio for *R. pumilio* was 1:0.83 (n=22). No juveniles were present but all animals were in breeding condition and 80% of *R. pumilio* females were gravid.

In contrast, *O. irroratus* showed a female biased sex ratio (1:1.57) (n=18). The entire population of *O. irroratus* trapped during summer was in breeding condition and 73% (n=8) of the females were gravid.

4.8.3 *R. pumilio* diet

The summer diet was dominated by dicots (35.9%) followed by insects (19.9%), monocots (17.1%) and grass seed (14.9%). Dicot consumption in early summer was significantly higher than in spring (q=4.962; p<0.01) while insect consumption was significantly lower (q=4.880; p<0.01). Grass seeds were present in abundance in the stomach contents with the main contribution coming from *Melica decumbens* which seeds during summer and a minor contribution from *Sporobolus* sp. The proportion of grass seed was significantly higher (q=5.059; p<0.01) than in spring (Table 8). A corresponding increase in the proportion of monocot plant material was not significant. Dicot seed consumption declined significantly (q=12.83; p<0.001). Root was consumed again in summer. Fruit constituted 5.4% of the diet while root, flowers, dicot seed and bark constituted but 4.3% of the diet.

4.8.4 *O. irroratus* diet

The proportion of monocot in the stomach content of *O. irroratus* reached its peak, 72.0%, in summer. Dicot plant material formed 20% of the diet and this is slightly lower than autumn and winter intake. Fruit, monocot seed and dicot seed were also consumed at above the 2% level in summer and constituted 8% of the diet (Table 10).

4.8.5 Interspecific comparison of rodent diets in summer

High quality food items (insects, seeds, flowers and fruit) constituted 42.5% of the diet of *Rhabdomys* (Table 8) and only 6% of that of *Otomys* (Table 10).

Significantly more dicots were eaten by *Rhabdomys* (t=1.76; p=0.043) while *Otomys* ate significantly more monocots (t=-9.937; p<0.001).

Monocots and dicots constituted 92% of *Otomys* diet and 53% of *Rhabdomys* diet indicating a possible source of dietary overlap. As shown previously, the overlap is minimal (see Tables 9 and 11) where *Asparagus* and *Oxalis* constituted similar proportions of the rodents' diets (<9%). *Sporobolus* was again important for *Otomys* (19.6% of the diet) but of limited importance to *Rhabdomys* (2.4%).

4.9 OVERALL CHANGES IN DIET

4.9.1 Frequency of occurrence

The frequency of different food items in the stomach of *R. pumilio* showed that insects were the most regularly occurring item and were present in 72% of the stomachs, followed by dicot seeds which were found in 40% of the total number of the stomachs examined (Table 12a). Of the ten dietary items listed, seven were present in more than 30% of *R. pumilio* stomachs.

The two most abundant grass species in the habitat, *Sporobolus fimbriatus* and *Melica decumbens* (Table 3a) were the two most frequently occurring plant materials in the stomach contents of *O. irroratus* (Table 12b). Only two of the ten most frequently occurring dietary items eaten by *O. irroratus* were present in more than 30% of the stomachs. *Sporobolus fimbriatus* was found in 67%, and *Melica decumbens* in 35% of the total number of the stomachs examined.

Out of the ten most frequently occurring items listed for *R. pumilio* and *O. irroratus*, only three items, grass seed, fruit and bark were present in the top ten dietary items of both species. All of the shared dietary material was present in fewer than 20% of the stomachs of *O. irroratus* and collectively constituted only 3.4% of its annual diet. In the case of *R. pumilio* the three items collectively constituted 18.7% of the annual diet.

Table 12a. Ten most frequently occurring food items found in the stomach contents of *R. pumilio* (n=82); (* indicates the food items which are common to *R. pumilio* and *O. irroratus*).

Dietary item	**No. stomachs with item**	**Percentage frequency**	**Order of importance**
Insects	59	72	1
Dicot seeds	33	40	2
Fruit*	31	38	3
Grass seed*	30	37	4
Bark*	29	35	5
Themeda triandra	28	34	6
Oxalis sp	26	32	7
Flower	14	17	8
Berkheya sp	14	17	8
Solanum tomentosum	13	16	10

Table 12b. Ten most frequently occurring food items found in the stomach contents of *O. irroratus* (n=37); (* indicates the food items which are common to both *R. pumilio* and *O. irroratus*).

Dietary material	**No. stomachs with item**	**Percentage frequency**	**Order of importance**
Sporobolus fimbriatus	25	67	1
Melica decumbens	13	35	2
Panicum maximum	10	27	3
Trachyandra sp	09	24	4
Cynodon dactylon	08	22	5
Grass seed*	07	19	6
Asparagus sp	07	19	6
Fruit*	06	16	8
Acacia karroo	05	14	9
Bark*	04	11	10

4.9.2 Annual abundance

The greatest proportional contribution (18.0%) in the entire stomach contents of *R. pumilio* was insects (Table 13). *Sporobolus fimbriatus*, a grass species, formed the single most abundant dietary item (26.9%) in the total stomach contents of *O. irroratus*. Out the ten most annually abundant food items found in the diet of both species, only three items, *Berkheya* sp., *Pelargonium* sp. and *Asparagus* sp., were shared. None of the shared items account for any significant proportion (>5%) of either diet.

Among the annually abundant foods listed for each species, three items in *R. pumilio* and seven items in *O. irroratus* were monocots. Out of the ten items listed, the first four items for *R. pumilio* and first two items for *O. irroratus* were identical in frequency and percentage contribution estimates. Seven out of the ten most abundant dietary materials listed for *R. pumilio* were also listed among the ten most frequent items found in their stomach contents. Five of the ten most abundant dietary items present in *O. irroratus* were listed among the ten most frequent dietary items listed for their stomach contents.

Table 13. The ten most abundant dietary items found in *R. pumilio* and *O. irroratus* expressed as the annual mean percentage contribution (* indicates the shared food items).

R. pumilio	**Annual mean %**	***O. irroratus***	**Annual mean %**
Insect	18.0	*Sporobolus fimbriatus*	26.9
Fruit	9.3	*Melica decumbens*	11.2
Dicot seed	7.5	*Trachyandra* sp	11.1
Grass seed	6.6	*Cymbopogon plurinodis*	5.4
Oxalis sp	6.2	*Berkheya* sp*	5.0
Berkheya sp*	3.9	*Asparagus* sp*	4.3
Pelargonium sp*	3.3	*Themeda triandra*	2.1
Solanum tomentosum	2.9	*Panicum maximum*	2.1
Bark	2.8	*Pelargonium* sp*	2.1
Asparagus sp*	2.8	*Hermannia* sp	1.9

4.9.3 Differences in overall consumption of dicots, monocots and high-quality foods

Dicots constituted the most important dietary item for *R. pumilio* when considering the overall contribution to the diet (Table 14). Leaves and stems of the monocots and dicots formed close to half of the overall stomach contents of *R. pumilio* . The average dietary percentage of monocots was 19.9% while that of dicots was 27.2% and together they formed 47.1% of the total. High quality foods such as insects (18%), seeds (14.1%) and fruit (9.3%) constituted 41.4% of the diet. Bark (2.8%) and roots (0.5%), both containing highly structural carbohydrates, were also consumed.

Table 14. Relative contributions of the major categories of food items found in the diets of *R. pumilio* and *O. irroratus* expressed as annual mean percentages.

Diet category	*R. pumilio* N=82	*O. irroratus* N=37
Bark	2.8	0.4
Dicot	27.2	20.2
Flower	0.6	0.5
Fruit	9.3	1.5
Insect	18.0	0
Monocot	19.9	67.9
Root	0.5	0
Seed	14.1	2.7

The largest proportion, 67.9%, of *O. irroratus* diet comprised of monocots (Table 14). Dicots formed 20.2% of the stomach content and this was significantly lower ($t=1.76$; $p=0.043$) than that in *R. pumilio* (27.2%). The combined proportion of these two categories of plant materials (88.1%) was significantly higher ($t=-8.989$; $p<0.001$), than that found in *R. pumilio* (47.1%). The proportion of high quality food material was however significantly lower ($t=9.912$; $p<0.001$) since the combined percentage of all such items constituted only 4.2% of the total versus 41.4% in *Rhabdomys*. The relative proportion of bark in the stomach contents of *Otomys* (0.4%) was lower than in *Rhabdomys* (2.8%) and the former did not consume root at all.

5. DISCUSSION

5.1 REPRODUCTION

Pregnant *R. pumilio* were trapped from the end of spring (Oct) to early autumn (Mar) while most individuals caught in September and April were regarded as being in reproductive condition (perforate or scrotal). The percentage of pregnant females changed from October 17%, to 100% in December and January and 50% in March. The majority of animals caught between May (67%) and August (50%) i.e. during winter were regarded as being out of reproductive condition (Fig 4a & 4b). The proportion of non-reproductive animals declined from a peak of 83%, observed in June, to 8% in October. This decline in the number of non-reproductives was matched by increasing breeding activity (Fig. 4a). This gives a good indication of a breeding season extending from Sep-Oct to Mar-Apr with its peak in mid-summer. Similar findings were reported by David & Jarvis (1985) from the Cape Flats where the breeding season of *R. pumilio* extended from October to the end of May (i.e. the end of spring to early winter). This small difference in breeding season might be attributed the small sample sizes of the present study.

Rainfall (Taylor & Green 1976) and temperature decline (Perrin 1980c) have both been cited as possible cues for breeding cessation. Brooks (1974) reported a correlation between breeding, rainfall and warm temperatures on the Transvaal Highveld, where he found that the summer rainfall from October to March, coincided with the breeding season of *R. pumilio*. Coetzee (1965), reported similar results for *Praomys (=Mastomys) natalensis* from the Transvaal Highveld. Several studies conducted in the tropics where the temperatures are less variable, also reported a strong correlation between rainfall and breeding (Delany 1972; Taylor & Green 1976; Neal 1977). In the present study, large reductions in rainfall (72.8 - 6.7 mm) and mean temperature (18.5 - 12.8^{o}C) from autumn to winter coincided with significant increases in the consumption of monocots and bark (low quality foods), significant decreases in the consumption of insects, seeds and fruit (high quality foods) and the cessation of breeding. Declining consumption of high quality foods would have reflected their reduced availability or absence during the cold, dry winter as reported from other studies (Rautenbach *et al.* 1988; Wolda 1988). Obviously the quality of diet must also play a role in determining the breeding season. There are many reports where breeding activity is stimulated by improving nutritional quality and quantity of available food during rains (Field 1975; Delany & Happold 1979) and this suggest that the species involved are opportunistic breeders and their reproduction cycle may continue unhindered if the food supply is regular and adequate (Neal 1999).

Because of their high reproductive rate (De Graaff 1981), rodents often epitomize breeding changes in response to environmental variables better than many other vertebrate populations. Population increase is often synonymous with increased breeding even though other factors such as growth, survival, emigration, disease and fecundity also play a role (Vaughan *et al.* 2000). Both quality and abundance of food available in the natural habitat has been linked to breeding in rodents (Field 1975; Taylor& Green 1976; Delany & Happold 1979; Swanepoel 1980; Neal 1984; Oguge 1995; Perrin, 1980a; 1980b; 1980c). The proportion of breeding individuals amongst *R. pumilio* in the present study was highest in mid-summer (Fig. 4a) and this corresponded with their stomachs containing over 40% high quality food. Bronson (1985; 1989) suggested that the timing of peak energetic demand (the breeding period), with the peak net energetic availability is the most successful strategy for a seasonal breeder. During summer in the present study, the habitat received its highest rainfall and mean temperatures (Fig 1&2) and the quality of food eaten by *R. pumilio* was at a peak, thus reflecting Bronson's suggestions. In similar fashion, the onset of breeding in spring coincided with significant increases in the consumption of high quality insects and dicot seeds, the two of which constituted over 50% of the diet.

R. pumilio in the present study did not show any evidence to suggest complete cessation of breeding and individuals in reproductive condition were caught throughout the year, though their numbers were low during winter. In addition to the declining food quality and availability, increased energy expenditure for thermoregulation in winter would also reduce the amount of energy available for reproduction. Increased dependency on low quality perennial monocots and bark during the adverse winter period, however, indicated that *Rhabdomys* was able to find emergency food resources which probably proved inadequate to shield them from an externally enforced refractory period as reported for herbivores living under extremely seasonal climatic conditions (Christian 1980; Ascaray *et al.* 1991).

Juveniles were trapped only in winter and spring when they constituted 41% and 5% of the population respectively. With a suggested breeding season extending from spring to autumn, one would have expected the recruitment of juveniles into the population to start much earlier and their absence is probably an artefact of sampling. Perrin (1980c) reported a dramatic increase in sub-adults during April-May period, which corresponds well with the present study. Davis (1973) reported two peaks in juvenile recruitment, one in early summer (Oct-Nov) and a second in autumn, which he described as the end of breeding season. The present study indicated a single peak in breeding (mid-summer) and the reason for the difference between the two populations is probably different climatic conditions at the different geographic locations.

Because of small sample size, the breeding pattern of *O. irroratus* was impossible to decipher. During the present study, no juveniles were trapped. This fact, together with low overall *Otomys* numbers trapped, can probably be attributed to *inter alia* Taylor's (1996 p. 49) assertion that "*O. irroratus* is notoriously trap shy".

The consumption of ephemeral high quality food has often been correlated with increased nutrient and/or caloric intake in rodents for seasonal reproduction (Perrin 1980a; 1980c). There was no dietary or demographic evidence that suggested seasonal reproduction in *O. irroratus* and they were probably not dependent on a temporal increase in energy expenditure for breeding reflected by only three of 37 individuals being out of reproductive condition. Monocots, which consistently dominated (>60%) their diet throughout the year indicated that they did not experience any shortage of preferred food group during winter. The dietary constancy of *O. irroratus* indicated that they were probably capable of balancing their energy requirement to that of the available energy in the diet by regulating their energy expenditure for reproduction. Absence of seasonal reproduction does not mean a species never suffers an energy deficit for reproduction in any month of the year. Reproduction in *O. irroratus* may be continuous except for a short winter period when reduced environmental temperature may compel them to direct additional energy for thermoregulation, insulation, activity phasing or microhabitat orientation. The continuous availability of perennial grasses may ensure that the food resource for *O. irroratus* during winter remains stable when compared with that of *R. pumilio* and thus they must be able to maintain a more consistent breeding rate throughout their annual cycle (Perrin 1980a; 1980c).

Despite the small sample of *O. irroratus*, the litter size and pregnancy period indicate that there were clear differences in the patterns of reproduction of the two coexisting rodents within an apparently uniform environment, an observation supported by (Perrin 1980c). Delany (1972) observed a similar non-uniform response to rainfall among the sympatric rodents he studied. No single reason could be found for their differing responses and he suggested diet as the possible reason for such disparity in breeding response among coexisting rodents. High rainfall has been often associated with increased growth and development in plants and this maximizes the food supply to the rodents. However species-specific food preferences may affect the food supply differently for different rodents and thereby the reproductive pattern, intensity and duration. In the present study, *R. pumilio* were dependent on a high quality seasonal diet (Table 8) while *O. irroratus* relied on a annually abundant lower quality diet which included >60% monocots (Table 10). In the case of *R. pumilio*, rainfall and temperature influenced the availability of their high quality diet and thereby their reproduction. Because of their heavy dependence on high quality food items, the adverse conditions in winter may affected *R. pumilio* more than *O. irroratus*, which is less dependent on the quality of their food items. These findings mirror those reported by (Perrin 1980a; 1980c).

5.2 PHYSICAL ASPECTS

The mean body weight and head body length of adult female *R. pumilio* was slightly above that of adult males. Smithers (1971) reported a similar observation among the *R. pumilio* population he studied from Botswana where not only body weight and head body length but also the tail length of females were slightly greater than that of males. However it was not possible to draw conclusions from this result alone since the size difference observed in favour of females may be an artefact of the smaller sample size used here. This finding however suggests that with better sample size it may be possible to formulate diagnostic parameters for rodent populations, which inhabit in different regions.

In *O. irroratus*, sexual dimorphism was apparent with males being larger than females in terms of mass and hind foot length. The significance of this is not known.

5.3 DIET

The stomach contents of the coexisting rodents was categorized into high quality nutritious food substances and poor quality food substances at a macro level on the basis of their nutrient contents and the presence of indigestible structural materials such as fibre and lignin. Perrin (1980a) distinguished insects, seeds and fruits as high quality food and leaves, stems, roots, bark and rhizomes as lower quality food while Wirminghaus & Perrin (1992) reported that flowers were easily digestible and were a valuable source of protein. The same categorization was adopted in this study.

The diet of *Otomys irroratus* was dominated by two grass species, *Sporobolus fimbriatus* and *Melica decumbens*. The flora at the study site was also dominated by the same grass species and one can conclude that they formed a reliable, easy to find food source (see Tables 3a & 13) for *O. irroratus*. The uniform distribution and higher cover by these two grass species also must be a contributing factor for their increased consumption by *O. irroratus*. The high proportion of *S. fimbriatus* and *M. decumbens* in *O. irroratus* stomach contents and their intensive and continuous use throughout the year together with other grass species such as *Cymbopogon plurinodis* and *Panicum maximum* (Table

13) suggested a specialization for grasses in general, probably because of their continuous availability as most grass species are perennial. In contrast, the diet of *Rhabdomys pumilio* was dominated by high quality items such as insects, fruits and seeds that were transient in the habitat (compare Tables 3a; 3b& 13). While over 50% of the annual diet of *Rhabdomys* was from perennial plant species, these plants were not dominant in the habitat. Generally *Rhabdomys* consumed a mixed diet throughout the year. The dominant items of their diet changed from one category of food to another as the seasons changed. With the exception of winter, they always managed to keep the high quality food items as dominant in diet. Their ability to pick and choose from a changing repertoire of preferred high quality foods resulted in greater dietary variation from season to season when compared with the diet of *O. irroratus,* which remained more or less constant over the various seasons.

Approximately 50% of the available plant species were present in the stomach contents of the two rodents studied here. This indicated a degree of specialization, which was not possible to quantify as most of the unconsumed plants were relatively uncommon in the plant community in the study area. Davis (1973), however, found that *Otomys* do eat nearly all of the plant species that occur in their habitat. Consequently their absence could have been due to infrequent encounter rather than undesirability.

Otomys had a far more specialized diet with only two food items having a frequency of occurrence >30%. In contrast, *Rhabdomys* had seven food items with a frequency of occurrence exceeding 30%.

The total number of food items identified in the stomach contents of *R. pumilio* was higher than that of *O. irroratus* but the mean number of plant species and the mean number of families per stomach was lower. This indicated that *O. irroratus* was capable of eating a wider range of plant types and this could be related to their better digestive efficiency (Curtis & Perrin 1979) to handle complex carbohydrates common to most plants. The same was suggested for *Otomys angoniensis,* another specialist herbivore, which eats a broad range of plants and Perrin & Curtis (1980) explained this in terms of their morphological adaptations.

Complex polysaccharides such as cellulose, hemicellulose and lignin (fibre) are important structural constituents which are abundantly available in plants (Van Soest 1977; 1982), but are unavailable to herbivorous vertebrates as potential food due to their low digestibility (Howe & Westley, 1987: In Bozinovic 1995). Grasses have a very high fibre content and low digestibility (Stenseth *et al*., 1977). The grasses, which formed the major monocot content of the diet of *O. irroratus*, probably had a high percentage of indigestible fibre that made them less attractive to an omnivore like *R. pumilio*, which does not have the anatomical adaptations to extract maximal nutritional value. Specialist herbivores have an enlarged caecum that accommodates symbiotic bacteria to digest complex structural carbohydrates (McBee 1971). Microbial fermentation in the caeca not only releases valuable energy but also amino-acids and vitamins necessary for growth and development (Perrin & Curtis 1980). The feeding tactics and preference for certain dietary items that was evident in *R. pumilio* and *O. irroratus* can be related to anatomical specializations reported for various rodent species (Golley 1960; Vorontsov 1961; 1962; Dearden 1969; Carleton 1973). Perrin and Curtis (1980) suggested that on anatomical grounds, fermentation of complex structural carbohydrates is relatively efficient in *Otomys* sp. The specialist herbivore features of the digestive anatomy of *O. irroratus* includes a small band of cornified epithelium in the stomach which enhances carbohydrate digestion, large caeca with a double row of haustra and numerous papillae which act as fermentation chambers, a colon with four loops and internal ridges that increases its surface area (Perrin & Curtis 1980). In contrast, *R. pumilio* has a smaller caecum, fewer small haustra and spiral colic loops, and some individuals have a gallbladder indicating adaptation towards proteinaceous (insects and seeds) diet in their digestive anatomy. This suggests an omnivorous diet (Perrin & Curtis 1980) and presence or absence of a gallbladder is an indication of polymorphism in *Rhabdomys*..

It thus seems likely that the increased digestive efficiency for complex carbohydrates in *O. irroratus* enabled them to select from a broader range of plant species and they were able to focus on the most abundant, most stable plant species which potential competitors such as *Rhabdomys*, were not be able to exploit. This ability to digest complex structural carbohydrates efficiently was probably the reason why *O. irroratus* consumed significantly more grass than *R. pumilio*.

The dominant grasses found in the stomachs of *Otomys* are perennial and they ensured a steady food supply throughout the year even though their quality may have varied with season.

5.3.1 Diets in Autumn

In autumn the diet of *R. pumilio* was varied and it utilized available seasonal food items such as fruit (27.8%), dicot seeds (14.8%) and insects (16.7%). Collectively these items constituted nearly 60% of the diet while permanently available food sources such as dicots (20.9%) and monocots (10.3%) constituted a further 30%. Grass seed and monocot consumption both declined significantly from summer values probably indicating the end of seeding in grasses and a preference for the higher quality dicot seed over monocots. Monocots were not considered a preferred food item for *R. pumilio* (Curtis & Perrin 1979) and the significant decrease in the consumption of monocots may have been a reflection of the availability of preferred foods. The fact that high quality seasonal foods were still available probably accounts for the continuation of reproduction into autumn. This food would also have allowed the juveniles to grow rapidly in preparation for the onset of winter and overwintering adults and sub-adults to improve their fat reserves.

In *O. irroratus* monocots and dicots together formed over 90% of the stomach contents during autumn. The proportion of both dicots and fruit was greater than in summer while the proportion of monocots declined slightly. The other food items eaten included grass seeds, dicot seeds and flowers but these were regarded as minor components while fruit constituted 3.9% of the diet.

The slight decline in the consumption of monocots, a preferred food item for *O. irroratus*, probably resulted from a diet shift towards more hydrated dicots and fruits as the monocots started to dry out (see Table 10).

The proportion of monocots eaten by *O. irroratus* (67.9%) far exceeded that taken by *R. pumilio*, which accounted for only 10.3%. The four most abundantly eaten plant species for *Otomys*, all monocots, accounted for the bulk (58.6%) of their stomach contents during autumn. These monocots were *Sporobolus, Trachyandra, Cymbopogon* and *Melica*. *O. irroratus* stomach contents contained 25.4% dicot material in comparison with that of *R. pumilio* which contained 20.9% dicots. The proportion of fruit taken by *O. irroratus* was very low, approximately 4%, in comparison with 27.8% taken by *R. pumilio*.

O. irroratus ate significantly more monocots in autumn than *R. pumilio* (67% vs. 10.3%). This heavy dependence on a monocot diet was similar for all seasons and has also been reported by Curtis & Perrin (1979) and Perrin (1980b). In contrast there was no significant difference in dicot consumption (25.4% vs. 20.9%). Curtis & Perrin (1979) regarded dicots as a preferred food for *Rhabdomys* and this was borne out by a contribution to their annual diet of 27.2% (15-36%). In autumn, however, dicot consumption decreased significantly from summer, probably due to the abundance of fruit, seeds and insects, and the reduced quality of dicots (see below).

There was a slight increase in dicot consumption in *O. irroratus* (20-25.4%) that coincided with increased rainfall in autumn. Perrin (1980a) reported an increase in the consumption of leaves in March following a peak in rainfall received in February. He explained this dietary shift in terms increased vascularity and coarseness of dicot stems and consequent decline in their nutritional quality compelling the rodents to look for alternate food resources like dicot leaves. Though the seasonal change in the food quality was not tested in this study, the fact that the dietary shift observed here, resembled that described by Perrin (1980a), suggested that the poorer quality of dicot diet may be the reason for reduced consumption of dicots by *R. pumilio* in autumn. *O. irroratus*, on the other hand, may have been less affected by declining digestibility or changing palatability due to their better digestive efficiency. Davis (1973) and Perrin (1980b; 1980c) reported that *Otomys* was able to process a wider variety of plant materials than *Rhabdomys* and this may have enabled them to eat dicots in large quantities during autumn when the digestibility of this food resource may have been declining.

The peak in the fruit consumption evident in *R. pumilio* stomach contents during autumn, coincided with the peak in rainfall. A similar association between rainfall and fruit consumption was reported for primates living in gallery forest in Kenya (Wahungu 1998). The similar increase in dicot seed and fruit consumption reflected the fact that *Grewia* and *Lycium* were fruiting and seeding in autumn. The consumption of fruit by *O. irroratus* peaked at 3.9% during this period.

R. pumilio was regarded as an opportunistic feeder by Curtis & Perrin (1979) and Perrin (1980a) and this was reflected in the present study by the exploitation of transient dicot seeds, insects and fruit, which play a minor role in the diet of *O. irroratus*. *O. irroratus*, as a specialist herbivore (Perrin, 1980a) did not need to exploit the transient food sources as their better digestive efficiency enabled them to obtain adequate nutrition from the lower quality monocots. The consumption of different categories and quantities of food items during autumn ensured a low dietary overlap between the two coexisting species.

5.3.2 Diets in Winter

Significant increases in both monocot and bark consumption in the winter coincided with significant reductions in the presence of insects, seeds and fruits in the stomach contents of *R. pumilio*. Both monocots and bark are well known for their poor nutritional quality, which is often determined in terms of the food value and the digestibility of the food. Food value depends on the nutrient contents while digestibility is determined in terms of the presence of crude fibres. Fibres have been commonly regarded as the determinant of digestibility for a broad spectrum of plant food substances (Maynard & Loosli 1959, Grodzinski *et al.*, 1977). For example Hansson (1971) reported that the food value of grasses in winter might be equal to or lower than in summer but their digestibility may drop from the peak digestibility of 60% estimated for the spring and summer to between 30 and 50% in winter. This clearly showed that the nutritional value of the grass in winter is lower even if the nutrient content in the grass remains the same, because of the lowered digestibility. Becker (1955: In Stenseth *et al.* 1977) estimated the digestibility of bark at around 40%. In comparison with seeds, which have a digestibility of 90-95% (Drozdz 1968), both bark and grass have low digestibility and therefore low nutritional value.

For rodents in general and herbivores in particular, relative habitat harshness is largely dependent on plant growth, which determines the abundance of their food supply (Brown 1986). Plant growth is inhibited by low water and low temperature (Van Riper 1971; Caldwell 1975). Harshness can therefore generally be assessed on the basis of climatic data, although other factors such as soil fertility also need to be taken into account. Despite the lower nutritional quality, *R. pumilio* significantly increased its intake of monocots and bark in winter, which is characterized by a decline in rainfall and temperature i.e. increased habitat harshness. The diet switch towards low quality food must have been forced on *Rhabdomys* by a marked reduction in the abundance of highly nutritious but seasonally unavailable food sources such as seeds, insects and fruit. The winter decline in plant growth and consequent food scarcity was observed in the present study site (personal observation). The increase in the intake of these poor quality food substances during food scarcity indicated that they are not the preferred food items of *R. pumilio*. It has been shown that for *Sigmodon hispidus* monocotyledons require lower harvesting and handling time than the dicotyledons (Randolph *et al.* 1991) and consequently the significant increase in monocot consumption that occurred in winter might have been profitable in energetic terms as they required lower energy expenditure for harvesting and handling by *R. pumilio* especially when alternative food items were scarce.

The high monocot consumption of *Rhabdomys* superficially appeared to increase dietary overlap with *O. irroratus*. However, a breakdown of the monocots to species level indicated that this was not the case. The major monocot species in the diet of *O. irroratus*, *Sporobolus*, accounted for 42.6% of the total while it was present at <2% in the stomach contents of *R. pumilio*. None of the preferred monocots listed for the two species was shared at above the 2% level. This suggests that the overlap between the two species in winter was minimal. The stomach contents of *O. irroratus* did not show any significant change in monocot consumption but a slight increase in the bark consumption was evident. This suggested that they are less inconvenienced by the harsh habitat conditions of winter since the availability of their staple food, which are monocots, was less affected by the adverse winter condition. The water content of monocots, however, is reduced by approximately 60% (Ntshebe 1997) but the inclusion of succulents such as *Delosperma* (2%) and bark which is moist (1.3%) may have reduced their water deficit. Willan (1982) reported that *O. irroratus* managed to acquire all its water requirements from food.

Monocot consumption by *R. pumilio* in winter reached a peak with the absence of high quality foods, while there was a slight increase in the quantity of dicots eaten despite their reduced availability on account of the absence of the annual dicots. The grasses lost large amounts of moisture during winter (Table 4) and as this rodent depends on preformed water available from plants when surface water is unavailable (Perrin 1980a; De Graaff 1981), some form of hydrated food needed to be included in the diet. Bark, which Ntshebe (1997) has shown to have a high moisture content in winter, was consumed in significantly higher quantities and contributed 7.4% of the diet. Similarly, *Opuntia ficus indica*, a highly succulent xerophyte was present among the dicots eaten by *R. pumilio* though its contribution was <2% in the winter diet.

In the semi-arid Karoo, seasonal shift towards an herbaceous diet by two sympatric rodents, *Parotomys brantsii* and *Otomys unisulcatus* was attributed to the combined effects of plant availability and water requirements (Du Plessis *et al.* 1989; 1991). The selective feeding on bark and succulent dicots by *R. pumilio* must have been related to the need to secure moisture during dry winter months when grasses and plants in general lose a large amount of water.

In the present study, the diet of *O. irroratus* with a significantly higher consumption of monocots than *R. pumilio* in winter, indicated that they were probably less waterconstrained and consequently needed less water from their diet. This is borne out by the fact that *R. pumilio* consumed a higher quantity of bark.

Field observation indicated that *R. pumilio* is a proficient tree climber. Tail length is often linked to the tree-climbing ability of rodents. The Pouched Mouse (*Saccostomus campestris*) has a low tail to body ratio and this has restricted these rodents from climbing on vertical substrates in its habitat (Earl & Nel 1976). *O. irroratus* also has a low tail:body ratio (De Graaff 1981) (see also Table 5b) and is likely to be less proficient in climbing on thin branches where a longer tail would be of more use in balancing the body. Among *R. pumilio*, the tail length of the adult does not show any significant variation from that of the juveniles. The higher tail:body ratio of *R. pumilio* and the similarity of adult and juvenile tail length suggested (see Table 5a) that *R. pumilio* in general and juveniles in particular were morphologically well adapted to tree climbing. The higher proportion of bark in the diet *R. pumilio* compared with that of *O. irroratus* could be related to their better climbing ability and the larger bodied *O. irroratus* may be restricted to feeding only near ground level. This conclusion differs somewhat from Atkinson (1993), Taylor (1996) and Baxter & Hansson (2001) where *O. irroratus* is considered as a prominent bark-gnawing rodent in various habitats especially in pine plantations.

The stomach contents of *R. pumilio* and *O. irroratus* showed approximately 56% potential overlap in monocot and dicot consumption during winter (compare Tables 8 & 10). When the diets were examined in detail (Tables 9 & 11), it was immediately apparent that there was no major overlap. *Sporobolus* constituted 42.6% of the diet of *Otomys* and less than 2% of that of *Rhabdomys*. A large proportion (28.6%) of the stomach contents of *Rhabdomys* was unidentifiable monocots. Since the diet of *O. irroratus* contained no unidentified monocots, it is unlikely that there was dietary overlap in the unidentifiable matter. The selective consumption of certain parts of the monocots that were not included in reference collection may be the reason for the greater amount of unidentified material in *R. pumilio*. If this was the case, it would also indicate dietary partitioning on the basis of selective utilization of monocot parts.

Similar to the monocots. the amount of overlap in the dicots was small. *Berkheya*. was the dominant dicot in *O. irroratus* diet where it constituted approximately 17%. The only common species was *Oxalis* (see Tables 9 & 11), which constituted 2.0% of the diet of *Otomys* and 7.9% of that of *Rhabdomys*. *Solanum*, *Pseudognaphalium*, and *Pelargonium*, which accounted for 11.6% of the diet of *R. pumilio*, occurred in very small quantities (<2%) in the stomach contents of *O. irroratus*.

The overlap in monocot and dicot consumption between the two rodents was minimal. Selective feeding among coexisting rodents of food would be important, as it would reduce interspecific competition for food.

5.3.3 Diets in Spring

The dramatic increase in the availability of high quality food items such as insects, dicot seeds and flowers was exploited by *R. pumilio* during spring. In late spring the first gravid females indicated that reproduction had started. Juveniles present in the population would have grown rapidly and achieved adulthood. The initiation of breeding coincided with an increase in mean temperature from the winter low of 12.8^{0}C to 14.9^{0}C, and in mean rainfall from 6.7 to 43.2mm.

The increase in the proportion of high quality food items such as insects, dicot seeds and flowers in the stomach contents of *R. pumilio* coincided with the wetter and warmer climatic conditions. The increase in insect consumption clearly coincided with the emergence of termites, which were identified as a major dietary item in *R. pumilio* during spring. The increase in seeds and flowers (Fig.8) coincided with the spring flowering and seeding observed in many dicotyledonous plants. A similar but much lower percentage increase of dicot seeds consumption by *O. irroratus* was observed, indicating an abundance of this food in the habitat. For *R. pumilio* the dietary change in the spring was highly significant as it represented a breakaway from the lower quality food taken in winter to high quality items required for the beginning of breeding activity as reported by a number of authors (*inter alia* Perrin 1980a; Fuller & Perrin 2001).

Golley (1961) observed that seeds have the highest caloric value of any plant material and they may be second only to insects in providing the highest number of calories per gram (Richman 1975). The consumption of high quality food by *R. pumilio* in spring resembled that of autumn but the focus changes from fruits to insects and seeds according to their changing availability. The strategic selection of transient but high quality food material by *R. pumilio* confirms the view that they are r-strategists capable of exploiting seasonal windfalls of highly nutritious food items available in their natural habitat (Perrin, 1980a; 1980b).

The seasonality of breeding could not be confirmed for *O. irroratus* as they could not be trapped in adequate numbers continually throughout the study period. No gravid *O. irroratus* females were trapped during spring but all individuals were in reproductive condition (scrotal; perforate). Despite obvious climatic changes, the diet of *O. irroratus* remained little changed in spring and as in winter they consumed large quantities (64%) of monocots (Fig 10). *Microtus agrestis*, an herbivorous cricetid, not only grows, moults and breeds on an essentially monocotyledonous diet (Ferns 1976) but achieves this at a time when the protein content of the grass is not optimal (Evans 1973). In the present study, *O. irroratus* achieved a similar feat without any dietary switch from a low quality monocot diet to high quality foods such as insects, fruits, seeds or flowers.

The absence of variation in the feeding habits or reproductive condition that was evident in *O. irroratus* from winter to spring when compared with the major changes that were observed in coexisting *R. pumilio*, confirmed Curtis & Perrin's (1979) and Perrin's (1980a; 1980b) assertions that they are characteristically k-strategists.

5.3.4 Diets in Summer

The significant drops in insect and dicot seed consumption from spring to summer were compensated for by significant increases in grass seed (14.9%) and dicot (35.9%) consumption. Insect consumption, however, still constituted some 20% of *R. pumilio* diet but was lower than 26.71% reported from Natal by Wirminghaus & Perrin (1992) and below the 35% reported by Perrin (1980a) from Fish River Valley scrub.

High quality food materials constituted 42.5% of the diet in summer that is lower than in spring and autumn seasons, all of which are identified as breeding seasons, but is more than twice that of winter. These results suggest that a diet which contains >40% high quality food might be necessary to sustain the reproductive effort in *R. pumilio*.

The consumption of dicots peaked (35.9%) during summer, similar to the omnivorous fulvous harvest mouse, *Reithrodontomys fulvescens*, which inhabits coastal prairie habitat in the USA (Kincaid & Cameron 1982). Forbs, which are dicots, digest easily because of their low fibre content (Gebczynska 1970) and *R. pumilio* in the Kenya highlands was able to exist largely on dicotyledonous plants with clover, a dicotyledon forb, as its main dietary item (Taylor & Green 1976). Evans (1960: In Taylor & Green 1976) reported that clover contained up to 30% crude protein.

Nearly 50% of the dicots taken by *R. pumilio* in summer in significantly increased quantities were *Berkheya* and *Oxalis*. Clearly these plants were selectively fed on and they, together with insects, seeds, fruit and flowers, would have provided the nutrients and energy needed to sustain an intensive summer breeding effort. During summer season both the quantity and variety of dicot plants in the field increased. Annually appearing dicots were observed to be abundant during summer and this might have accounted for the significant increase in dicot consumption. This abundance means that they can be found easily and processed rapidly thereby saving valuable search and handling time. This would translate into an increase in energy return. Herbivores increase their consumption of mopane leaves in summer when their palatability and crude protein content reaches its annual peak (Styles & Skinner 1997). The increased preference for dicots was most probably related to their increased palatability or nutritional quality.

Monocot consumption by *O. irroratus* peaked during summer at 72% of the diet, as did the diversity of plant species (14) that constituted more than 2% of their diet (see Tables 9 & 11). As with the other seasons, monocots were clearly the preferred food items. With the increased diversity of plant species in the diet, the *Sporobolus* component decreased to its lowest level, which was more than 50% lower than winter levels. Specialist herbivores are known to have a broad trophic range (Curtis & Perrin, 1979) and while *O. irroratus* in this study specialized in monocots, in summer it was not particularly selective. Consumption of broader food resources among coexisting species occurs only when there is an abundance food in the habitat (Kincaid & Cameron 1982). The variety of plants in the diet of *O. irroratus* in summer increased with the increasing food availability of summer. This confirmed that they were able to exploit a wide variety of plant species as has been reported for other herbivore species such as *Otomys unisulcatus* and *Parotomys brantsii* (Du Plessis *et al.* 1991).

O. irroratus has been shown to be anatomically adapted to exploit different plant species (Curtis & Perrin 1979) and this may enable them to focus on exclusive plant resources such as grasses and herbs in preference to seeds and fruits, thereby reducing dietary overlap with *R. pumilio*. Frequent interaction is likely to promote ecological segregation (Hoffmeyer 1975) an undesirable outcome for coexisting species. Dietary divergence may be more important for winter when the habitat is under severe environmental hardship and food availability is limited. During summer the abundant supply of plants in the habitat may permit a considerable dietary overlap. The above appears to be the case in the present study and dietary overlap was greatest in summer.

While plant material was the dominant food supply in summer for both *R. pumilio* and *O. irroratus* (77.5% and 100% respectively) (Tables 8 & 10), the actual overlap was restricted to *Asparagus* and *Oxalis* which constituted similar proportions of the rodents' diets (<9%) (see Tables 9 & 11). This degree of overlap in summer was more than twice that for any other season. Kincaid & Cameron (1982) reported that in summer the dietary overlap between *Sigmodon hispidus* and two other sympatric rodents they studied increased dramatically. They suggested that the "resource co-utilization" during maximum resource diversity in the habitat was the reason for this increase in overlap. In addition, Camillo & Garofalo (1989) have suggested that increased food availability permits a considerable overlap in food selection among the coexisting animals with out direct interaction and the risk of escalating competition. The suggestions of Kincaid & Cameron (1982) and Camillo & Garofalo (1989) probably explain the increased dietary overlap of *Rhabdomys* and *Otomys* during summer when good rains and warm temperatures (see Figs 1 & 2) ensure better food availability thus allowing a higher degree of dietary overlap.

The higher proportion of *R. pumilio* in the small mammal population in summer was probably an indication of their increased population density. While reproduction had started in spring, no juveniles were trapped and this was probably a sampling artefact. The entire adult population was in breeding condition and this reflected the optimal conditions prevailing in the habitat during summer. The high proportion of gravid females found among *R. pumilio* caught during summer confirmed their intensive reproductive effort and their need for a high quality diet.

5.4 OVERALL VARIATION IN DIET

The frequency occurrence of high quality food materials such as insects, grass and dicot seeds, and fruits showed that they were present in more than 35% of *R. pumilio* stomachs (Table 12a) with insects occurring most frequently. These four items also dominated in terms of abundance in the diet where insects again dominated by constituting 18% of *Rhabdomys*' annual diet (Table 13). Collectively, the four items constituted 41.4% of the annual diet, and if one bears in mind that out of the breeding season (winter), they constituted 18% whereas in the breeding season they exceeded 60%, their importance in reproduction can be inferred.

It was also evident (see Tables 8, 10, 12a & 13) that none of these dietary items were present in sufficiently high proportions so as to confer a total dominance of any single item or group of items in the entire diet of *R. pumilio*. It is clear that *R. pumilio* in the present study selected different food items from time to time depending on their availability in the habitat. Temporal variation in diet composition became more apparent when the prominent dietary categories eaten during various seasons were compared. The major diet category changed from fruit (27.8%) in autumn, to monocots (32.9%) in winter to insects (34.3%) in spring to dicots (35.9%) in summer (Table 8). The selective feeding on a highly nutritious but transient diet according to its availability and its omnivorous habit, confirmed Perrin's (1980a; 1980b; 1980c) assertion that *R. pumilio* is an opportunistic omnivore. The dietary composition of this species in the present study differed markedly from studies on other populations where it is reported to be either granivorous (Davis 1942; Choate 1971; Smithers 1971; Brooks 1974) or herbivorous (Roberts 1951; Hanney 1965; Rosevear 1969; Delany 1975; Kingdon 1975). The diet did, however, resemble that reported for a *R. pumilio* population studied from Fish River Valley Scrub, Eastern Cape by Perrin (1980a; 1980b; 1980c) and one from Zimbabwe (Churchfield 1985).

Captive *R. pumilio* preferred shrubs over herbs (Curtis & Perrin 1979). In contrast, this study found that all the major dicot plants that *R. pumilio* consumed were herbs thereby indicating that captive conditions, with water *ad libitum*, might influence food selection. This would also imply that diets might vary according to the presence or absence of freestanding water. This suggestion warrants further investigation.

The difference between the diets of juvenile and adult *R. pumilio* was interesting. All four categories of food (dicot and monocot seeds, fruit and bark) where the juveniles consumed more than adults are well hydrated (see Table 3). It seems likely that the juveniles must be more vulnerable to water shortages on account of their relatively higher metabolic rate caused by their unfavourable surface area:volume ratio (see Eckert & Randall 1983). Thus they were forced to secure food that contained adequate water while adults could utilize the drier monocots. This in turn would lead to a degree of intraspecific resource partitioning which could improve the survival of the juveniles.

The seasonality of bark feeding as reported in various studies (Davis 1942; Hechter-Schulz 1962; Willan 1984; Perrin 1980a; Taylor 1996; Baxter & Hansson 2001) is not surprising since peak juvenile recruitment was observed in winter for *R. pumilio* (Fig 4a) and this coincided with the increased bark consumption. However the findings made here regarding bark consumption must be viewed with caution due to the small sample size used in his project. Further research involving bigger sample size representing different age categories could provide more comprehensive evidence to support the age related variation in bark consumption in *R. pumilio*. In the present study, bark consumption by *Otomys* was low but did occur in winter. The seasonality of bark feeding as reported in various studies (Davis, 1942; Hechter-Schulz, 1962; Willan, 1984; Perrin 1980a; Taylor, 1996; Baxter & Hansson, 2001) is not surprising since peak juvenile recruitment was observed in winter for *R. pumilio* (Fig 4a) and this coincided with the increased bark consumption. However the findings made here regarding bark consumption must be viewed with caution due to the small sample size used in his project. Further research involving bigger sample size representing different age categories could provide more comprehensive evidence to support the age related variation in bark consumption in *R. pumilio*.

In the case of *O. irroratus*, monocots dominated the diet throughout the year and constituted between 64% and 72% of it. The second most abundant item was dicots, which except for spring when only one animal was trapped constituted 20% to 25.4% of the diet. Transient, high quality food items never constituted more than 8% of the seasonal diet (see Table 10). Thus, the diet taken by *O. irroratus* showed little variation regardless of the seasonal and phenological changes in plants which form their main food source, and they survived on lower quality foods that were available more or less continually. The larger number of plant species present per stomach content and their obvious specialization on plant food indicated that they were capable of exploiting a wide range of plant resources, thereby confirming that they can be regarded as a specialist herbivore (Perrin 1980a; 1980b; 1980c). Other populations of *O. irroratus* are reported to have a similar diet (see Davis 1973; Perrin 1980a; Rowe-Rowe 1986; Kerley 1989; Monadjem 1997) containing only plant material, the majority of which comes from the leaves and stems of various grass species.

Captive *O. irroratus* selected large quantities of grasses and herbs in preference to fruits and seeds (Curtis & Perrin, 1979) and this seemed to be the order in the natural habitat as well (Table 13 & 14). Captive *Otomys* do not utilize freestanding water (Baxter pers. com.) and thus could not have influenced their food selection as seems to be the case in *Rhabdomys*.

Perrin (1980a) reported that *O. irroratus* from a semi-mesic Fish River Valley Scrub habitat fed entirely on green plant material with the exclusion of decaying vegetation, rhizomes, roots and seeds (Perrin, 1980a). In the present study no active exclusion of seeds was detected and especially those of grass were present in the diet during all the four seasons of the year though they formed only a small portion of the diet. The increase in monocot seeds in summer coincided with an increase in the amount of monocot plants eaten and also with the seeding of most grass species. A similar correlation was also evident between the increase in dicot seed and dicot plant material eaten during the autumn season. The rare presence of seeds and other transient dietary resources in the diet content of *O. irroratus* confirmed the view that they are not adapted to exploit temporarily available high quality food materials unlike the coexisting *R. pumilio*.

The major factor that distinguished the diet of *R. pumilio* from that of the *O. irroratus* was the fact that the latter species completely avoided insects. Furthermore, the annual mean percentage of high quality food consumed by *O. irroratus* was 4.7%, nine fold less than *R. pumilio* at 41.4% (see Tables 8 & 10). In contrast, the former specialized on a monocot diet (67.8%) supplemented by dicots (19.2%) giving an annual average of 87% while the latter had (17.4%) monocots and (24.1%) dicots (total=41.5%) in its diet. Where there appeared to be dietary overlap, close examination of the diet indicated selection of different species within a food category. *Sporobolus, Trachyandra* and *Melica* were very important monocots in the diet of *Otomys* while they were of little importance to *Rhabdomys* (see Tables 9 & 11).

The dietary versatility of *R. pumilio* has allowed them to exploit more habitats than the dietary conservative *O. irroratus*. Consequently one finds that the former has a large distribution covering much of southern and eastern Africa while the latter is restricted to the southern African subregion (distributions based on Skinner & Smithers 1990). Where they occur sympatrically, the present study shows emphatically that dietary overlap is minimal thus allowing successful coexistence with minimal competition.

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Appendix 1. Species list of plants found in the study area on the University of Fort Hare Research Farm, Alice, Eastern Cape.

Monocotyledonae

1. Family Poaceae (Gramineae)
Aristida conjesta
Cymbopogon plurinodis
Cynodon dactylon
Digitaria eriantha
Eragrostis chloromelas
Eragrostis curvula
Eustachys mutica
Heteropogon contortus
Hyparrhenia hirta
Karroochloa curva
Melica decumbens
Panicum maximum
Panicum stapfianum
Setaria neglecta
Sporobolus fimbriatus
Themeda triandra

2. Family Juncaceae
Juncus lomatophyllus

3. Family Asphodelaceae (formerly Liliaceae)
Bulbine asfeloidea
Bulbine frutescens
Drimiopsis sp
Trachyandra sp

4. Family Asparagaceae
Asparagus capensis
Asparagus retrofractus

5. Family Hyacinthaceae
Albuca sp

6. Famiily Iridaceae
Tritonia sp

Dicotyledonae

1. Family Loranthaceae
Viscum sp

2. Family Mesembryanthemaceae
Trichodiadema sp
Delosperma sp

3. Family Cruciferae
Raphanus raphanistrum

4. Family Crassulaceae
Crassula lycopodoides

5. Family Fabaceae
(Leguminosae)
Acacia karroo

6. Family Geraniaceae
Pelargonium alchemilloides
Pelargonium sidoides

7. Family Oxalidaceae
Oxalis sp

8. Family Anacardiaceae
Rhus lancea
Rhus longispina
Rhus lucida
Rhus refracta

9. Family Celastraceae
Maytenus polycantha
Maytenus heterophylla

10. Family Rhamnaceae
Ziziphus mucronata

11. Family Tiliaceae
Grewia occidentalis
Grewia robusta

12. Family Malvaceae
Hibiscus atromarginatus
Hibiscus pusillus
Hibiscus sp

13. Family Sterculiaceae
Hermannia sp

14.Family Cactaceae
Opuntia ficus indica

15. Family Primulaceae
Anagallis arrensis

16. Family Loganiaceae
Buddleja saligna

17. Family Ebenaceae
Diospyros lycioides

18. Family Oleaceae
Jasminum sp
Olea europaea

19. Family Salvadoraceae
Azima tetracantha

20. Family Convolvulaceae
Falkia sp

21. Family Boraginaceae
Ehretia rigida

22. Family Verbenaceae
Lippia javanica
Verbena tenera

23. Family Lamiaceae
(=Labiatae)
Teucrium capense

24. Family Solanaceae
Lycium sp
Solanum tomentosum

25. Family Scrophulariaceae
Sutera sp

26. Family Selaginaceae
Selago corymbosa

27. Family Plantaginaceae
Plantago lanceolata

28. Family Cucurbitaceae
Kedrostis africana

29.Family Compositae (=Asteraceae)
Arctotheca sp
Berkheya sp
Brachylaena elliptica
Chrysocoma tenuifolia
(Karroid shrub)
Cineraria sp
Cirsium vulgare
Conyza sp
Felicia sp
Helichrysum aureonitens
Lasiospermum bipinnatum
Pseudognaphalium sp
Senecio pterophorus
Senecio leptophyllus
Senecio lobeta
Sonchus dregeanus
Tagetes minuta

APPENDIX: 2

1. Monocots

Fig. 1a. *Cynodon dactylon* X 500 (A= inter-costal zone: B= prickle hair C= stomata: D= silica body)

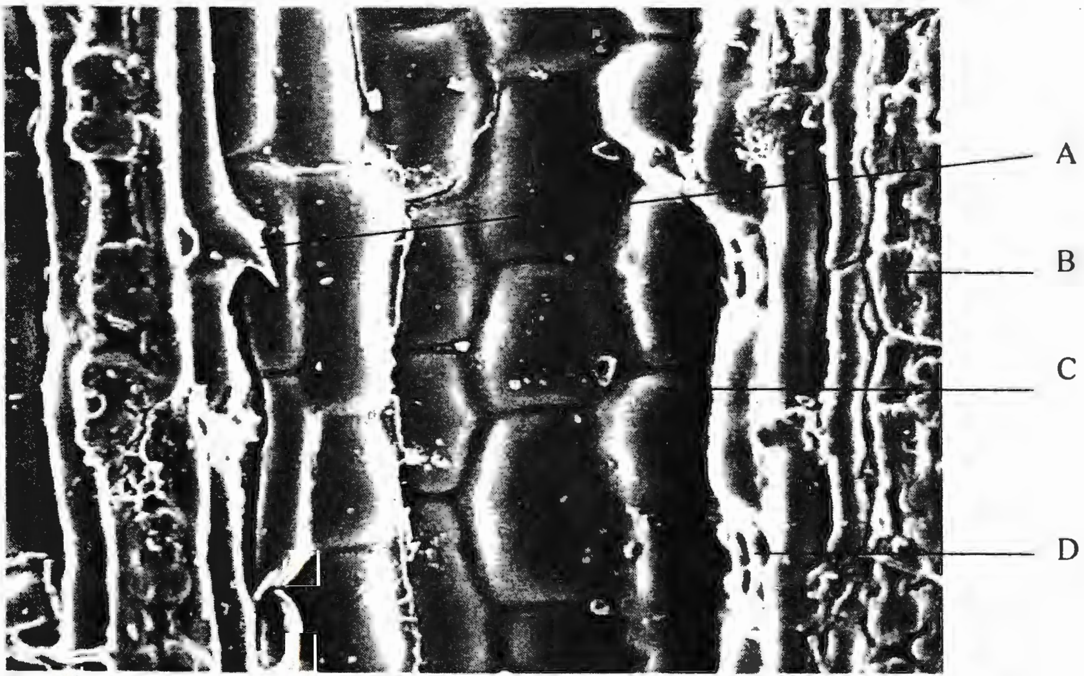

Fig. 1b. *Digitaria eriantha* X2000 (A= prickle hair: B= silica body: C= regular cell: D= stomata)

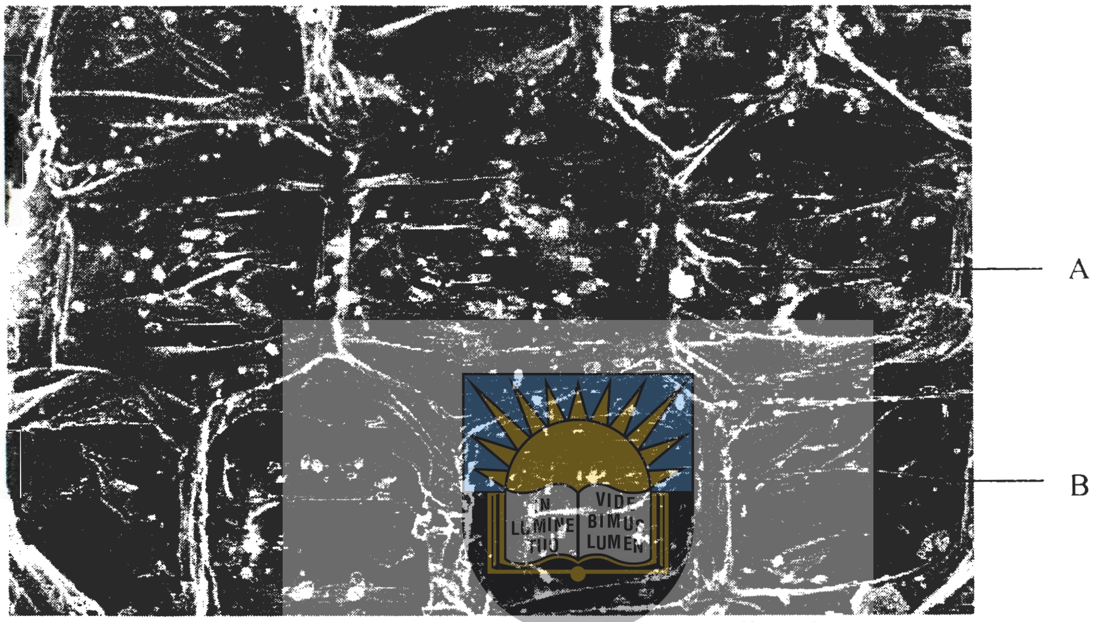

Fig. 1c. *Melica decumbens* X2500 (A= prickle hair: B= cell wall)

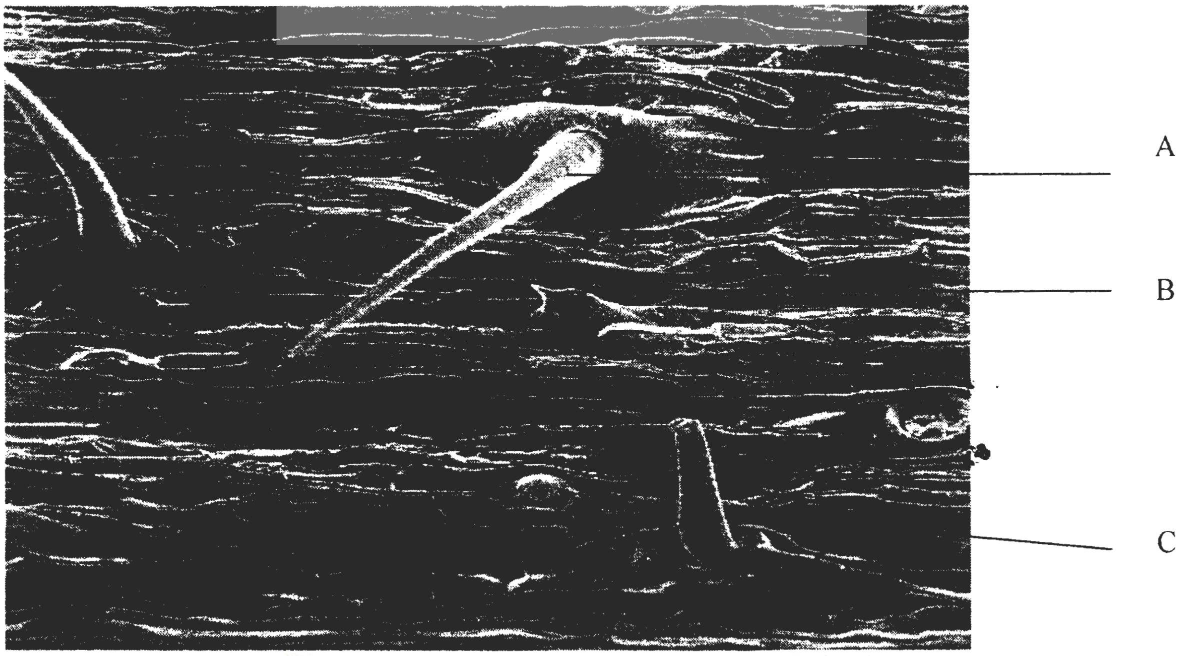

Fig. 1d. *Panicum stapfianum* X500 (A=micro hair: B= prickle hair: C= stomata)

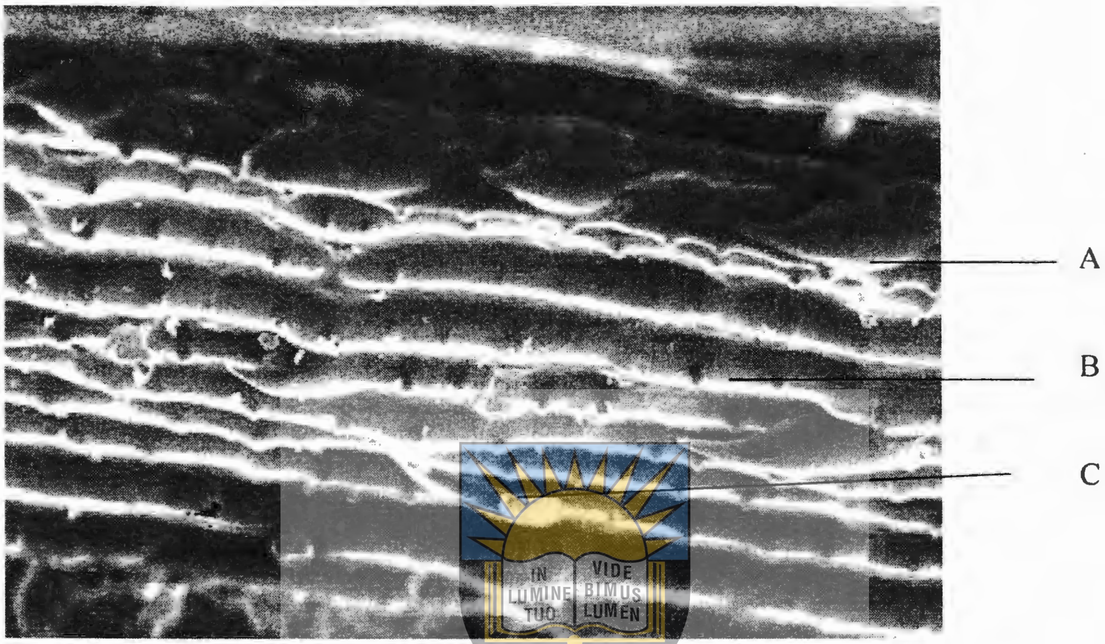

Fig. 1e. *Sporobolus fimbriatus* X350 (A=prickly hair: B= inter-costal zone: C= micro hair)

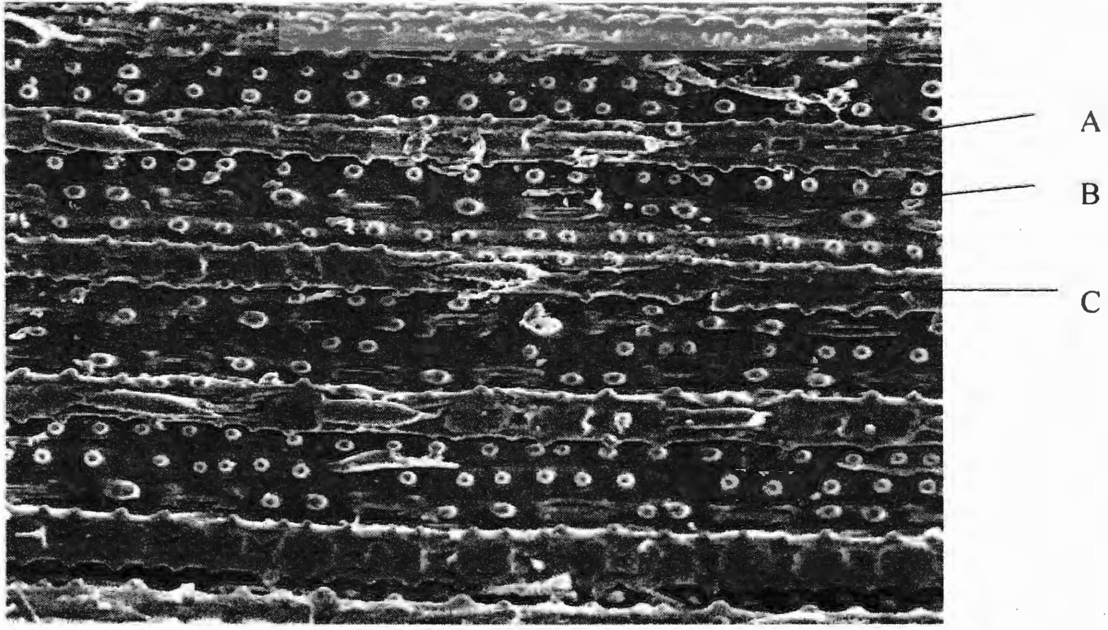

Fig. 1f. *Themeda triandra* X300 (A= silica body: B= stomata: C= short cell)

2. Dicots

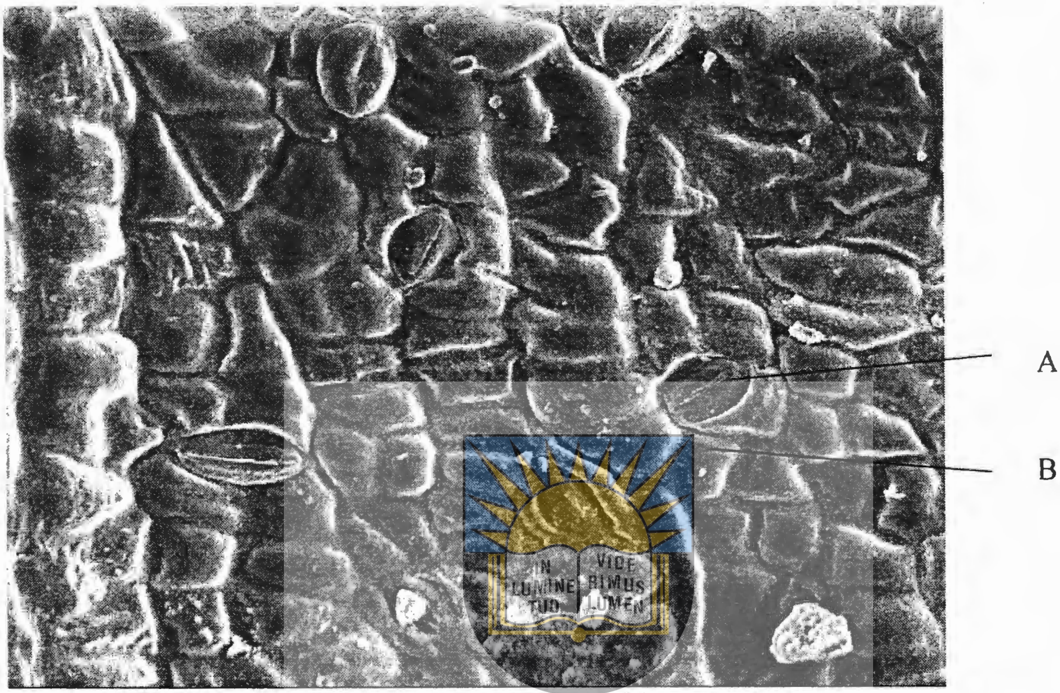

Fig. 2a. *Acacia karroo* X740 (A= stomata: B= epidermal cell)

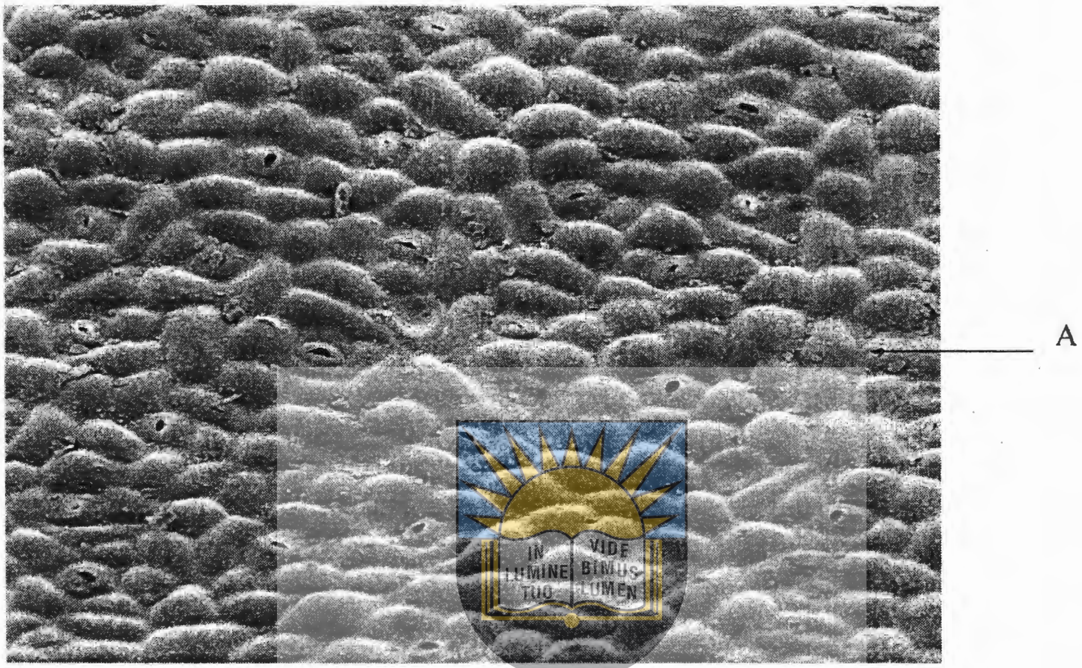

Fig. 2b. *Jasminum sp* X380 (A= stomata)

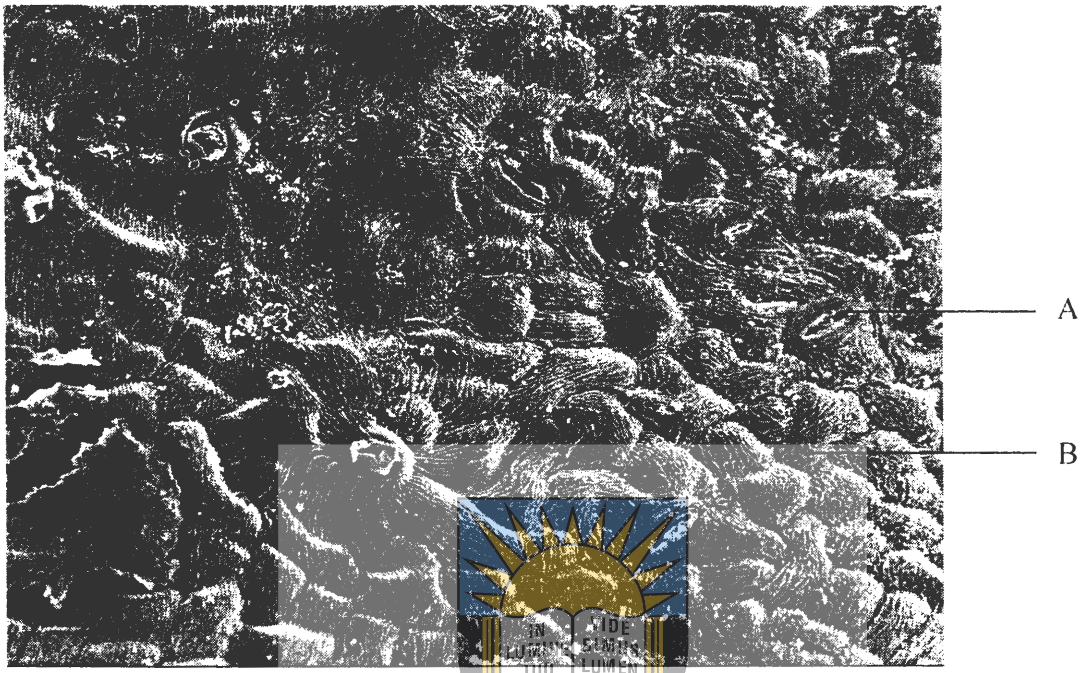

Fig. 2c. *Lycium sp* X450 (A= stomata: B= epidermal cell)

Fig. 2d. *Oxalis sp*X320 (A= parenchyma cell: B= vascular tissue)

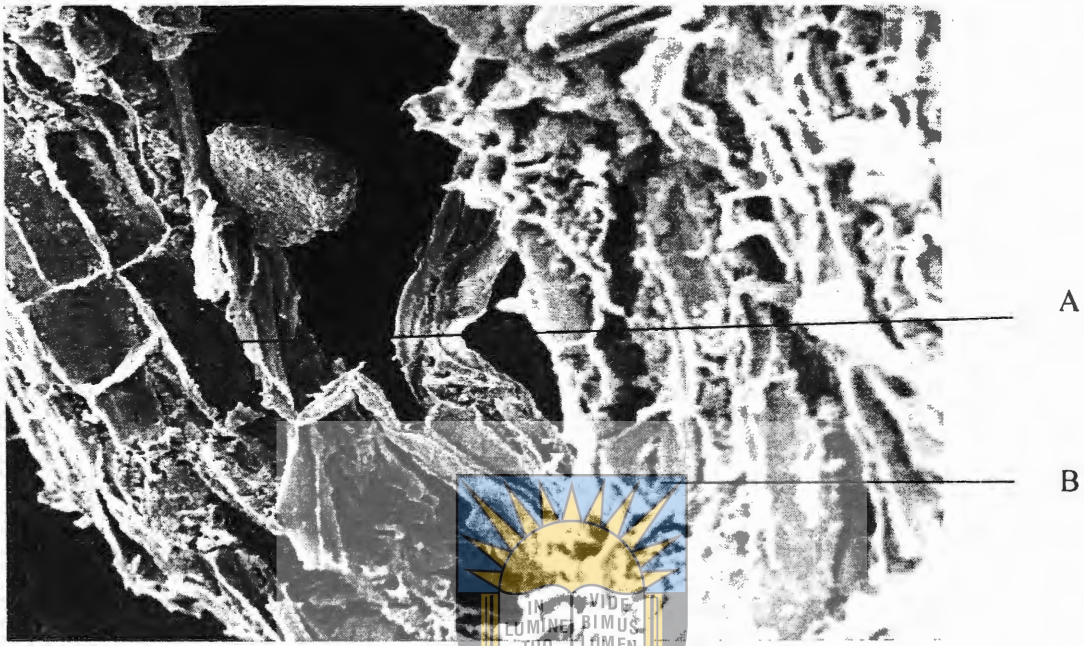

Fig. 2e *Senecio pterophorus* X540 (A= parenchyma cell: B= stomata)

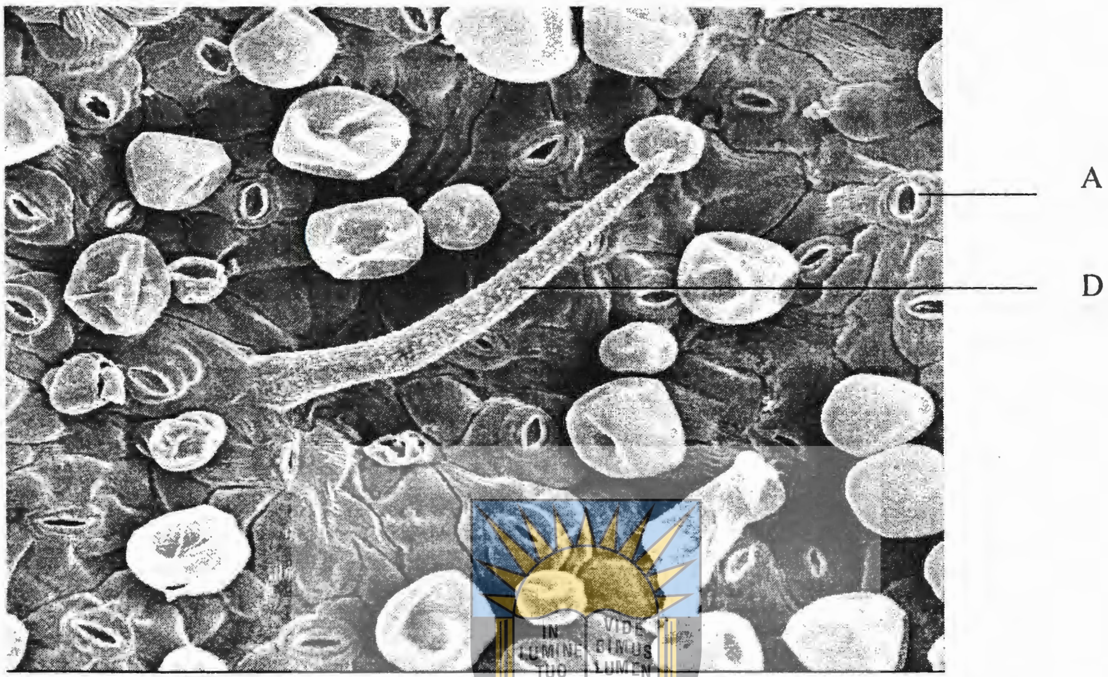

Fig. 2f. *Teucrium capense* X800 (A= stomata: B= trichome)