Demography and population dynamics of the striped fieldmouse, Rhabdomys pumilio, in alien Acacia vegetation on the Cape Flats, Cape Province, South Africa.

by

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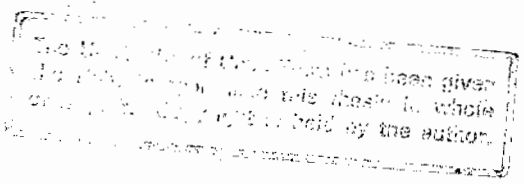
1980



This work is dedicated to my mother,

MURIEL SANDERSON DAVID, Wick, Bristol.

-----oOoOo-----

Parturient montes; nascetur ridiculus mus.

The mountains will be in labour; an absurd little mouse will be brought forth.

HORACE 65 - 8 B.C.

Ars Poetica 139

PLATE 1

An adult male striped fieldmouse, Rhabdomys pumilio.

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I. INTRODUCTION

I.1 Preamble

Rodents are abundant throughout the world in terms of numbers of both species and individuals. In recent years, various species have been subjected to intensive study, mainly in Europe and Africa. The literature on small mammals has expanded at such a rate that it has become a daunting task to attempt to read everything that might be relevant to a study of rodent ecology. Despite this considerable activity, it remains true that "Africa is a continent awaiting intensive ecological study", (Delany, 1972).

Delany demonstrates the comparative richness of the tropical African rodent faunas by comparing the numbers of genera and species of seven tropical African countries whose faunas are reasonably well-known, with those of France, Spain and Portugal combined and California. The mean number of 28 genera and 54 species for the seven African countries (mean area 1,258,374 km^2) compares with 11 genera and 18 species for France, Spain and Portugal, (1,130,575 km^2) and 17 genera and 71 species for California. California is considerably smaller than most of the African countries selected though larger than Uganda which has 33 genera and 58 species (Delany, 1972). Thus, the African faunas have considerably more genera than in either of the temperate regions, and appear particularly rich in comparison with

France, Spain and Portugal. It would appear that the South African rodent fauna matches this diversity as Roberts (1951) lists 28 genera and 46 species of Muridae for the Republic alone (area 1,221,120 km^2 excluding South West Africa). However, Misonne (1971) lists only 23 genera and 41 species.

At the time of writing (1980) scarcely any of these have received more than a superficial investigation, mainly due to the paucity of workers in the field. Those that have been studied are chiefly genera of medical or agricultural importance.

In the present case a fairly large study area (700 ha) was made available, in which preliminary trapping revealed that the striped fieldmouse (Rhabdomys pumilio, Sparrmann 1784), was abundant in areas dominated by alien Acacia spp. It was decided to start a long-term population study of this animal by livetrapping, using the capture-mark-release method; since as far as was known, no detailed long-term field study had been conducted on any South African Murids. Brook's (1974) thesis on the ecology of R.pumilic appeared about half way through the present study. However, as the aims of the present study were rather different and his work was conducted in the Transvaal Highveld, about 1600 km northeast of the present study area, it was felt that there was no serious overlap between the two studies.

It soon became apparent that R.pumilio on the Cape Flats

experienced severe seasonal fluctuations in numbers. Continued trapping then revealed that there were marked inter-annual changes too. Peak numbers in one year could be over three times the peak of the previous year. The question, therefore, arose as to what controlled population size in R.pumilio - what prevented unlimited population growth and what prevented extinction during population declines? An attempt was, therefore, made to investigate the main ecological factors which could have influenced population size in Rhabdomys. These included food supply and predation as possible limiting factors.

The possibility that R.pumilio might be a species exhibiting a periodic cycle in numbers was also investigated in view of the extensive research of Krebs and his co-workers on Microtus spp. (e.g. Krebs (1966), Krebs et al (1969), Krebs et al (1973), Krebs & Myers (1974), Myers & Krebs (1974). This was done by a careful documentation of various demographic parameters such as population size and density, individual growth rates, reproduction, mortality, immigration and emigration rates throughout the study.

I.2 Study area

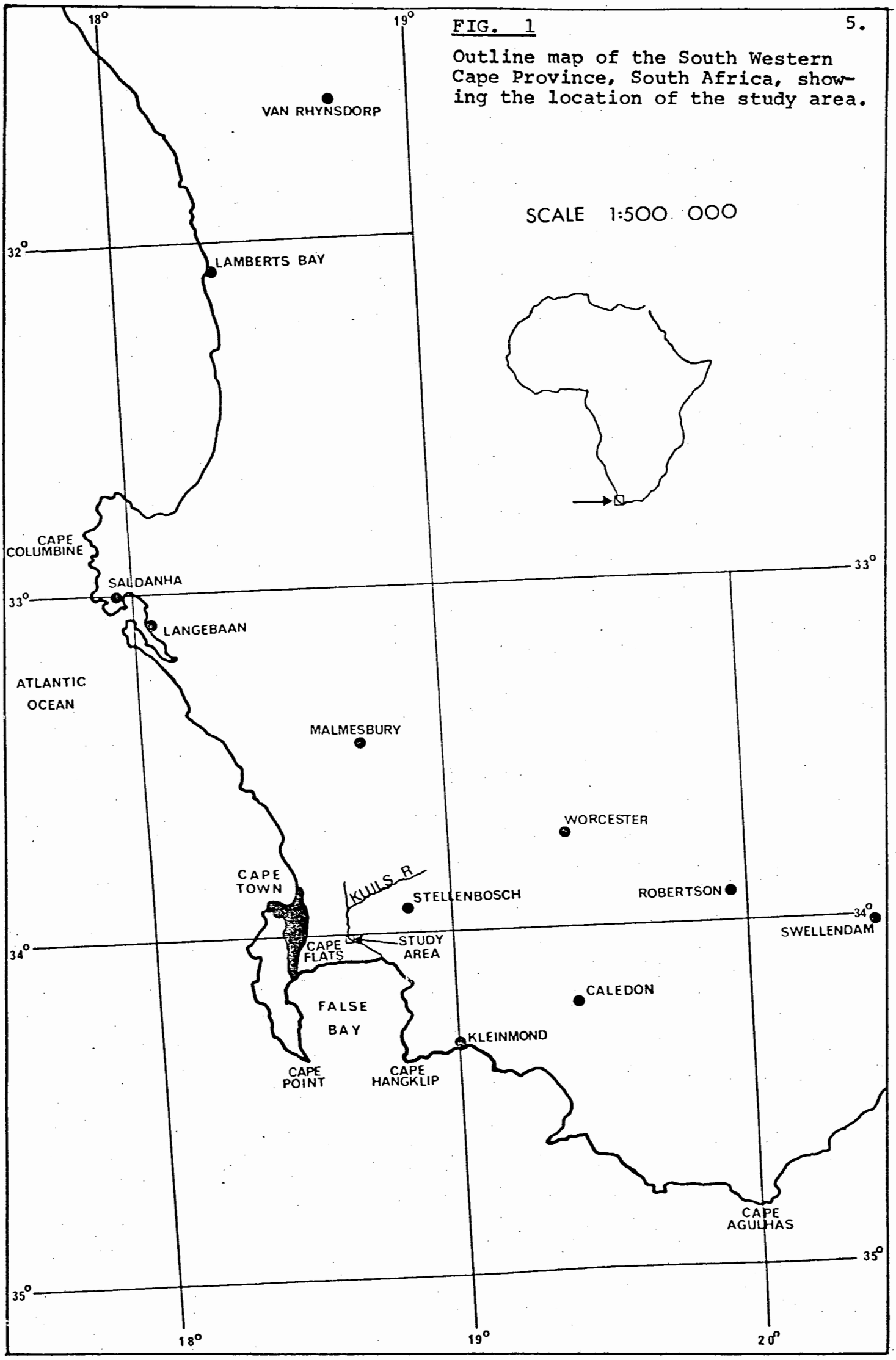
The study area was situated near the West bank of the Kuils River on the Cape Flats, about 24km east of Cape Town, South Africa. The history and vegetation of the area have been discussed by Roux (1961), Roux & Middlemiss (1963) and Taylor (1969). The Cape Flats cover an area of about 400km^2 and form a broad, sandy isthmus connecting the Cape Peninsula to the mainland (Fig. 1). A sea-strait formerly separated the mainland from the present peninsula (Taylor, 1969). Most of the area which now forms the Cape Flats was submerged until a series of coastal elevations combined with recession of the sea, occurred during the late Pleistocene (Walker, 1952). The Flats are composed mainly of sand of recent (Quaternary) origin, which may extend to depths of over 30m and rests on an uneven foundation of Malmesbury rocks and granite. The sand was deposited mainly as beach drifts, which now have a dune topography due to the prevailing south-easterly wind. The whole area is very low-lying, with an average elevation of about 34m (Taylor, 1969).

The soil is fine white sand riddled with mole-rat burrows; chiefly those of the Cape dune mole-rat, Bathyergus suillus, which digs a maze of tunnels at least 30cm below the soil surface (Roberts, 1951), usually about 7 - 9cm in diameter (pers. obs.).

Taylor (1969) recognised three main indigenous inland communities:

FIG. 1

Outline map of the South Western Cape Province, South Africa, showing the location of the study area.



1.) Euclea-Rhus Inland Dune Scrub, occupying chiefly the ridge crests. Typical woody species are Euclea racemosa, Rhus lucida and R.glauca. The Dune Scrub is characteristically dense and 2 - 3m tall.

2.) Metalasia Inland Dune Fynbos. This is typically about 1m tall, and covers most of the undulating country. Its composition is complex and varies strikingly within short distances, with no obvious change in site conditions (Taylor, 1969). The oldest fynbos tended to be dominated by Metalasia muricata and Passerina spp. Two species which are confined to this community and, therefore, regarded as character species, are Psoralea fruticans, a virgate legume and the grass Ehrharta villosa (Pypgras). Another species characteristic of the Dune Fynbos is the woody shrub Rhus mucronata, up to 1m high, occurring in pure spreading stands.

3.) In the low-lying parts, inundated by the Kuils River in winter, there is a Grass-Rush community in which the families Gramineae, Cyperaceae, Restionaceae and Juncaceae show local dominance.

The Cape Flats have been very extensively invaded by alien vegetation, notably Australian wattles. Over large areas the indigenous communities have been obliterated or drastically reduced in size. The two most important aliens are two species of phyllode-bearing Acacias, A.cyclops (Rooikranz) and A. saligna (Port Jackson), which were introduced as sand-binders some time after 1845 (Roux, 1961). The first hard

road built across the flats, connecting the Peninsula with the mainland, quickly became impassable for miles of its length due to wind-blown sand drifts. It became a matter of urgency to fix the shifting sands and by the 1870's an effective method of establishing the wattle seedlings had been developed. Once established, the wattles quickly began to spread naturally, by dispersal of their own seeds, faster than by artificial planting (Roux, 1961).

Both species are fairly robust trees with dense foliage which provides good shade and cover. They tend to cluster in thickets, commonly formed of both species. Acacia saligna attains a height of 5 - 6m compared with 3m or 4m for A.cyclops. The pods of A.saligna are deciduous whereas those of A.cyclops are not. In the latter species, the seeds are held in the pods by a bright red funicle (seed stalk), which is eaten by rodents and birds (Middlemiss, 1963). In A.saligna there is a burst of flowering in August and September, whereas A. cyclops flowers spasmodically throughout the year (Roux & Middlemiss, 1963). The flowers of A.saligna are in dense, bright yellow, clusters whereas those of A.cyclops are pale yellow and rather inconspicuous.

Apart from R.pumilio, other small mammal species found in the study area were as follows: Tatera afra, the Cape gerbil; Gerbillurus paeba, pygmy gerbil; Otomys irroratus, the vlei rat; Mus minutoides, the pygmy mouse; Rattus norvegicus, brown rat; Myosorex varius, common shrew; Bathyergus suillus, Cape dune mole-rat; Genetta genetta, common genet;

Herpestes pulverulentus, Cape grey mongoose; Atilax paludinosus, water or marsh mongoose.

I.3 Climate

The south western Cape Province has a so-called Mediterranean type of climate with dry, warm summers and wet, cool winters. In summer the temperature can rise to over 38°C and in winter may fall to below 0°C. Records of temperature and rainfall for the study period were taken from the weather office at D.F. Malan airport, approximately 4km west of the study area. Normal mean annual rainfall is 575mm, the majority of which (69%) falls in the winter months, May through August. Rainfall for each month of the study (1972-77) is presented in Table 1 and mean monthly rainfall for the study period, together with mean monthly maximum and minimum temperatures, is shown in Fig. 13 (d).

I.4 Description, Distribution and Habits

Rhabdomys pumilio belongs in the family Muridae, subfamily Murinae, and is monospecific. Roberts (1951) describes it as: "the well-known Striped Field Mouse of South Africa, with only one species, but many subspecies. Externally they may be at once recognized by the four black to brown stripes down the back, with three more or less white stripes between them". (Plate I). He describes 19 races for

TABLE 1.

Annual rainfall recorded at D.F. Malan airport, about 4 km W. of the study area.

RAINFALL (mm)

MONTH	NORMAL	1971	1972	1973	1974	1975	1976	1977
Jan.	8,6	9,1	25,2	1,8	8,9	20,2	0,0	14,4
Feb.	15,2	0,9	7,6	3,6	4,6	0,9	4,9	53,2
Mar.	13,8	10,2	17,4	17,0	7,2	10,5	18,0	13,7
Apr.	66,9	18,0	46,1	8,9	4,6	45,9	40,4	78,3
May	93,6	47,4	76,7	39,0	126,4	143,7	48,4	130,6
June	85,3	57,9	68,5	33,1	130,0	51,5	184,6	166,4
Jul.	100,3	60,3	38,5	81,7	82,8	155,5	61,6	108,9
Aug.	79,9	85,8	55,5	46,5	214,8	61,4	74,2	125,4
Sep.	47,4	29,6	34,9	50,4	38,3	9,3	47,3	28,0
Oct.	33,9	23,4	18,4	10,7	40,1	33,9	5,4	11,0
Nov.	21,4	3,4	0,1	5,7	19,2	25,0	56,7	14,4
Dec.	8,8	15,5	35,2	22,4	5,7	1,8	45,9	6,9
TOTAL	575,1	361,5	424,1	320,8	682,6	559,6	587,4	751,2

Southern Africa, but Ellerman et al, (1953) and Misonne (1971) accept only 12 races. Coetzee (1970) has shown that racial differences in tail length, expressed as a percentage of head-and-body length, are pronounced as between populations from relatively arid areas (long-tailed) compared with those from moist or wet regions of Southern Africa (short-tailed). Adults have a mean body mass of about 40g.

The distribution of Rhabdomys has been examined by several authors, including Shortridge (1934), Swynnerton & Hayman (1950), Roberts (1951), Ellerman et al (1953), Davis (1962), Hanney (1965) and Misonne (1971). R.pumilio is evidently a highly adaptable species. It is found widely, though discontinuously, distributed over much of Africa south of the Sahara. It is found over the whole of Southern Africa, including South West Africa, to central Angola and southern Malawi (Misonne, 1971). However, Hanney (1965) also recorded it from the Nyika Plateau in Northern Malawi. It is also found in southern Zaire, Tanzania, western and central Kenya and eastern Uganda, (Misonne, 1971).

Its adaptability is emphasized by the fact that, though Davis (1962) considers Rhabdomys to be primarily a savanna form (though absent from tropical savanna woodlands) it ranges extensively into both the South West Arid (under 500mm rainfall) and the South-West Cape (winter rainfall) biotic zones. In addition, it has a considerable altitudinal range. Hanney (1965) recorded R. pumilio in Malawi only from the high plateaux of Nyika (2132 - 2284m) and Mlanje (1800m).

Swynnerton & Hayman (1950) record it at 2436m in Kenya and on the Shira Plateau at 3685m. Delany (1972) records it up to about 3200m on Mt. Kenya.

Roberts (1951) describes R.pumilio as: "being diurnal, hiding in holes in the ground, frequenting pathways amongst dense vegetation and feeding mainly upon green vegetable matter and sometimes seeds". Rhabdomys is partial to fields and vegetable gardens and is, therefore, moderately well-known. Ellerman et al (1953) describe it as: "one of the commonest mammals of the Union". Shortridge (1934) says that striped mice concentrate in scrub and long grass and may avoid dense continuous forest. "They are to some extent arboreal in Great Namaqualand, and were often observed climbing among bushes and low thorn-threes ...." (Shortridge). He also states that Rhabdomys is normally a burrower and the burrows contain fine grass and other soft nesting material. Smithers (1971, 1975) says that it inhabits grassland, is diurnal and a burrower. According to him, the burrows have a depth of about half a metre and have a chamber excavated, which is lined with soft grass in which they nest.

It was not uncommon to see Rhabdomys climbing among the low branches of Acacia trees on the Cape Flats and one could often find seed pods still attached to the trees, which appeared to have been chewed by rodents. This is also reported by Middlemiss (1963). On the other hand, it is less certain that Rhabdomys is an active burrower in the western Cape. It certainly takes refuge in holes when released from a live-

trap, and one may catch it by setting live or killtraps at the entrance to a burrow. However, it appeared that the majority of these holes in the area were dug by the gerbil, Tatera afra, which shares the habitat with R.pumilio, and is an active burrower. A captive colony kept in an outside cage 10m long by 5m wide for nine months at the University of Cape Town, did not appear to dig any burrows but were quite happy to live on the surface in the boxes provided. However, a second colony introduced into the same cage dug some shallow burrows, while also occupying surface nests (G. Jones, pers. comm.). Hanney (1965) does not mention Rhabdomys using burrows in Malawi. Choate (1971) says that field observations showed that they bred both in underground holes and above ground nests. Choate (1972) says that R.pumilio "usually nests above ground, as indicated by the locations of nine surface grass nests ... and only two each in crevices and burrows". The grass nests were spherical, having a central chamber lined with fine grasses. Brooks (1974) states that they did not use burrows in his study area in the Transvaal. He suggests that local conditions may determine whether burrows are used or not. It would be interesting to know what these conditions might be. It is possible that lack of sufficiently dense cover at ground level may lead to the greater use of burrows. In the present study there was abundant ground cover supplied by grass, shrubs and fallen branches from the Acacia trees. In a study with captive animals, Stiemie & Nel (1973) found that Rhabdomys built well-constructed spherical enclosed nests from cottonwool in a laboratory aquarium. We found a few enclosed surface nests in the field, constructed from grass.

Rhabdomys does not appear to be of significant medical importance. The study of one of the most widespread rodent-

carried diseases, plague, in South Africa has resulted in the identification of the most important rodent vectors - the gerbils, Desmodillus auricularis and Tatera brantsi. According to Davis (1964), Rhabdomys may sometimes act as a secondary reservoir for the disease. It has been identified as a host of various plague-infected species of fleas (De Meillon et al., 1961), which it picks up through contact with gerbils, but is not considered to be an important vector (Davis 1964).

With regard to agriculture and forestry also, Rhabdomys appears to be of relatively minor importance. Davis (1942) reported rodent damage to forestry plantations in Natal and the Eastern Transvaal caused by ring-barking of the trees. Otomys sp. was apparently the main culprit, with Rhabdomys of secondary importance. Hechter-Schulz (1962) reported rodent damage amounting to a million trees a year, in 1950, in plantations in the E. Transvaal. The two main culprits were R.pumilio and Otomys sp. Satisfactory control was apparently achieved by poisoning. Damage to maize and wheat crops in Kenya in 1962 was reported by Taylor (1968), (cited by Delany, 1972). However, Rhabdomys was only one of four rodent species responsible. It appeared that there was a temporary increase in rodent numbers, believed to be due to a 40 - 50% increase in the average rainfall in the previous year. Smithers (1975) states that though Rhabdomys will eat any grain, and will feed on fallen maize seeds after harvesting, they "do not appear to climb the mealie stalks to get at the grain while still attached to the stalk". With regard

to Rhodesia he states: "..... they do not appear ever to become a serious pest".

II. MATERIALS AND METHODS

Information for this study was gained from two primary sources. Firstly, monthly livetrapping for five years on the control grid plus a total of 28 months livetrapping two other grids (Grids K and E). The first time they were caught, all new mice were marked with an individual number by toe-clipping. Secondly, monthly killtrapping, with traps set randomly outside the livetrap area, conducted simultaneously with the livetrapping. Trapping was conducted co-operatively with Prof. J.U.M. Jarvis.

II.1 Livetrapping on the Control Grid and Grids K and E (See Fig. 2).

A control grid 10 stations long (labelled 1 - 10) by five stations wide (labelled A - E) was originally established in April, 1972, when preliminary trapping was conducted (area = 0,36ha). Trap stations were 10m apart, and in the early stages of the study, due to a shortage of traps, one trap per station was used. As more traps were acquired, this was increased to two traps per station. On some occasions, when rodent populations were high, three traps were placed at some stations. Throughout the study an ad hoc policy was followed with regard to the deployment of traps. That is to say, at stations in areas of high rodent density, two or more traps were always set. Stations at which rodents were seldom or never caught had only one trap, and traps might be added to or

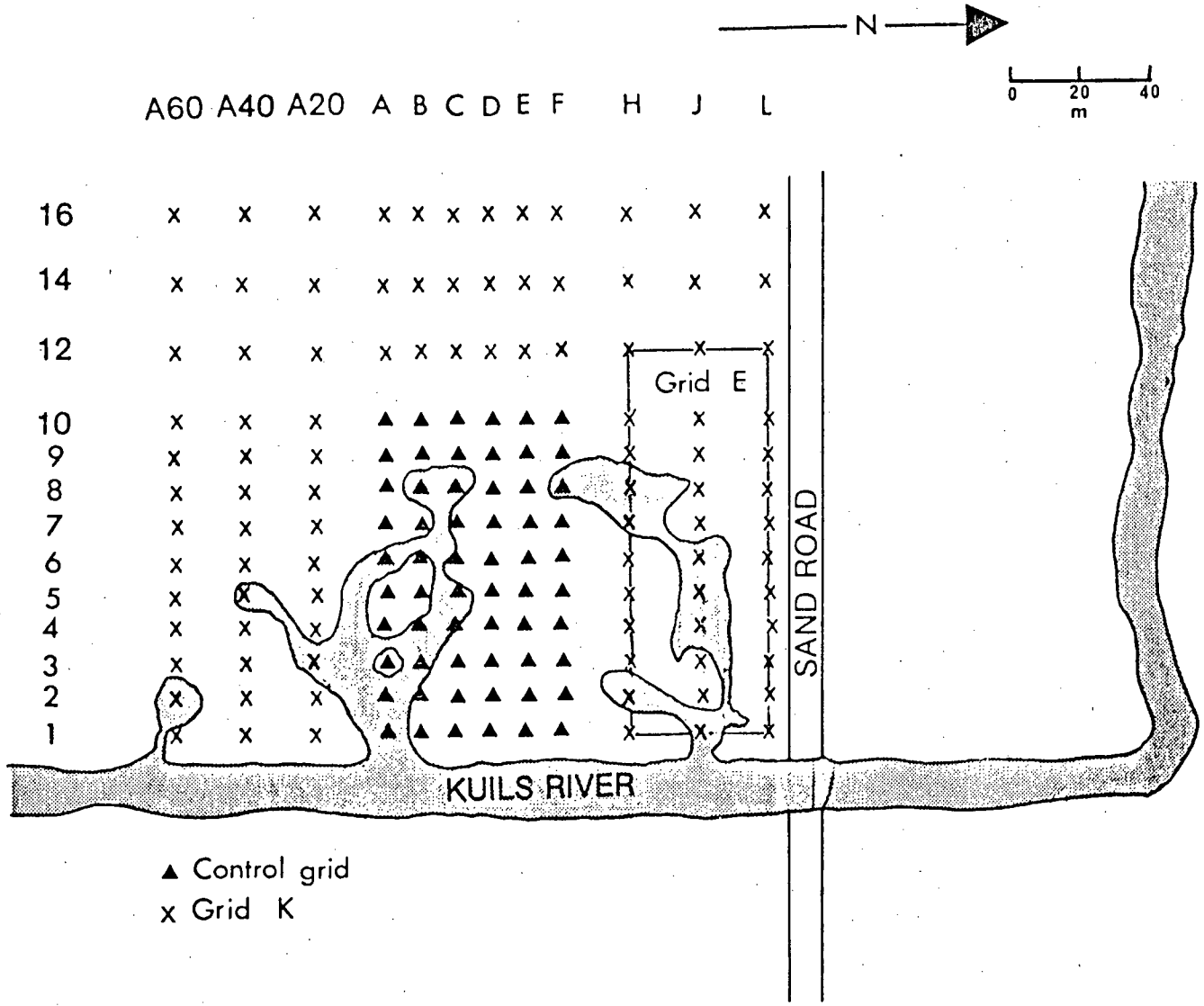


FIG. 2

Plan of the livetrapping grids used in this study. The control grid was trapped from April 1972 through May 1977.

Grid K was trapped from February 1975 through February 1976.

Grid E was an experimental grid in which supplementary food was supplied and was trapped from March 1976 through May 1977. The total area of the grids was 2,55 ha.

removed from stations as rodent numbers dictated. A limited supply both of traps and time made this policy necessary as this project was not conducted on a full-time basis. In general, a maximum of about 100 traps per grid were used in the summer months when rodents were abundant, which fell to a minimum of about 60 traps in the winter. From February 1975, the grid was extended by an extra column of 10 stations (F file), making a total of 60 stations. This increased the area of the control grid to a final area of 0,45ha.

Regular monthly grapping was commenced in July 1972, and continued during the last week of every month up to June 1977, with the exception of months when flooding in the study area rendered trapping impossible. This happened in some winter months when high rainfall caused the Kuils River to overflow its banks. (See Fig. 2 for the extent of flooding). The depth of the water, (if present) was measured at trap station 1A each month, as an indicator of overall flood level.

Traps were set for four consecutive days and nights each month and checked twice daily. The morning check commenced about 0815h and the evening check at about 1700h. The precise time of the latter depended on the season, since in winter it was too dark to work by 1800h. No prebaiting was done. Traps were baited with the mixture suggested by Taber & Cowan (1969), consisting of peanut butter, oatmeal, dried fruit, beef fat and paraffin wax. This was very attractive to Rhabdomys. Food preference experiments were conducted in the field and these showed that bait was preferred both to the naturally occurring Acacia seeds and to commercial rat cubes (Table 2).

TABLE 2

Rhabdomys food preferences in the field : natural and artificial foods. In each trial, food types to be tested were presented in pairs in the field. 10g of each food pair were presented per trial. After an interval of time, the amount of each food eaten was determined by weighing. The Table is a summary of all trials conducted.

	Bait x	versus	Acacia seeds	Rat cubes *	versus	Acacia seeds	Bait	versus	Rat cubes	Rat cubes	versus	Wheat	Rat cubes	versus	Oats
Amount (g) offered	50,0		50,0	50,0		50,0	340		340	320		320	370		370
Amount (g) eaten	50,0		14,2	36,7		34,1	144,6		58,0	95,0		29,4	70,8		126,4
No. Trials	5		5	5		5	34		34	32		32	37		37
% eaten	100		28	73		68	43		17	30		9	19		34

x Bait was composed of oats, peanut butter, dried fruit, beef fat and candle wax.

* Rat Cubes = commercial EPOL rat cubes (20% protein).

Traps used were the large, folding aluminium type made by H.B. Sherman, Florida, U.S.A. (dimensions 7.6 x 8.9 x 22.9cm). They weigh 160g each which is considerably less than Longworth traps (250g. Delany, 1974). The soft aluminium can be chewed by Rhabdomys and by Tatera and some traps were damaged. It was found simplest to repair holes with epoxy putty. Sherman does supply traps made of tin, which are too hard for Rhabdomys to chew. However, these are much heavier to carry and are less satisfactory to use in the field, chiefly due to a less sensitive trigger mechanism. Despite careful setting, tin traps seemed more prone to having the bait taken without catching the animal. One disadvantage of Sherman traps is the fact that there is no nest box. On cold, wet, winter nights some losses from exposure were suffered. Losses could be reduced by putting cotton wool in each trap during the evening check. In summer, great care had to be taken to adequately cover with grass and leaves all traps that were not in the shade. Some deaths from overheating in the traps were experienced. Overall deaths in the traps, from all causes including mice taken from the traps by predators, were about 1,3% in a sample of 7033 captures.

The control grid was established with its long axis running more or less E - W, with its eastern boundary close to the west bank of the Kuils River. In February 1975, trapping was commenced in a second grid, (Grid K), which surrounded the control grid on three sides, having the River as the fourth side. (Fig. 2). This was used in an attempt to detect immigration of mice into and emigration from the central

control grid. Grid K consisted of 96 trap stations arranged in three parallel rows, situated at distances 20m, 40m and 60m from the outer rows of the control grid. The area of grid K, excluding the central control grid, was 1,56ha; including the control grid the whole area was 2,55ha.

Trapping on grid K was conducted on the same plan as in the control grid - namely four consecutive days and nights each month. This normally took place in the middle of each month, about two weeks after the month-end trapping in the control grid, and was continued for 13 months, from February 1975 through February 1976. Due to other commitments it was only possible to trap for two days and nights in grid K in the months August through November 1975. From December 1975 through February 1976, trapping on grid K and the control grid was simultaneous (for 4 days and nights).

A third grid was established in March 1976, in the northern section of the old grid K. This was an experimental grid (grid E), in which supplementary food was supplied. It was the same size as the control grid, but a slightly different shape, being twelve stations long by five stations wide (total 60 stations). This was due to the restriction imposed by the sand road on the northern boundary (Fig. 2). This was considered to present a partial barrier to movements by Rhabdomys into and out of the grid. This in turn was considered to be an advantage in the attempt to detect the movements of marked animals in the experimental area. Trapping in grid E was conducted for four consecutive days and nights

per month, at the same time as the control grid, from March 1976 through May 1977. Uniform spacing of 10m between trap stations was achieved in grid E by placing two extra columns (I and K) of 12 stations per column inbetween the original 20m-spaced lines of grid K (Fig. 2). In all grids trap stations were marked by four foot metal fence droppers, or bamboo poles, tagged with the station identification.

All animals caught in the livetraps were examined for toe-clip identification marks while still in the traps; it was found easiest to see the feet spread against the shiny metal background. They were then shaken into a 5mm diamond mesh plastic bag, where they could be examined and marked. Marking was done by toe-clipping, using the 1-2-4-7 system (J. Nel, pers. comm.), with which a total of 9999 animals can be marked without taking more than two toes from any foot.

The question of marking animals by mutilation is a somewhat vexed one. The disadvantages are that there is always the risk of infection; the animal may be hampered in some way or its behaviour may be permanently changed. However, it is a method which seems to have been used successfully for many years (e.g. Blair, 1941).

In the present study, the most important consideration was ease and speed of marking in the field, when one person had to process a large number of animals. For this reason, toe-clipping offered the best alternative. Although a mouse was occasionally found with a toe missing naturally, it is con-

sidered that extremely few errors were introduced into the records on this account. With regard to behaviour, it is possible that the trauma of being captured and marked may have dissuaded animals from entering the traps again. This is a problem implicit in any mark-recapture programme - how to account for trap-shy animals. It is questionable, however, whether marking alone is responsible for producing trap-shyness. The fright associated with being caught in the trap and being handled for examination may be quite sufficient to do this. Choate (1971) found, in trials with captive Rhabdomys, that the tendency of satiated animals to enter traps, whether baited or unbaited, quickly waned. If animals were starved for 12 hours prior to the test, the tendency to enter baited traps shot up again.

One can only say that, in the present study, animals appeared to suffer little discomfort from the toe-clipping and often did not react at all to the removal of the toe. Bleeding was usually slight and it was not uncommon to find an animal that had been marked in the morning back in the traps the same afternoon. In most cases, the toes were healed within a day or two of marking.

The alternatives to toe-clipping were ear-tagging or leg-banding. Both methods require more equipment, more expense and are more difficult to apply single-handed in the field. There is a real likelihood of ear-tags tearing out, especially as many small individuals (10 - 20g) were marked in the present study. It is possible that ear-tags may make mice more

conspicuous and so possibly render them more prone to predation. However, Brant (1962) and Krebs (1966) used ear-tags successfully on species as small as Microtus californicus (mean body mass 40 - 50g) and Stoddart (1970) used them on the water vole (Arvicola terrestris) - but this animal is several times heavier than R.pumilio. Leg bands have also been used on mice e.g. Chitty (1937), Chitty & Phipps (1966) and have even been developed for species as small as shrews (Linn & Shillito, 1960). However, Rhabdomys is an inveterate chewer, so it is doubtful how long such bands would have lasted. There is also the problem of fitting bands to small juveniles and allowing for growth. Extensive field trials would have been necessary to prove either method, involving much extra time - which was simply not available at the start of this study. One advantage of using tags or bands is the possibility of recovering them from predator scats, e.g. Brant (1962).

After being examined for marks, each animal was weighed to the nearest gram by holding the bag suspended from a spring balance. This was normally done only on the first occasion that an animal was caught in each trapping session. In addition, the sex, the point of capture and the reproductive condition of each animal were recorded. Males were recorded as having descended or undescended testes, and females as having perforate or imperforate vaginas. Pregnancy was recorded for females in the late stages, when it could be detected by eye, as well as the condition of the teats. These were recorded as large, medium, small or none. Attempts

were made to accurately detect lactation by squeezing a drop of milk from the nipples (as reported for example by Brooks, 1974), but this was scarcely ever successful, even in females in which the condition of the nipples showed evidence of recent suckling. Such attempts were then abandoned. The presence of large teats was taken as good evidence that the female had recently given birth. In winter, females seldom had detectable teats. The ability to express milk from the nipples did not appear to be a reliable guide, since it was often found impossible to get milk from dead females which, dissection of the uterus showed, had very recently given birth. All information was recorded on field data sheets and then transferred to a permanent file where the complete history of each animal was kept. The method of storing the data was basically the "Calendar of Captures" method of Petrusewicz and Andrzejewski (1962).

II.2 Killtrapping

Killtrapping was conducted every month, in conjunction with the livetrapping, in order to obtain material for post mortem examination. This is the only way in which accurate and detailed data on reproduction and food habits can be obtained, as well as skulls and skins for age determination. Traps were set randomly, well away from the livetrap grid and often on the east bank of the Kuils River (Fig. 2). In fact, despite precautions, a few marked animals were taken in killtraps, which gave some useful ancillary information on move-

ments. For the first three years of the study, killtrapping was continued until a minimum of five females had been caught each month, or until the end of the four day livetrapping period, whichever should occur first. From October 1975 the sample size was increased to a minimum of ten females per month.

Mass in grams and standard body measurements were taken from all dead animals. Stomachs and carcases were kept and deep frozen. In males, testes were measured and the presence of sperm noted in the vas deferens. This was recorded by eye as absent, present or abundant. One testis, epididymis and the paired seminal vesicles were weighed.

In females, whether perforate or lactating, size of teats, general condition of the uterus (whether small and immature or large and well vascularised, etc.) was noted. The number of grossly visible embryos, uterine scars and corpora lutea in the ovary were recorded. Reproductive tracts were fixed in Bouin's fluid and stored in 70% alcohol.

All skulls were carefully boiled, cleaned, labelled and stored. They were examined and assigned to one of eight age classes on the basis of tooth eruption and wear by Henschel (1977).

II.3 Food availability and supplementary food

Analysis of stomach contents revealed that the major item of

Rhabdomys diet was Acacia seed, (Shelton 1975, King 1976). Accordingly it was decided to monitor the supply of Acacia seeds throughout the year in the study grids. This was done by catching the seeds falling from the trees in black plastic bags attached to 0,5m diam. wire rings (area $0,2m^2$). The bags were mounted on bamboo tripods and placed at random under the closed canopy of Acacia thickets. In January 1976 40 bags were set out in the control grid and in March 1976, 25 bags in the experimental grid. These bags were emptied at the end of each month. All the seeds collected were sorted by species from the rest of the debris, dried at $60^{o}C$ and then weighed. The area covered by the bags was less than 0,4% of the area of the Acacia in the control grid, so food supply to the mice was not being significantly affected.

In addition to monitoring the seeds falling from the trees, the seed available in the leaf litter in the control grid was measured at the end of each month by taking 10 x $0,25m^2$ quadrats of leaf litter at random under areas of closed Acacia canopy. All seeds in the litter were sorted, dried and weighed.

The percentage cover of Acacia in the control and experimental grids was measured using the line-intercept method of Mueller-Dombois & Ellenberg (1974). Two ten metre long line transects, at 90^{o} to each other, were measured from each of the sixty station markers in each grid. The length of projected canopy along each line was recorded, as was the proportion of trees bearing seeds or flowers. Dead trees were ignored.

In order to test the response of the mouse population to an excess of food, and to remove the possibility of food shortage in winter being responsible for the decline in rodent numbers, supplementary food was supplied in the experimental grid. This food took the form of standard EPOL rat cubes (composition: protein 20,0%, fat 2,5%, fibre 6,0%, calcium 1,4%, phosphorus 0,7%). Two 750g glass jars filled with the rat cubes were placed on their sides at each of the 60 trap stations in the experimental grid. Food was first set out at the beginning of April 1976 and replenished weekly until June 1977, when floods in the study area rendered further field work impossible. Approximately 20 kg of food was supplied per week. The palatability of rat cubes was tested against other possible foods before the experiment began (Table 2). Abundant rodent faeces in some bottles made it clear that the mice were eating the food, although it was also being taken by birds, such as laughing doves (Stigmatopelia senegalensis) and turtle doves (Streptopelia capicola).

II.4 Predation by mongoose

Throughout the study a few carnivore livetraps were set in the grids whenever rodent trapping was being conducted. Results over the first three years showed plainly that the Cape grey mongoose was the most abundant mammalian predator in the area. Its scats were frequently found. In addition, water mongooses and genets were occasionally captured. All carnivores captured were sexed, weighed, examined for reproductive condition, marked and released. In the early stages of the study they were marked with ear notches. Later on, when fingerling fish tags were obtained from the National Band and Tag Co., U.S.A., they were ear-tagged. However, this did not prove very satisfactory, as mongoose ears are flimsy and the tags quite often were lost. Another problem was that mongooses proved to be quite trap-shy. It was not difficult to capture and mark a mongoose on the first occasion, but thereafter they tended to avoid the traps and recaptures were sometimes difficult to obtain. Abundant evidence that mongooses were in the area was obtained from traps that had been dug under or even turned right over in the animals' attempts to get at the bait without entering the trap. The traps used were the rabbit size traps made by the Tomahawk Live Trap Co., Wisconsin. These will catch large water mongooses (about 4 kg) as well as the much smaller grey mongooses (up to 1 kg).

A more intensive effort to quantify the amount of grey mongoose predation was begun in July 1976. The scats of this species are relatively easy to find, once one is familiar

with them. They are usually deposited on open sandy ground. It was decided to make a systematic collection of scats over a one year period and to analyse these in order to ascertain the main prey items. Accordingly, from July 1976 through July 1977, a section of the sandy road bordering the north side of the experimental grid (Fig. 2), about 300m long, was patrolled regularly every week and all scats found were collected and stored in plastic bags. These were dried and later analysed for remains such as teeth, bone fragments, insect cuticle, etc. Many of the scats consisted mainly of rodent hair. Hairs were identified by making casts of a sample of hairs from each scat in gelatine on microscope slides. The impression of the cuticular scale pattern of each hair left in the gelatine can then be identified under a compound microscope (Keogh, 1975).

The scat collection was divided into bi-weekly samples (two samples per month); usually 1 - 15th of the month and 16th to the end of the month. Scats were taken singly from each sample and broken up by hand for gross examination. If there was rodent hair present in the scat one slide of 20 hairs was prepared. If no hair was present, another scat was examined and this was continued until a total of ten slides of 20 hairs each had been prepared for each sample (one slide per scat). If microscopic examination of a slide showed that more than one prey species was present, a second slide was prepared from the scat. Preliminary analysis of scats showed that very few teeth or

bones were present. Incisors, which might have been expected to be common and which were useful in prey identification, were rather rare.

In order to check the feeding behaviour of the grey mongoose a nearly full grown male (about 90% of adult weight at capture), was captured near the study area and kept in an outside cage, 10m x 5m, for five weeks. It was fed controlled quantities of dead Rhabdomys, laboratory mice and commercial dog food. It was weighed every week and scats were collected daily. From these data the approximate daily food requirement of the mongoose was calculated.

III. ESTIMATION OF POPULATION SIZE AND GROWTH RATE : RESULTS AND THEORETICAL PROBLEMS

III.1 Introduction

In this study monthly estimates of population size were calculated from the capture-recapture data using the Jolly-Seber method (Jolly, 1965; Seber, 1965). All calculations were performed on the UNIVAC 1100 computer at the University of Cape Town. Jolly-Seber population estimates are a modified and sophisticated form of the Petersen-Lincoln Index (Petersen, 1896; Lincoln, 1930). However, since the validity of capture-recapture estimates of population size is open to considerable question, it was considered preferable to follow the lead of Krebs (1966) and to use numbers derived from direct enumeration for estimates of population density and for most other purposes (see Section III.4). Direct enumeration yielded the parameter 'minimum number of mice alive' or MNA each month, which was the number of mice actually caught plus the parameter Z of Jolly (1965). The parameter Z represents the number of mice marked prior to the i^{th} trapping occasion, which were not captured on the i^{th} occasion but were captured subsequently. These mice are, therefore, assumed to have been present in the population at time i.

The changes in the R.pumilio population throughout the study are discussed below, as well as a discussion of the relia-

bility of the Jolly-Seber estimates and the justification for using direct enumeration as a reliable guide to population size.

III.2 Population estimates of Rhabdomys pumilio on the control grid

The minimum number of mice alive (MNA) each month throughout the study, together with the numbers of new (unmarked) mice and the numbers of juveniles each month are presented in Fig. 3. The numbers of males and females caught are shown separately in Fig. 4. The Jolly-Seber estimates of population size, together with standard errors and probabilities of survival are given in Table 3. Fig. 3 records the fluctuations in the trappable segment of the population only. The young leave the nest when about 14 days old at a weight of about eight grams. They are readily trappable at that age as the youngest mice livetrapped were in the range 6 - 9g and mice of 10 - 14g were often caught during the breeding season. With respect to trappability of the very young, R.pumilio appears to be an easier species to work with than, for example, the voles Microtus pennsylvanicus and M.ochrogaster since in those species the youngest animals caught were 4 - 6 weeks old and weighed about 25g (Krebs et al, 1969). The duration and intensity of breeding can be gauged from the number of new juveniles (< 30g) captured each month (Fig. 3).

FIG. 3

Fluctuations in the minimum number of R.pumilio alive on the control grid (0,45 ha) from 1972 - 1977 (sexes combined). Also shown is the total number of new (unmarked) mice and number of new juveniles (body mass less than 30g at first capture) caught each month. Grid size was increased from 0,36 ha to 0,45 ha in February 1975. Dashed curve represents theoretical population size for a grid of 0,45 ha for 1972 - 1974. Extent of breeding season can be judged from months when juveniles were captured.

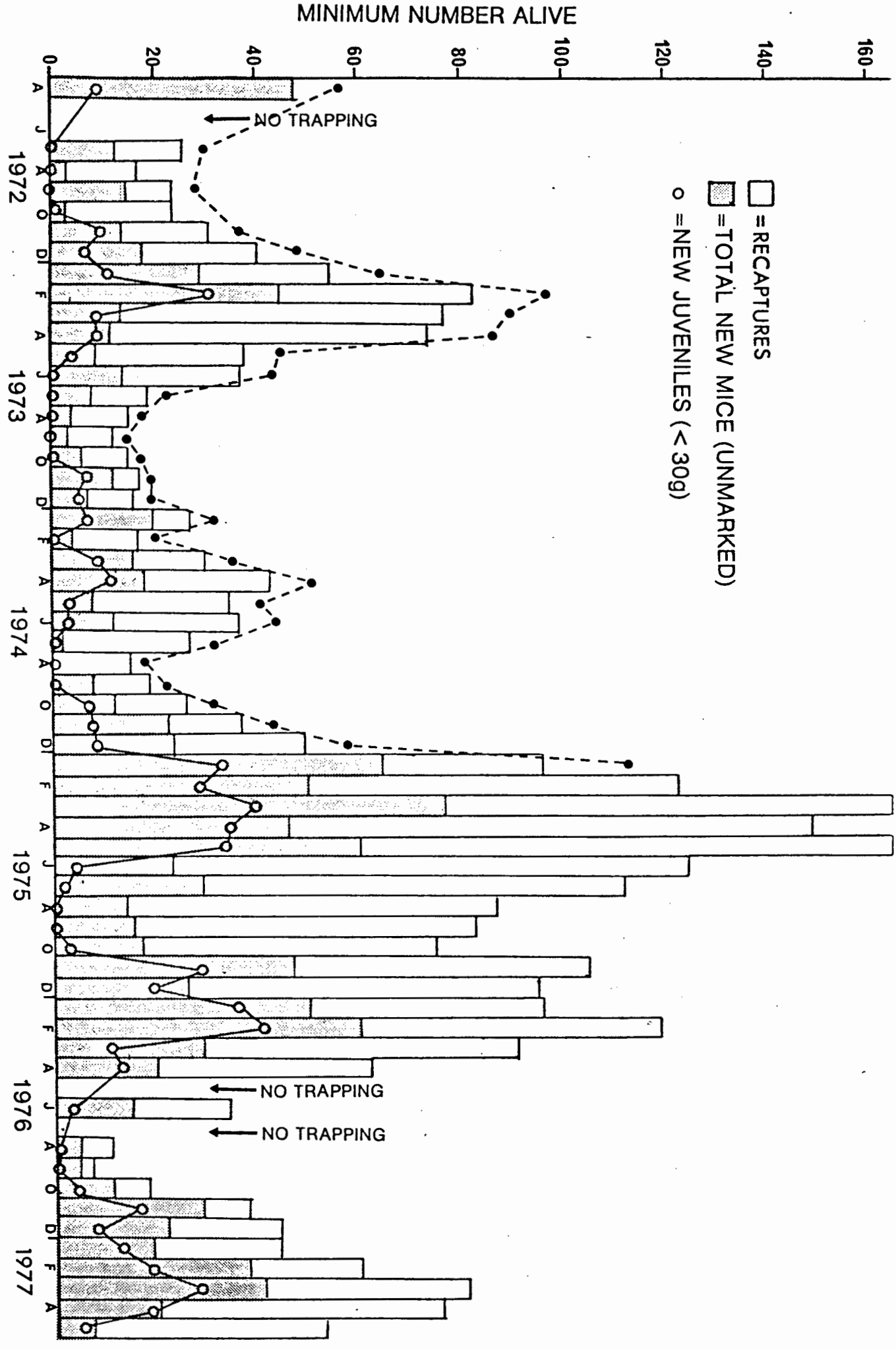

MINIMUM NUMBER ALIVE
0
20
40
60
80
100
120
140
160
NO TRAPPING
NO TRAPPING
NO TRAPPING
1972
1973
1974
1975
1976
1977
A
J
A
O
D
F
A
J
A
O
D
F
A
J
A
O
D
F
A
J
A
O
D
F
A
J
A
O
D
F
A
= RECAPTURES
= TOTAL NEW MICE (UNMARKED)
o = NEW JUVENILES (< 30g)

FIG. 4

Fluctuations in minimum number of R.pumilio alive on the control grid from 1972-1977. Sexes separately. Breeding season is shaded.

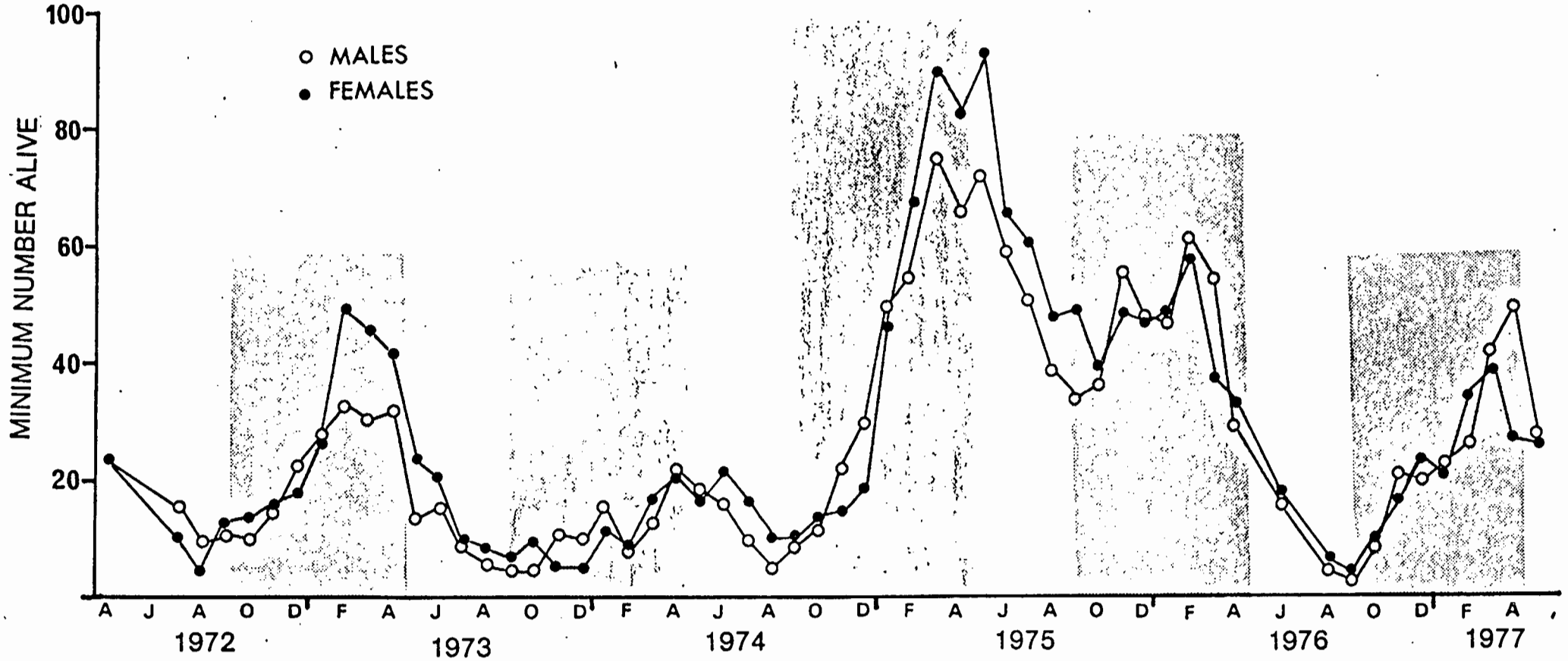


TABLE 3

Jolly-Seber (Jolly, 1965; Seber, 1965) population estimates 1972 - 1977 for R.pumilio on the control grid.

P = probability of surviving until the next trapping session : time i - (i + 1).

The estimates and standard errors were calculated on a UNIVAC 1100 computer.

Date	MNA minimum number alive	Jolly-Seber estimate	S.E. of estimate	P	MNA as % of estimate	Estimated no. births + immig. time i - (i + 1)
1972						
Apr.	48	-	-	-	-	-
Jul.	26	27,0	2,4	,538	96,3	3,0
Aug.	17	17,0	2,9	,529	100,0	15,0
Sep.	24	24,0	2,6	,875	100,0	3,0
Oct.	24	24,0	2,8	,772	100,0	14,0
Nov.	31	31,0	3,0	,780	100,0	20,7
Dec.	41	44,9	4,8	,694	91,3	37,6
1973						
Jan.	55	68,0	8,6	,675	80,9	42,9
Feb.	83	88,8	6,3	,799	93,5	11,9
Mar.	77	80,5	5,9	,855	95,7	12,1
Apr.	74	80,9	7,5	,384	91,4	9,5
May	38	40,6	5,5	,583	93,6	13,3
June	37	37,0	4,2	,337	100,0	9,4
Jul.	19	21,2	4,3	,593	89,6	3,9
Aug.	15	16,5	3,6	,571	90,9	2,6
Sep.	12	12,0	2,6	,750	100,0	6,0
Oct.	15	15,0	2,5	,357	100,0	12,0
Nov.	17	17,0	2,0	,646	100,0	9,0
Dec.	16	19,4	4,8	,495	82,5	25,9
1974						
Jan.	27	35,0	9,6	,521	77,1	3,4
Feb.	17	21,2	4,8	,874	80,2	21,3
Mar.	30	38,9	7,1	,898	77,1	16,7
Apr.	43	51,6	6,7	,713	83,3	10,4
May	35	47,1	8,0	,754	74,3	16,7
June	37	52,3	9,4	,727	70,7	3,9
Jul.	27	34,1	6,7	,525	79,2	0,6
Aug.	15	17,3	4,5	,788	86,7	7,5
Sep.	19	21,1	4,0	,791	90,0	12,5
Oct.	26	28,4	4,4	,585	91,5	24,7
Nov.	37	40,2	4,9	,754	92,0	31,9
Dec.	49	62,2	8,7	,660	78,8	89,1

continued ...

TABLE 3 continued ...

Date	MNA minimum number alive	Jolly-Seber estimate	S.E. of estimate	P	MNA as % of estimate	Estimated no. births + immig. time i-(i + 1)
1975						
Jan.	96	129,4	16,0	,771	74,2	35,0
Feb.	123	134,8	8,2	,763	91,2	86,2
Mar.	165	186,8	11,2	,695	88,3	55,8
Apr.	149	181,5	12,9	,774	82,1	71,7
May	165	209,8	15,7	,685	78,6	13,8
June	125	149,9	12,3	,629	83,4	26,4
Jul.	112	119,4	9,0	,686	93,8	13,1
Aug.	87	90,2	7,7	,862	96,5	15,2
Sep.	83	86,8	7,5	,705	95,6	16,2
Oct.	76	76,7	6,6	,767	99,1	48,0
Nov.	105	106,8	6,6	,731	98,3	30,6
Dec.	95	107,9	9,4	,490	88,0	61,6
1976						
Jan.	96	114,5	10,9	,680	83,8	61,4
Feb.	119	135,1	10,9	,576	88,1	31,3
Mar.	91	109,1	11,2	,543	83,4	23,4
Apr.	62	81,6	13,7	,332	76,0	17,6
Jun.	34	44,7	13,2	,365	76,1	12,1
Aug.	11	28,0	25,3	,111	39,3	9,0
Sep.	7	12,0	7,9	1,000	58,3	6,0
Oct.	18	18,0	1,7	,540	100,0	35,2
Nov.	38	44,9	8,2	,679	84,6	27,1
Dec.	44	56,9	9,1	,561	77,3	16,9
1977						
Jan.	44	48,8	6,0	,586	90,2	45,4
Feb.	60	73,4	9,4	,707	81,7	48,5
Mar.	81	100,4	10,4	,700	80,7	12,3
Apr.	76	81,9	6,9	-	92,8	-
May	53	81,7	-	-	64,9	-

Analysis of the killtrap data showed that pregnant or oestrus females were normally first caught in September (spring) each year (Table 20). Fig. 3 shows that the first young of the year did not appear in the livetraps until the end of November in 1972 and 1973, but in 1974 - 76 the first young appeared at the end of October. Females normally stopped breeding during April and few young appeared in the traps as late as the end of May. In general, the population showed a clear seasonal (annual) cycle which was correlated with summer breeding. Numbers began to increase in October or November (late spring) and usually rose steadily to a peak in either February or March (summer) but in 1974 the peak was as late as April and in 1975 the numbers in May were as high as those in March. There was then a steady decline in numbers during winter after breeding had stopped, with the population reaching its nadir in August or September each year, just before the start of the new breeding season.

Although it is clear from Fig. 3 that the increase in numbers each year was largely due to the influx of new juveniles yet the difference between the total number of new mice and the number of juveniles each month appears to show a substantial immigration of adult mice as well. Table 33 shows the number of new heavy adults (>40g) caught on the control grid each year. These were believed to have immigrated from elsewhere. Thus Table 33 shows that from 21 - 33% of new (unmarked) mice each year were immigrants as opposed to births in situ. See discussion of immigration on p. 196.

Due to the presence of trap-shy mice some of the apparent 'immigrants' may have been mice which had been in the grid but had avoided capture. Nevertheless, if one examines Fig. 3, the rather consistent difference which existed each month between the total new mice and the number of new juveniles caught makes it probable that immigration was occurring throughout the year. This is also born out by the evidence from trapping in grid K: namely, that of 125 new mice marked in the control grid during the winter of 1975, 21% were immigrants which had already been marked in grid K. The apparently continuous movement of mice at all seasons as revealed by this immigration is an interesting facet of their ecology.

Although the timing of the breeding season and hence of the annual cycle of numbers was reasonably constant each year, Fig. 3 shows that there was considerable inter-annual variation in the amplitude of this cycle. These results would be influenced to some degree by the fact that an extra column of 10 stations was added to the grid in February 1975, increasing its area from 0,36ha to 0,45ha. Including a border strip (see Chapter IV) this was an effective increase in area of 17,5%. For comparative purposes, therefore, in Fig. 3 a dotted curve has been added showing the computed number of mice had the grid been 17,5% larger from 1972 - 1974. If one takes the breeding season of 1972 - 73, the first year of the study, as a starting point, the population peak of MNA of 83 mice on the control grid was reached in February, 1973, which coincided with a peak in the number

of new juveniles captured. In the following year (1974) the annual peak was the lowest of the whole study, which was apparently due to failure of the 1973 - 74 breeding season. The peak MNA of 43 animals was only half that of the previous year and was attained unusually late (end of April). As can be seen from Table 4, the total number of juveniles captured that season was little more than half that of 1972 - 73. The 1973 - 74 breeding season was also remarkable for the complete absence of juveniles in February which is normally a month when juveniles are abundant. The following breeding season (1974 - 75), by contrast, was the most successful of the whole study when 201 new juveniles were captured (Table 4) and this led to the highest peak recorded - a MNA of 165 mice in March and May 1975. This was twice the peak recorded in 1975 and nearly four times the peak of 1974. This was followed in February 1976 by the second highest peak of the study resulting from the second most successful breeding season (155 juveniles), about three times that of 1974. Finally, in 1977, the last year of the study, the peak was the same size as that of 1973, although the 1976 - 77 breeding season (114 juveniles) was more successful than that of 1972 - 73 (81 juveniles).

The marked correlation between the success of the breeding season each year (as reflected in the total number of juveniles captured) and the size of the population peak can be seen from two facts. Firstly, that every year the peak population was recorded in the same month that the largest number of juveniles was captured (Fig. 3) and, secondly,

TABLE 4

Index of breeding success.

Total number of new juveniles (< 30g) livetrapped on the control grid each year compared with the minimum number of R.pumilio known to be alive on the control grid during the population peak (from Fig. 3).

MNA = minimum number of R.pumilio alive on the control grid.

* start of breeding season.

Period	Total No. Juveniles livetrapped	Peak MNA	RJ	RP	No. adult ♀♀ in Sept. *
Oct - Jun 1972/73	81	83	1,8	1,9	13
Oct - Jun 1973/74	44	43	1,0	1,0	7
Oct - Jun 1974/75	201	165	4,6	3,8	10
Oct - Jun 1975/76	155	119	3,5	2,8	48
Oct - Jun 1976/77	114	81	2,6	1,9	3

RJ = Ratio of number of juveniles each year to the year of lowest numbers (1973 - 74).

RP = Ratio of population peak each year to the year of lowest peak (1973 - 74).

from the ratio of the total captures of juveniles each year to the size of the peak. Thus, from Table 4 it can be seen that the ratio of total juveniles captured each year in the sequence 1972/73:1973/74:1974/75:1975/76:1976/77 is 1,8:1:4,6:3,5:2,6 compared with the ratio of the population peaks for the same years of 1,9 : 1 : 3,8 : 2,8 : 1,9. There thus appears to be consistent correlation between the total number of juveniles and the size of the population peak.

After breeding stopped in autumn the population declined steadily during the winter and, as already mentioned, reached its lowest point in August or September. With the exception of 1975, the population declined to about the same level each year at this low season irrespective of the size of the preceding peak. Thus the minimum numbers of mice recorded in 1972, 1973, 1974 and 1976 were 17, 12, 15 and 7. The exception was October 1975 when the minimum recorded was 76 mice - yet this unusually large number of mice entering the breeding season did not result in an exceptionally high population peak; the peak reached in February 1976 was only 72% of the peak in March 1975. It is interesting that the breeding season commenced with the minimum number of mice each year and that the future of the population apparently depended on the survival of just a handful of mice. Yet these low numbers did not appear to hinder population growth each spring. The population could not grow at a maximum rate until the offspring of these females were themselves breeding and this explains why population size did not reach a peak until February or March each year.

III.3 Rate of population growth

Table 5 shows the rate of population growth (r) during the increase phase and of decline during the decrease phase as well as the number of times the population multiplied from the minimum in a standard six month period each summer. According to figures presented by Krebs and Myers (1974 p. 281-2) the usual increase for a rodent population during a six month increase phase is between three and six times. The increases in the R.pumilio population on the Cape Flats during the first two years of the study was 4,15 and 3,07 times (Table 5) so although 1974 was a year of generally low numbers yet the summer increase still seems to have been of normal magnitude. The following year the rate of increase doubled and the population increased by more than 8 times in the summer of 1975. That year was somewhat exceptional in that the summer peak was followed by the slowest winter decline of the study so that numbers remained far higher than usual throughout the year. The subsequent increase in the summer of 1976 was the slowest of the study resulting in a subnormal population increase of only 2,35 times by February 1976. In complete contrast to the winter of 1975, this was then followed by a very swift 'crash' decline to very low numbers during the winter of 1976. This in turn was followed by the fastest recovery of the study resulting in a population increase of over eleven times by March 1977.

TABLE 5

Measured rates of population growth (r) in increase and decrease phases of control grid population of R.pumilio. r is measured as an exponential rate of increase per week over the periods indicated.

$$\log_e N_t = \log_e N_o + r\,t$$

PERIOD	INCREASE			DECREASE	
	r	m	Range MNA	Period	r
Sep 1972 - Feb 1973	0,057	4,15	24-83	Feb - Sep 1973	-0,064
Sep 1973 - Apr 1974	0,042	3,07	12-43	Apr - Aug 1974	-0,061
Sep 1974 - Mar 1975	0,083	8,68	19-165	Mar - Oct 1975	-0,0256
Oct 1975 - Feb 1976	0,026	2,35	76-119	Feb - Sep 1976	-0,093
Sep 1976 - Mar 1977	0,094	11,57	7-81		

m = number of times population has multiplied in standard 6-month period

MNA = minimum number alive of R.pumilio on the control grid

III.4 Review of theoretical problems connected with capture-recapture estimates

The validity of the capture-recapture model depends upon certain premises holding true in the population under study as well as on the frequency of trapping occasions and the proportion of the population captured. Amongst the most important of these are the assumptions that marked animals distribute themselves randomly in the population and that there is an equal chance of catching all individuals, both marked and unmarked.

The most commonly recognised factor influencing probability of capture is 'trap-addiction' and 'trap-shyness' of individual mice. In the first case certain individuals have a greater than average probability of capture due to some mice developing a penchant for entering the traps. In the second case some individuals may have a diminished probability of capture due to them avoiding the traps. A second factor is 'heterogeneity' (Carothers, 1979) which implies that the probability of capture varies between individuals but for any one individual is unaffected by the previous capture history.

Caughley (1977) has pointed out that many authors pay lip service to these ideals by acknowledging that their population may not obey them, but that they then go ahead and present their results as though there were no possibility of error! The following considerations are presented in an attempt to avoid this pitfall.

Krebs (1966), during a study of the vole, Microtus californicus, in California, rejected the population estimates based on the capture-recapture method as being biased. This was because two equal catchability tests devised by Leslie et al (1953) to test whether his marked and unmarked voles were occurring in the expected proportions and also whether there was equal catchability within his marked population showed that the observed and expected frequencies of capture were significantly different. He relied instead on simple enumeration of the population as revealed by intensive livetrapping. However, this also involves an unknown margin of error since one can never know what percentage of the population is being captured each month without knowing first the true population size - which is precisely the parameter one is attempting to measure. Theoretically one can approach this problem by first of all conducting a series of mark-recapture samplings in a given area to enable an estimate of population size to be made and then following this up by trapping out the study area completely and so capturing every animal within the area. This then yields a known total population size for comparison with the estimates. Clearly, this method cannot be used in cases where one wishes to monitor a population over a long period of time.

In the present study the method of Leslie et al (1953) was used to test for equi-catchability of marked and unmarked mice. This test can only be applied at a time when there is no dilution of the population occurring through births or immigration. Mortality is assumed to fall equally on the marked and unmarked

segments of the population. Thus, any unmarked animals appearing in the population are assumed to have been there all the time, but to have previously avoided capture. For a full explanation of the method Leslie et al (1953 p.145 Table 4) should be consulted. The distribution of recaptures during the period of no dilution is tabulated according to the month of initial capture and marking. The expected proportions of marked and unmarked animals each month are calculated and compared with the observed values by means of chi-square.

In the case of the Rhabdomys population, the non-breeding winter months May to August were chosen as being the only time such a test could be applied. Only during the winter of 1975 were sufficient recaptures obtained to yield a statistically valid sample. Since the study grid was open to immigration on three sides the supposition of no dilution was suspect. The trapping conducted in grid K (Fig. 2), which surrounded the control grid, from February 1975 to February 1976 enabled this to be tested. As already mentioned, this trapping showed that of 125 new mice marked in the control grid from May to August 1975, 26 (20,8%) were immigrants which had already been marked in grid K. This high proportion of immigrants may invalidate the test but the analysis is, nevertheless, presented in Table 6, which shows the observed and expected numbers of marked and unmarked males and females each month.

The high value of chi-square appears to indicate a very

TABLE 6

Test for equal catchability of marked and unmarked mice on control grid in non-breeding season 1975. Expected numbers in parentheses. Test taken from Leslie et al (1953).

Date of Sample	MALES CAPTURED			FEMALES CAPTURED		
	Marked	Unmarked	Total	Marked	Unmarked	Total
1975 May	35 (27,6)	25 (32,4)	60	47 (41,6)	34 (39,4)	81
June	37 (32,5)	13 (17,5)	50	41 (39,5)	10 (11,5)	51
July	31 (36,4)	18 (12,6)	49	44 (46,5)	11 (8,5)	55
Aug.	30 (36,5)	7 (0,5)	37	36 (41,4)	7 (1,6)	43
CHI-SQUARE	94,23			21,49		
DF	3			3		
P	< 0,001			< 0,001		

significant difference between the observed and expected numbers of animals caught each month and hence that there was not equal catchability between marked and unmarked mice. This result is, however, very difficult to interpret, since Table 6 shows that there is no consistent trend in the relationship of the observed to the expected numbers caught each month. In both sexes the expected numbers of unmarked mice start by being higher than the observed numbers in May and decline progressively until they are considerably less than the observed numbers in August. It is impossible to say, therefore, that there is a consistent under-representation of unmarked mice in the samples, as found by Krebs (1966) for Microtus. Thus, in this case the meaning of the high value of chi-square obtained must remain in doubt. It may be that it indicates a learned trap avoidance on the part of marked mice which enter traps progressively less readily. It is very probable that the 21% of immigrants caught each month and included in the 'unmarked' sample was enough to invalidate the test. If so, this was due to there being no period of 'zero dilution' in the study population and hence it becomes very difficult to test the underlying assumptions of the model. It would appear from the Jolly estimates of the number of new animals joining the population each month (Table 3, births + immigration), that there was in fact no period of zero dilution.

III.5 Assessment of reliability of Jolly-Seber estimates and justification for using MNAs

Thus, it would seem that another way must be found to decide on the reliability of the Jolly-Seber estimates. In Table 3 the Jolly-Seber population estimates and standard errors can be compared with the minimum numbers alive each month. In general, it can be seen that the population estimates are very close to these MNAs. During the time when the highest population densities were recorded between October 1974 and September 1975, the MNAs lay between 74 - 95,6% of the estimates. Another aid to assessing the accuracy of the estimates is the 'trappability' of the mice. This was calculated as the proportion of the MNA which was actually caught in each period and is shown in Table 7. The estimates of trappability are maximum values since the MNAs are minimum values. There is, therefore, an inherent error factor here. The generally high values in Table 7 indicate that R.pumilio is highly trappable (many values over 90%) and also that marked animals alive in the population were being recaptured regularly and, therefore, that reluctance of marked animals to enter traps was not causing errors in the estimates.

Another parameter designed to assist in assessing the accuracy of one's results is the standard error. It can be seen from Table 3 that the standard error of the population estimates is usually small and that the MNA each month falls within the range of the estimate plus or minus two standard

TABLE 7

Trappability of R.pumilio on the control grid 1972 - 1977; trappability measured by the percentage of mice known to be alive which were actually caught in each 3-month period.
MNA = minimum number alive.

PERIOD	MALES		FEMALES	
	MNA	t (%)	MNA	t (%)
Jul - Sep 1972	37	100	31	100
Oct - Dec 1972	48	97.9	48	97.9
Jan - Mar 1973	92	91.3	123	95.1
Apr - Jun 1973	62	98.4	87	95.4
Jul - Sep 1973	20	100	26	92.3
Oct - Dec 1973	26	100	22	95.5
Jan - Mar 1974	37	86.5	37	86.5
Apr - Jun 1974	56	82.1	59	81.4
Jul - Sep 1974	24	75.0	37	78.4
Oct - Dec 1974	64	95.3	48	91.7
Jan - Mar 1975	180	91.1	204	95.1
Apr - Jun 1975	197	82.2	242	85.5
Jul - Sep 1975	124	94.4	158	92.4
Oct - Dec 1975	140	98.6	136	95.6
Jan - Mar 1976	162	94.4	144	93.1
Apr - Jun 1976	45	95.6	51	94.1
Jul - Sep 1976	8	100	10	80.0
Oct - Dec 1976	49	95.9	51	94.1
Jan - Mar 1977	91	92.3	94	92.6

t = trappability

errors, with very few exceptions (e.g. April and May 1975). It thus appears that a high proportion of the total population was being captured each month - certainly more than the sample size of 60% of the population necessary for an accuracy of to within 0,1 of the true population size if dealing with a population of 150 - 200 animals (Robson & Regier, 1965; quoted by Begon, 1979, p.49). It would thus appear that the statistical criteria for accuracy of the Jolly-Seber estimates are being met. Even this conclusion, however, is unfortunately open to question, since Manly (1971) and Roff (1973), quoted by Begon (1979, p.48), questioned the validity of the standard error formulae used in capture-recapture estimates. They found that estimates and standard errors were highly correlated so that underestimates appeared more accurate than they really were and overestimates less so.

It is necessary now to consider what the effects of violations of the biological criteria on which the Jolly-Seber model is based might be. Because of the doubtful interpretation of the Leslie test (above) it seems impossible to say whether unmarked (new) mice were being captured in the expected proportions. Trap-shy mice are bound to be present in any population and constitute an unknown error factor, which would lead to some (unmeasured) bias in the population estimates. The same could apply to 'heterogeneity' of capture (Carothers, 1979). Thus, one falls very much between two stools in these attempts to obtain an accurate population estimate. Capture-recapture censuses contain an unknown element of bias, but equally, so do direct enumeration methods, since one can

never know what proportion of the population remains uncaptured. If marked animals were being recaptured at less than the expected frequency, then this would cause the population to be overestimated but violation of the assumption that all individuals were being caught at random would not affect the estimates of the rates of survival, but would cause total population size to be underestimated (Begon, 1979, p.57). Begon also states that if the assumption that all individuals are equally likely to survive is violated, then the estimates of population size will be largely unaffected and the estimates of survival will reflect the average rates within the population.

Prima facie then, it seems that the Jolly-Seber estimates obtained in the present case were a useful approximation to the true population size. This assumption remains untested, however, and one cannot be sure that any tendencies to overestimate or underestimate the population size will cancel out. Bearing in mind Caughley's (1977) injunction, that having acknowledged the errors in one's model one should not then blithely treat the results as being completely accurate, it would seem preferable to use the known MNA each month for most purposes in this study, as outlined below. Although capture-recapture assumptions are never truly valid, it would be a mistake to assert that, therefore, the models should never be used, as this would often deny us any information at all. There is usually no reliable alternative which makes more realistic assumptions than does capture-recapture (Begon, 1979).

Hilborn et al (1976) have examined the reliability of enumeration for mark and recapture censuses of voles (Microtus spp.) using computer simulation models. They conclude that the two parameters to which enumeration is most sensitive are: (a) a low probability of capture for any individual (below 0,5) and (b) low trappability of unmarked individuals. In general, their models showed that enumeration gave an accurate picture of changes in the population but that it was usually 10 - 20% below the actual population size.

Low trappability of some unmarked individuals ('trap-shyness'- point (b) above) will always remain a problem in any live-trapping study, but low probability of capture (point (a) above) does not seem to apply to R.pumilio, as illustrated by the high trappability shown in Table 7. In the present study, therefore, it is considered legitimate to use the MNA each month as a reliable index to the population size and that changes in this parameter will accurately reflect changes in the population as a whole.

IV. POPULATION DENSITY AND BIOMASS

IV.1 Population density

The figures given below of R.pumilio population density and biomass apply only to the trappable segment of the population. Population density will closely follow the fluctuations in population size (Fig. 3). However, there is some interest in converting these figures to numbers and biomass per ha for comparison with other species. There are a few complications in deciding on the area to be used in the density calculation when working with a fixed grid size. Because mice caught on the borders of the grid may have their home ranges centred outside it, the effective area sampled by the grid will be larger than that of the grid itself. One must, therefore, add a border strip round the perimeter of the grid before calculating the full area sampled. The question then arises as to how wide this border strip should be.

From the analysis of movement (Table 9) it can be seen that for a sample of 101 mice of both sexes involving 557 recaptures the mean distance between successive recaptures was 8,6m. A strip 8,6m wide was accordingly added to the perimeter of the grid on three sides and an arbitrary 5m on the fourth side which was a few metres from the Kuils River and hence did not permit unrestricted immigration. The area sampled by the control grid was, therefore, considered to be 103,6m x 67,2m = 6962m^2, (0,7ha) from February 1975 when grid

size was increased and 5926m^2 (0,6ha) prior to that.

The highest density recorded during this study was in March and May 1975 when in both months the minimum number of mice alive on the control grid was 165 (Fig. 3). The peak density was, therefore, at least 238 mice per ha or 96 per acre (Table 8). The highest Jolly-Seber estimate of 210 mice or 303 per ha was in May 1975 (Table 3). During 1973 and 1976 the peak density attained during the summer months was 141 mice/ha in 1973 and 172 mice/ha in 1976. The figures for minimum density, which occurs in August or September annually, possibly illustrate the exceptional nature of 1975 just as well as those for peak density. These show that the minimum density was remarkably constant for the first three years of the study at 20 - 29 mice per ha (Table 8), but in 1975 was about four times the mean value for the previous three years. The population density, therefore, remained high throughout 1975 in contrast to 1976 which had the second highest peak density, but also crashed to the lowest density of the whole study (10 mice per ha).

Reference to the literature on small mammals shows that the peak densities reported here are very high. Brooks (1974) recorded a maximum density of only 30 Rhabdomys per ha on his 1,82 ha study grid in the Transvaal. However, Brooks added a border 20,1m wide to his grid before calculating the total area sampled. The width of his border was the average distance between successive recaptures of his mice (av. D of Brant, 1962). The relatively larger movement

TABLE 8

Density (no./ha) and biomass (kg./ha) of R.pumilio on the control grid. Annual peak and minimum given for each year of the study.

	1972	1973	1974	1975	1976	1977
*Area sampled (ha)	0,6	0,6	0,6	0,7	0,7	0,7
Peak density (no./ha)	-	141	73	238	172	117
Min. density (no./ha)	29	20	25	110	10	-
Peak biomass (kg/ha)	-	4,68	2,50	9,43	5,71	3,84
Min. biomass (kg/ha)	1,13	0,70	1,07	4,58	0,43	-
Mean body mass (g) ¤1	-	33,2	34,3	39,6	33,2	32,8
Mean body mass (g) ¤2	38,9	35,1	42,9	41,6	43,4	-

N.B.

Densities calculated from minimum numbers of mice known to be alive.

* Area sampled = grid area plus border strip (see text for details) Grid size increased in February 1975.

¤ 1 = mean body mass at peak density

¤ 2 = mean body mass at minimum density.

pattern for his mice was probably partly due to his larger trap spacing of 15m. If a border strip 8,6m wide, as in this study, is added to his grid, instead of the 20,1m strip, then his maximum density is about 40 mice per ha. This is still well below the maximum density recorded even in the lowest year of this study (1974), when it was at least 73 mice per ha (Table 8). It is worth emphasizing here that the figures for Rhabdomys have been calculated from the minimum numbers of mice known to be alive, not on the Jolly-Seber estimates of population size and no account has been taken of juveniles still in the nest. True densities would undoubtedly be higher.

Delany (1972) has reported on the results of research by Dieterlen (1967) and Misonne (1963) in Zaire. The highest density for a single species (Oenomys hypoxanthus) of rodent reported by Dieterlen was 99 animals per ha in elephant grass and grass-bush vegetation and his second highest was 61 Mus minutoides per ha. He recorded the very high average density for 12 spp. of 361 animals per ha. The highest density for a single species recorded by Misonne was 42 Otomys irroratus per ha close to villages. In temperate habitats some very high densities have been recorded for microtine rodents. Batzli (1968) estimated a density peak for Microtus californicus of 617 voles per ha (250 per acre) in June 1963, using the Lincoln index. Pearson (1966) estimated peaks of 308 voles per ha in July 1961 and 494 per ha in summer 1963 for this species and Krebs (1966) esti-

mated a peak in March 1963 of 1149 per ha (465 per acre) for the same species, both using Lincoln index. By direct enumeration Krebs recorded 803/ha (325/acre). For M.pennsylvanicus a peak density (MNA) of about 150 voles per ha in March 1966 and for M.ochrogaster a peak MNA of about 100/ha in June 1966 was recorded by Krebs et al (1969) in Indiana. Chitty (1952) estimated 750 M.agrestis per ha (300 per acre) in Wales in 1937, but during a 12 year study of rodent densities in deciduous woodland in England, Southern (1970) recorded only up to 20 Apodemus sylvaticus and 40 Clethrionomys glareolus per ha.

IV.2 Biomass

The biological significance of these densities is probably best indicated by converting them to biomass figures. The biomass of Rhabdomys was calculated by summing the weights of all mice captured in the month of peak, or minimum, numbers each year. Table 8 shows that the peak biomass attained in this study ranged from 2,5kg/ha in 1974 to 9,4 kg/ha in 1975. Delany (1972) has estimated a combined average biomass of 11,2 - 16,5 kg/ha for 11 - 12 species recorded by Dieterlen (1967) and 3,8 - 7,3 kg/ha for 7 - 9 species recorded by Misonne (1963) in Zaire. Delany (1972, Table 9, p. 24) also reports the estimates of Verschuren (1966) of combined average biomass of small Muridae in primary and secondary environments in Zaire. In most environments his estimates

are in the range of approximately 1,8 - 5 kg/ha, with a maximum estimate for marshy areas in the Garamba Park of 10 kg/ha.

It is, therefore, clear that the peak biomass estimates for Rhabdomys in this study, being minimum values for a single species only, are very high, though not applicable all year round; nor are they applicable to areas of indigenous fynbos vegetation, since the control grid was situated in alien Acacia vegetation, which provided abundant food and cover.

Owing to the paucity of published results of small mammal trapping in fynbos, it is very difficult to find comparable estimates of biomasses of fynbos fauna. Bigalke (1980) reports a mean collective biomass of about 0,5 kg/ha for four rodent species in fynbos. During a brief four day survey of rodents in undegraded fynbos on the Rooiberge (altitude 1500 - 1600m) near Ladismith, Southern Cape, David & Jarvis (unpubl.) found a biomass of about 0,5 - 2,0 kg/ha in two study grids in a community comprising seven species, at what was believed to be a peak season of the year (March, 1978). These figures are, apparently, high for fynbos. The contribution due to Rhabdomys alone was from 51 - 61% of the total, which gives a biomass of about 0,25 - 1,27 kg Rhabdomys per ha. This is a maximum of about half of the peak recorded in the lowest year of the study (1974) on the Cape Flats and shows the relatively very high biomasses recorded in the alien Acacia vegetation.

Another way to illustrate the significance of these small mammal biomasses is to compare them with estimates for large mammals. According to Pienaar (1966) the biomass of ungulates in the Kruger National Park, South Africa, is around 10 kg/ha. Schaller (1972) in his brilliant study of the African lion, calculated that in the woodland areas of the Serengeti Plains, Tanzania (where prey density varies seasonally due to their migratory habits), the prey biomass of large mammals was between 10 - 72 kg/ha at the leanest season. This was normally sufficient to support lion prides all year round. Schaller reported one pride of lions containing about 10 adults which was even able to live in an area for about nine months where the prey biomass was as low as 2,16 - 6,62 kg/ha. The pride was forced to leave the area only when prey biomass dropped to below 1,15 kg/ha. The biomass of mice on the Cape Flats at the leanest season was more than 1,0 kg/ha in 1972, 1974 and 1975 and at the peak was 2,5 - 9,4 kg/ha (Table 8), which thus seems quite significant. It seems surprising, therefore, that relatively little attention has been paid to the role of small mammals in community dynamics in Africa.

One reason for this apparent neglect may be the often highly unstable nature of rodent populations. A peak population may last usually for a few weeks at most and numbers may drop to a low level for months at a time. Thus their importance either as prey items or as consumers of primary production is likely to be quite variable. Another reason probably relates to the difficulties of studying small mammals in the

wild. They are almost impossible to observe in their natural habitat and an adequate study of their ecology is not easy. This tends to reduce their attractiveness as study subjects.

V. MOVEMENT AND HOME RANGE

V.1 Short distance movement

The movement pattern of R.pumilio was analysed from the recapture histories of individual mice. The mean distance moved between successive captures (Av. D. of Brant, 1962) was computed for a sample of males and females in 1975 on both the control grid and grid K. This movement pattern was taken as being an index of the size of the home range. For the majority of mice it was not possible to calculate an actual home range area, because there were too few recaptures of individuals. The results are presented in Table 9, which shows that on both grids the mean distance moved between successive recaptures was less than 10m, (mean for both sexes on the control grid 8,6m and on grid K 9,7m). This is taken to be indicative of a small home range for both sexes. Males moved slightly longer distances than females, but the difference was not statistically significant. The fact that the mean distance moved was slightly greater in grid K compared with the control grid was probably related to the greater trap spacing in grid K, which had trap rows 20m apart (see Fig. 2).

Johnson (1980) studied the home range of R.pumilio using the technique of Randolph (1973). This involves feeding live-trapped mice with marker bait containing individually coloured fibres such as feathers or wool. The animals are then released at their point of capture. The coloured fibres pass

TABLE 9

Analysis of movement. Mean distance (m) between successive recaptures (AV.D. of Brant, 1962) for a sample of livetrapped mice in 1975.

	CONTROL GRID				GRID K			
	No. mice	No. recaptures	Mean distance (m) between successive recaptures	S.D.	No. mice	No. recaptures	Mean distance between successive recaptures	S.D.
Males	59	275	9,3	9,31	74	277	10,4	11,24
Females	42	282	7,9	9,06	81	271	9,1	10,51
Total	101	557	8,6	-	155	548	9,7	-

Males vs. Females: t = 1,798; P < .1 >.05 t = 1,398; NS

through the digestive tract unchanged and can then be identified in the faeces of the individuals which are picked up on dropping boards scattered throughout the home ranges of the mice. The number of dropping boards visited by an individual will give an indication of the extent of the home range. This method has the advantage of not interfering with the animal's movements in any way whilst the range is being recorded.

The largest home range recorded by Johnson (1980) was a mean of about $528m^2$ for a sample of 12 adult males between October and March (range 90 - $1343m^2$); about $464m^2$ for a sample of 16 non-breeding females (range 179 - $792m^2$) and $76m^2$ for a sample of three breeding females (range 29 - $108m^2$). The maximum distances between extreme points of the largest home ranges (home range length, Stickel, 1954) were about 80 - 100m.

A home range of $500m^2$, if circular, would have a radius of about 13m. This is rather more than the average distance between successive recaptures of 8,6m (Table 9), which could be taken as the radius of a home range. This discrepancy is probably due to the restrictions on movement imposed by the spacing of the traps. Nevertheless, it still indicates severe limitations on the extent of normal movements of most mice.

V.2 Long distance movement

Because of the relatively small size of the trapping grids we used, mice can move off these areas quite easily and their fate is usually unknown. Animals which disappear from live-trapping grids are usually assumed to be dead whereas, in fact, some may have moved away to distant locations. Knowledge of long distance movement is important if one is attempting to study dispersal and wishes to know whether individuals may make extensive journeys to areas far from where they started.

The longest movements ever recorded between recaptures, which were therefore assumed to be part of the home range, were about 50 - 70m. This is in reasonable agreement with the findings of Johnson (above) of 80 - 100m. Therefore, movements greater than these may be of some interest. We were able to collect only a very few instances of longer distance movements in this study and these usually occurred when marked mice were accidentally killtrapped at various distances from where they were marked. There are seven records of these longer distance movements and the mice concerned were six adult males and one adult female. The female had moved 150m and the males distances of at least 300m, 270m, 120m, 122m, 154m and 162m. In the last two instances, the two males had crossed the Kuils River - a slow flowing stream about 10m wide. These few records constitute preliminary evidence that dispersal outside the normal home range can take place. Dispersal is discussed in Chapter XI.

VI. AGE DETERMINATION

One of the most vital requirements basic to work on population dynamics is a reliable method of ageing the animals. A variety of methods have been used on mammals with varying degrees of success, as reviewed by Morris (1972) and Spinage (1973). Animals such as small rodents pose special problems in that they generally have a very short life span. This means that several life stages are compressed into a brief period of time. It may, therefore, be important to be able to distinguish animals in different age classes which are separated in time by only a few weeks. Tooth eruption and wear is the most commonly used method on post mortem material. In the field, it is usually impossible to distinguish age classes in live animals. The most important distinction is usually that between breeding or sexually mature animals and non-breeding or sexually immature animals. For this purpose, body mass is the most often used criterion (e.g. Chitty, 1952; Smyth, 1966). Head-and-body length (hereafter called body length) may also be used (e.g. Brant, 1962), but this parameter is more difficult to measure in the field than body mass and was not recorded from live animals in this study, since speed was usually of the essence when handling a large catch.

Known-age mice were collected from the control grid and grid K during the course of livetrapping, using mice which were originally marked as juveniles identified from their

low weight (from 8 to 25g in most cases), and were then recaptured for a known number of months. In addition to these known-age juveniles there were some mice in the old age categories which were first captured as adults and whose precise age was not, therefore, known. However, these were then recaptured for a sufficiently long period (until old age) that they became invaluable for establishing the old age classes (7 & 8). A reasonable estimate of their age at first capture could usually be made and hence a minimum age could be arrived at.

Using this material, tooth eruption and wear in a sample of 53 known-age specimens of R.pumilio of both sexes, with an age range from 3 weeks to about 71 weeks, was studied by Henschel (1977).

On the basis of a subjective analysis of molar wear, Henschel (1977) was able to recognise eight age classes. He assigned all the skulls of mice collected during this study to one of these age classes. A body mass scatter graph of the known-age sample is shown in Fig. 5 and body length, mass and age range in Table 10. As body mass was the most useful criterion in the field, an attempt was made to relate age to body mass. Fig. 5 clearly shows the great range in body masses in each age class older than class 2. An attempt was made to fit regressions connecting the points in each age class. However, beyond class 3 the goodness of fit (r^2) was so poor that this was abandoned as being too inaccurate. It is evident from the mass scatter in Fig. 5 that any attempt

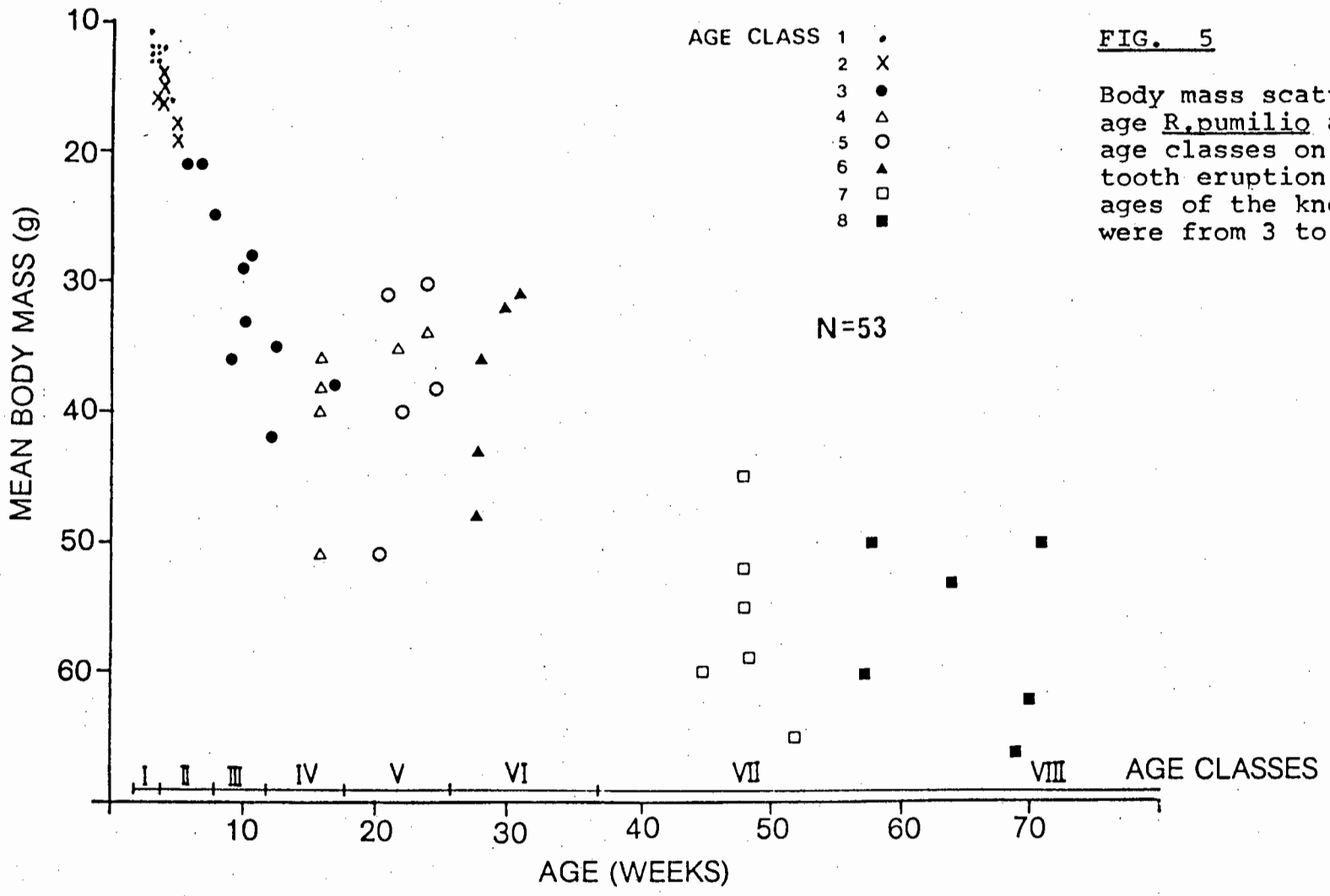


FIG. 5

Body mass scatter of 53 known-age R.pumilio assigned to 8 age classes on the basis of tooth eruption and wear. The ages of the known-age mice were from 3 to 71 weeks.

TABLE 10

Known-age mice : age range (weeks), body mass, length and age class; N = 53.
(from Henschel, 1977).
See also Fig. 5

	AGE CLASSES							
	1	2	3	4	5	6	7	8
No. of mice	9	6	10	6	5	5	6	6
Age range (weeks) of known age mice	3-4	4-5	6-12½	16-24	21-24½	28-31	45-52	55-71
Age range (weeks) of age class	2-4	4-6	6-12	13-18	19-26	27-37	38-54	≥ 55
Body mass range (g)	6-16	14-25	20-45	> 35	> 35	> 35	> 50	> 50
Head-body length range (mm)	60-70	70-95	90-115	105-120	> 110	> 110	> 120	>120

to age a mouse weighing over 30g from its mass alone would introduce a quite unacceptable margin of error. This point is further brought out by a look at the body masses of kill-trapped males in different age classes (Fig. 6). It is evident from the large standard deviations and resultant overlap in body masses of all age classes above class 2 that any attempt to age a mouse of over 30g solely from its body mass would be highly unreliable.

Brooks (1974) analysed the tooth wear of a sample of 36 known-age wild R.pumilio in the Transvaal, using the 6 tooth wear classes developed by Davis (1959) for Mastomys (Praomys) natalensis. His sample showed a poor correlation of tooth wear with age beyond 3 - 4 months. This further emphasises the very considerable problems with accurate age determination in the field.

Perrin (1979) identified 12 equal age classes in R.pumilio in the Eastern Cape based on eye lens mass and molar tooth wear. Each age class spanned exactly one month, since he assumed that the maximum ecological longevity (i.e. lifespan in the field) was 12 months, based on the work of Brooks (1974). However, he had no known-age animals.

Ecological longevity in this study was investigated by analysing the livetrapping records of all mice captured in the control grid. An approximate minimum age at first capture was calculated from the body mass of those mice with the longest recapture histories. By adding the age at first

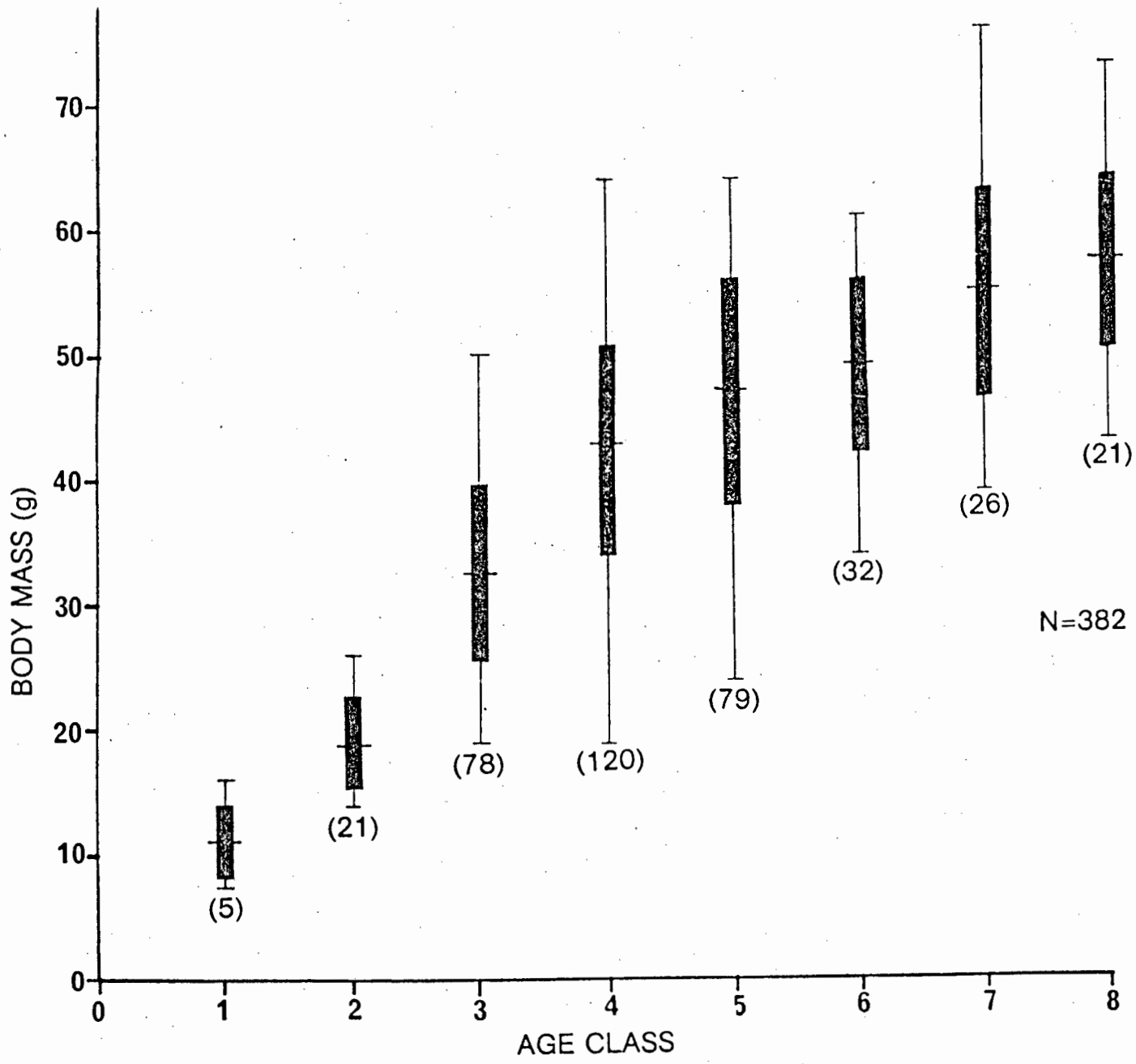


FIG. 6

Mean body mass and age class of 382 male R.pumilio killtrapped from 1972 - 1977. Also shown is the range and one standard deviation for each age class.

See TABLE 10 for chronological ages.

capture to the number of months for which they were caught, a minimum lifespan could be calculated. The results showed that there were 16 mice (15 of them female) which lived for 12 months or more (1,3% of the 1230 mice marked in the control grid up to March 1977). Twelve of these lived for over 12 months and the longest lifespans recorded were 19 months for 2 females and over 16 months for one male. The fate of these animals was unknown. These results should not be confused with the table of residency in the control grid (Table 26) where no allowance has been made for the ages of the mice at first capture.

Thus, though the percentage of mice surviving to 12 months of age is small, it is probably unwise to assume that the maximum ecological longevity is 12 months. In captivity R.pumilio can live for over two years (Choate, 1971; Brooks 1974). It also appears to be an arbitrary decision by Perrin (1979) that each age class should span exactly one month in time and this is unlikely to lead to accurate chronological ageing in practice. Biological material is far too variable to permit such neat pigeon-holing.

Caughley (1967, 1977) has pointed out that estimates of population parameters made from the age distribution of a population depend on the accurate determination of the age of the specimens. The character used for the determination must have a negligible variance at any age. Caughley points out that variance is often ignored on the assumption that errors in age determination are compensatory, but that this is

incorrect. Even when the percentage error is the same for all age intervals, the distribution of frequencies by age will be distorted. Caughley (1967) states that unless the ageing character has a quantal change with age (e.g. annual growth layers in teeth and bones), errors in ageing are inevitable. Ageing by growth measurements or tooth eruption and wear can lead to gross misinterpretation of the mortality pattern of the population if the age frequencies are used to construct a life table. "Where errors are suspected, only those statistics based on a minimum of ageing can be used with confidence", (Caughley, 1967).

In the present study the only readily available field criterion for ageing the mice was body mass. Due to great variations in growth rates, errors in age determination by this method were inevitable. It was, therefore, deemed best to divide livetrapped animals into only two categories, namely juveniles and adults. A body mass of 30g was chosen to demarcate the two groups. The reasons for this were that it approximated the mean body mass at which females became sexually mature (see Chapter VII), and mean growth rate up to this mass was fairly uniform and rapid (Fig. 9). Although males were in fact not sexually mature at 30g the difficulty in choosing a higher body mass lay in the slower growth rate and hence greater error in age determination above a mass of 30g (see Fig. 9). The best compromise seemed to be to consider animals of either sex under 30g to be juveniles.

VII. GROWTH AND BODY MASS

VII.1 Field growth curves for juveniles for each month of the breeding season

Mean monthly growth curves for juvenile Rhabdomys on the Cape Flats for each of the summer months, October through April, are presented in Figs. 7 & 8. The growth curves were prepared by pooling the information from mice first captured up to about one month old (< 20g) in each month October to April during the study period 1972 - 77 and which were subsequently recaptured in succeeding months. The figure at each point on the graphs is the sample size. The ranges and standard deviations of all samples are given in Table 11.

Statistical analysis of the initial monthly growth rates (i.e. between first capture and one month later), showed that the rates for each month were rather similar, with the exception of March and April when growth tailed off appreciably (i.e. at the end of the breeding season). Comparison of February with March growth rates by means of Student's 't' (Table 12) showed that in both sexes the growth for March was significantly less ($p < 0.01$) than in February. April growth was similar to March. In the case of females February growth was just significantly less than January ($p < 0.05$). Since trapping was always carried out during the last week of the month, 'February growth' means from the end of February to the end of March - hence growth which really occurs during March.

FIG. 7

Mean monthly growth curves of juvenile females first captured at a body mass of under 20g during the breeding season, October to April. Growth rates were computed from the body masses of marked mice recaptured at monthly intervals.

Numbers next to each point are sample sizes - ranges and standard deviations of all samples given in TABLE 11.

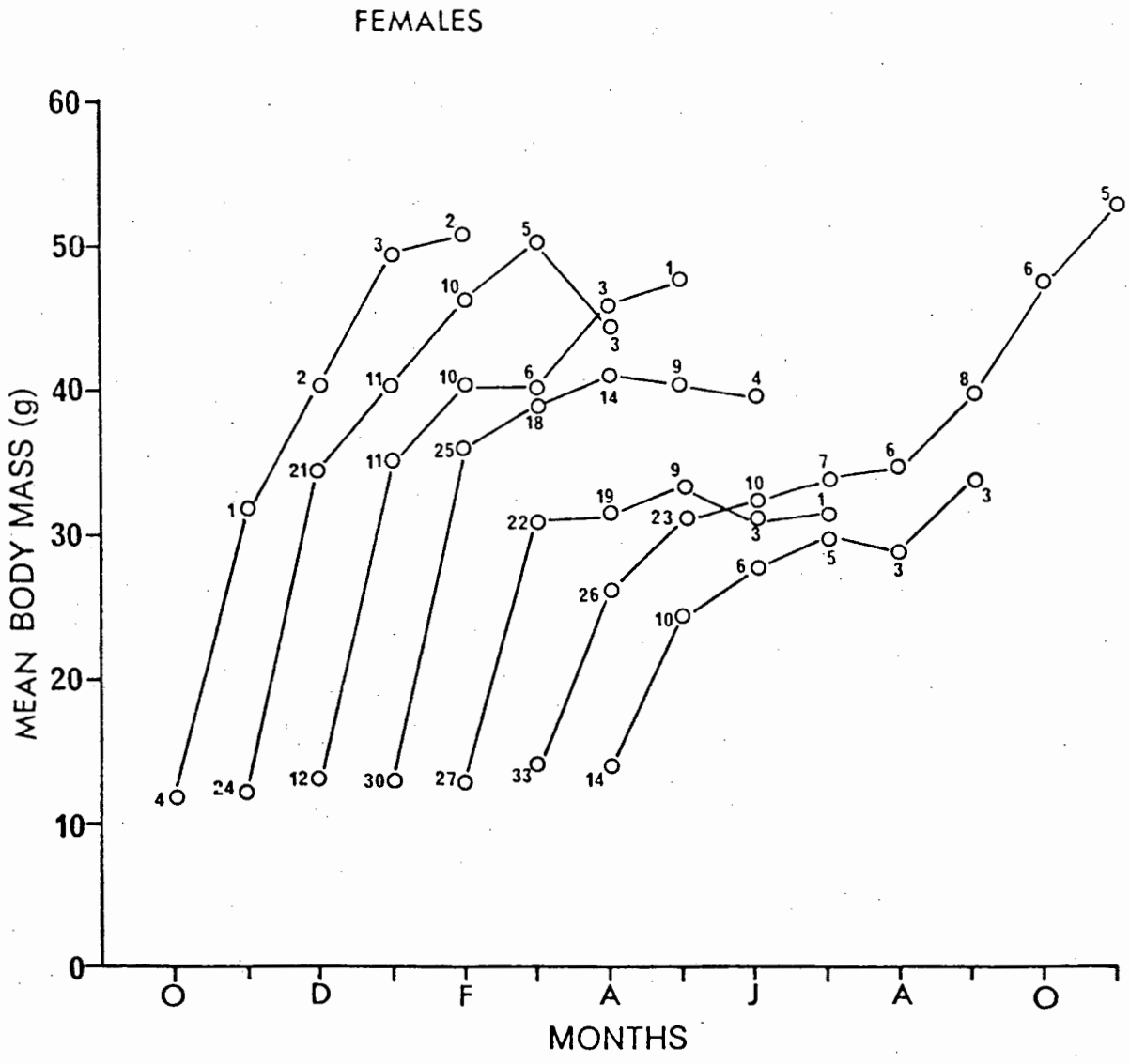


FIG. 8

Mean monthly growth curves of juvenile males first captured at a body mass of under 20g, during the breeding season October to April.
Growth rates were computed from the body masses of marked mice recaptured at monthly intervals.
Numbers next to each point are sample sizes - ranges and standard deviations of all samples given in TABLE 11.

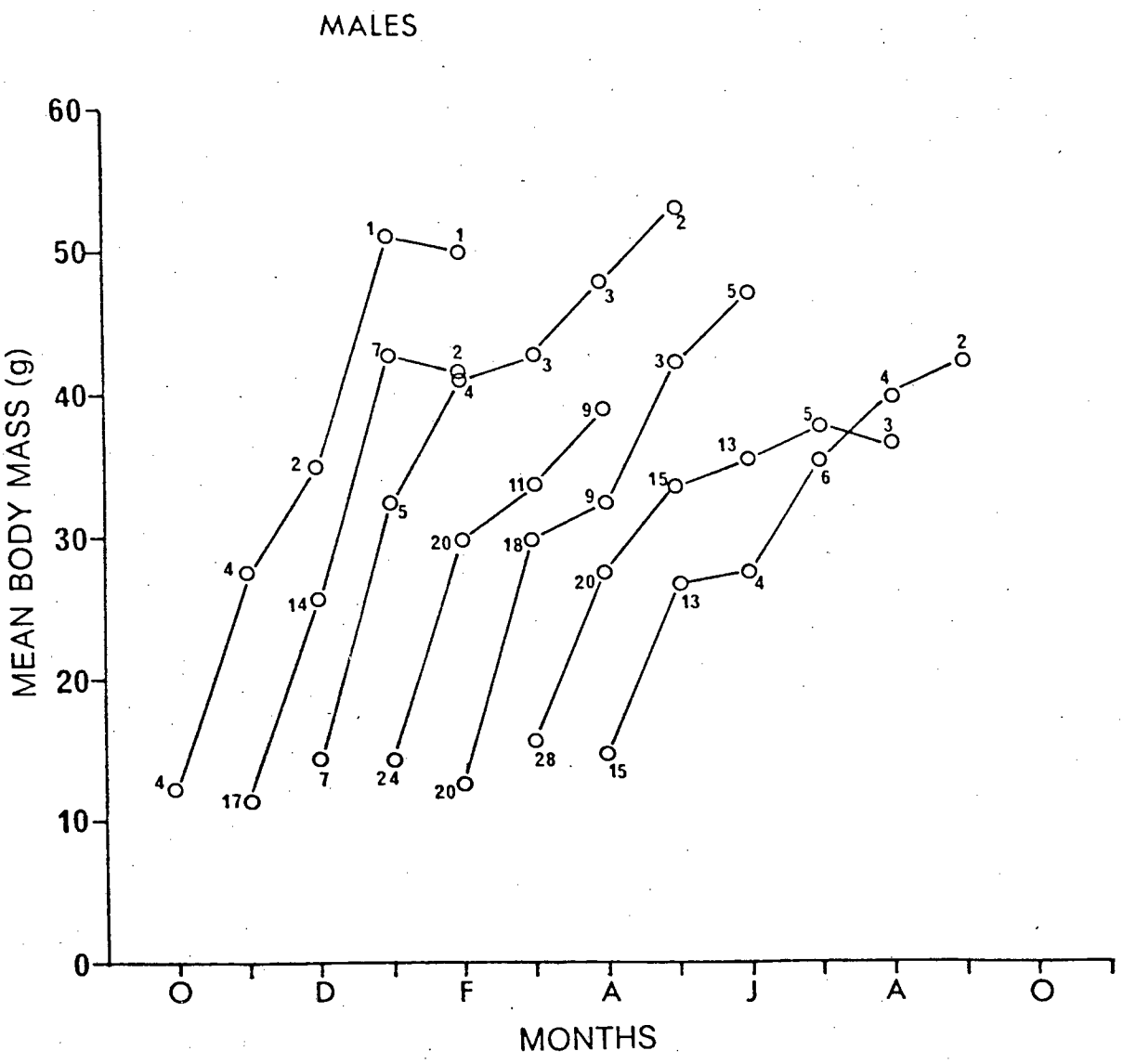


TABLE 11

Summer growth rates (October - April) of mice first captured up to one month old (<20g). Ranges and standard deviations of samples (see Figs. 7 & 8). For statistical comparison of growth rates see Table 12.

	MONTH FIRST CAPTURED													
	OCTOBER		NOVEMBER		DECEMBER		JANUARY		FEBRUARY		MARCH		APRIL	
MONTHLY WEIGHT RANGES (g)	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
MONTH 1 (g) Range	7-17	8-15	6-17	7-19	10-18	8-18	9-19	8-19	9-18	6-19	6½-19	7-19	10-18	6½-19
S.D.	4,43	3,56	3,14	4,0	3,74	2,93	2,97	3,42	2,91	4,45	3,75	3,85	2,51	4,26
MONTH 2 (g) Range	25-31	-	21-36	19-44	25-42	31-40	22-43	23-58	22-45	16-44	19-39	18-46	20-41	22-29
S.D.	2,52	-	4,22	7,29	6,34	3,28	5,22	9,76	6,18	8,08	5,56	5,84	5,36	2,84
MONTH 3 (g) Range	32-39	38-43	37-55	29-54	38-45	34-53	28-40	26-64	28-35	19-41	24-53	21-51	22-31	25-30
S.D.	4,24	3,54	5,70	7,12	2,99	5,42	3,47	9,92	2,64	5,77	6,23	5,38	3,97	1,79
MONTH 4 (g) Range		45-56	36-47	33-66	31-50	39-46	25-51	31-62	35-54	30-37	30-49	23-43	30-39	26-34
S.D.		5,69	7,78	9,03	10,21	2,88	7,70	8,96	10,44	3,10	5,24	5,82	2,99	2,66
MONTH 5 (g) Range		48-54		36-72	43-45	41-51		31-45	35-60	28-34	35-46	28-40	37-44	28-31
S.D.		4,24		14,29	6,43	5,0		4,65	10,63	3,06	4,77	4,79	3,40	1,73
MONTH 6 (g) Range				42-47	50-56			33-44			32-39	32-38	42-42	31-36
S.D.				2,52	4,24			4,99			3,79	2,10	0	2,65
MONTH 7 (g) Range												35-46		
S.D.												3,18		
MONTH 8 (g) Range												33-68		
S.D.												11,80		
MONTH 9 (g) Range												47,60		
S.D.												4,69		

TABLE 12

Comparison of the seasonal differences in the growth rate of juvenile mice (< 20g at first capture) for the first month after initial capture (see Table 11 and Figs. 7 & 8).

	Oct vs Nov	Nov vs Dec	Dec vs Jan	Jan vs Feb	Feb vs Mar	Mar vs Apr
Males t	0,57	-1,47	0,44	0,76	2,80	0,27
DF	16	17	23	36	36	31
SIGNIF	NS	NS	NS	NS	< 0,01	NS
Females t	-	-0,39	-0,17	2,18	2,93	1,12
DF		29	34	44	45	33
SIGNIF		NS	NS	< 0,05	< 0,01	NS

If mean growth rates for two months after first capture (Table 13) are compared by means of a 't' test for the different months (Table 14) then it seems that reduced growth in March has a greater effect on the older males than on the females. Thus, in the case of males, the mean growth rate from January to March is significantly less ($p < 0.02$) than that in the following months. Whereas, in females growth is only significantly reduced in the February to April period and following months, when compared with the January to March period (Table 14). This different pattern of growth in young females as compared to males when taken over a two month period is probably due to the influence of pregnancy - females grow faster than males for a longer time. Thus, females first captured in January grow to almost 40g by March whereas males only get to 33g in the same time (Figs. 7 & 8).

Figs. 7 & 8 and Table 14 show that young males first caught in October, November and December have similar growth rates which are significantly higher than those of mice caught January to March, when taken over a two month period. Young females have rapid growth from October to January and reduced growth from February onwards. This has a bearing on the attainment of sexual maturity and the question of what proportion of mice breed during the year of their birth (see Chapter VIII).

TABLE 13

Mean growth in body mass two months after first capture of juveniles up to one month old (< 20g) first captured between October and March.

(See Figs. 7 & 8).

	MONTHS						
SEX	O-D	N-J	D-F	J-M	F-A	M-M	A-J
No. of males	2	7	4	11	9	15	4
Mean growth (g)	26,0	32,6	26,3	19,2	17,9	18,0	12,0
S.D.	1,41	6,19	4,35	4,19	3,66	6,24	3,74
No. of females	2	11	10	18	19	23	6
Mean growth (g)	28,0	28,5	26,8	26,0	19,1	17,0	12,5
S.D.	0	6,06	6,44	9,82	6,51	4,84	4,68

TABLE 14

Statistical comparison of mean growth shown in Table 13.

	M O N T H S					
	O-D vs N-J	N-J vs D-F	D-F vs J-M	J-M vs F-A	F-A vs M-M	M-M vs A-J
Males t	-	1,795	2,86	0,72	0,034	1,805
DF		9	13	18	22	17
SIGNIF		NS	< 0,02	NS	NS	NS
Females t	-	0,623	0,23	2,52	1,20	2,49
DF		19	26	35	40	27
SIGNIF		NS	NS	<0,02	NS	< 0,02

VII.2 Field growth curves for juveniles for the whole breeding season

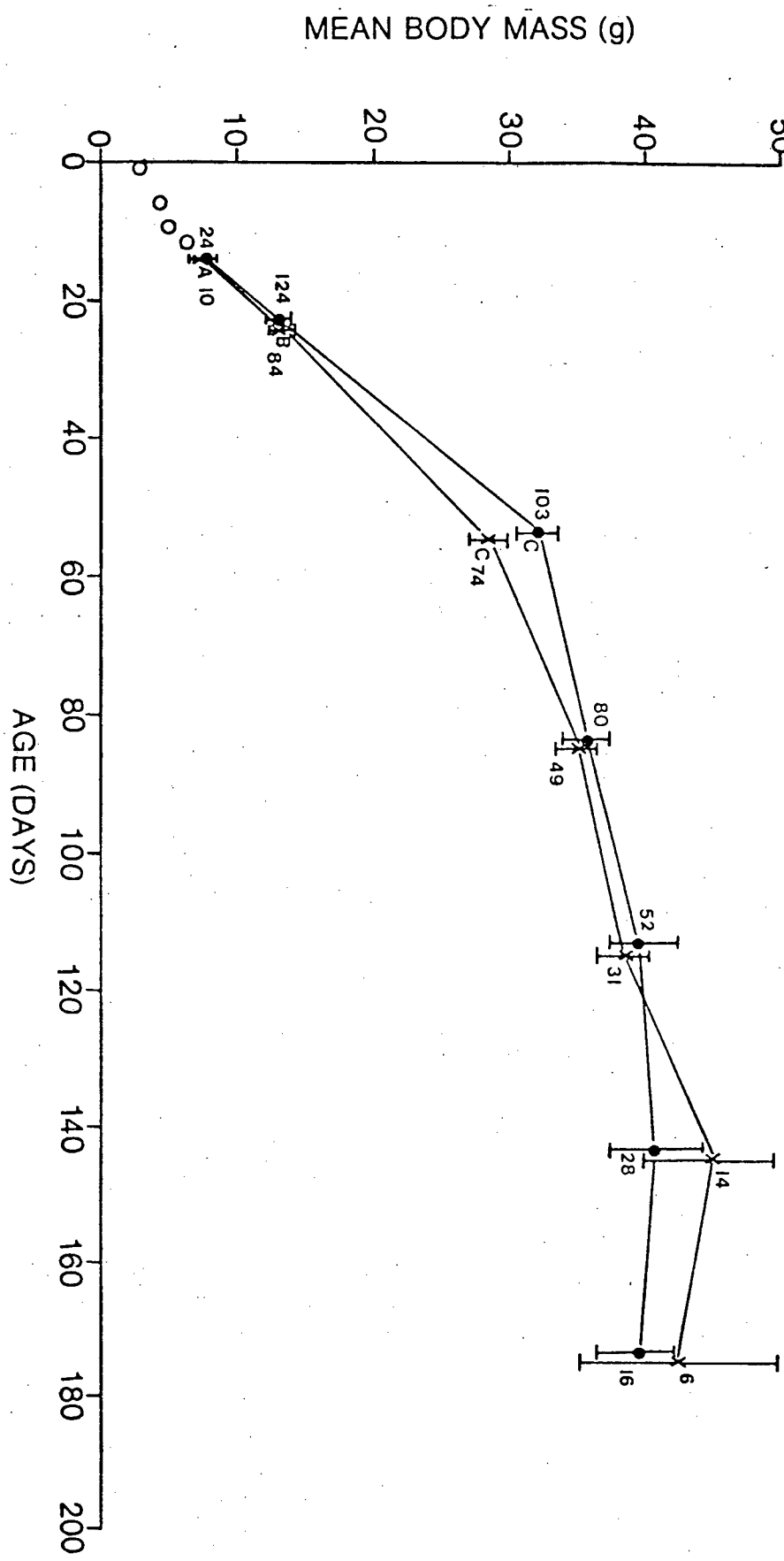
Although the growth rate for March was significantly less than the preceding months, the mean initial growth rate (from first capture to one month later) for October through March was not significantly different from the initial rate October through February (for males $t = 1,13$ $DF = 140$; for females $t = 1,87$ $DF = 182$, both NS). It, therefore, seemed justifiable to present a mean growth rate for the whole breeding season October to March. Therefore, a mean growth curve of juveniles in the field, from birth (sexes separate) for the summer months October through March is presented in Fig. 9.

Point A in Fig. 9 was established as follows:

A number of litters were raised in captivity by Mitchell (1973) and Henschel (1977). This enabled growth rate and tooth eruption from birth to weaning age to be established. The mass of R.pumilio at birth is about 2,5 - 3g. They grow to about 8g at 14 days of age. Meester and Hallet (1970) and Mitchell (1973) give 14 days as the age of weaning, though Choate (1971) says it is 22 days. Brooks (1974) says weaning is complete by 16 days. The youngest mice caught in livetraps weighed 6 - 8g. Fourteen days of age (point A in Fig. 9) was, therefore, taken as the starting point for the field growth. Numbers next to each

FIG. 9

Mean field growth curve from birth for male and female R.pumilio first captured in the summer breeding season October to March and subsequently recaptured at monthly intervals. From birth to point A (14 days old) established from litters reared in captivity. Point A to point B established from juveniles first captured in the field weighing less than 10g, which were recaptured one month later. Point B to point C established from juveniles first captured in the field weighing less than 20g, which were recaptured one month later. Figures at each point are sample sizes.


MEAN BODY MASS (g)
0
10
20
30
40
50
AGE (DAYS)
0
20
40
60
80
100
120
140
160
180
200
O GROWTH FROM BIRTH
IN CAPTIVITY
x MALES
• FEMALES
24
10
124
84
103
74
80
49
52
31
28
14
16
6

point are the sample sizes. Two standard errors are shown for each sample.

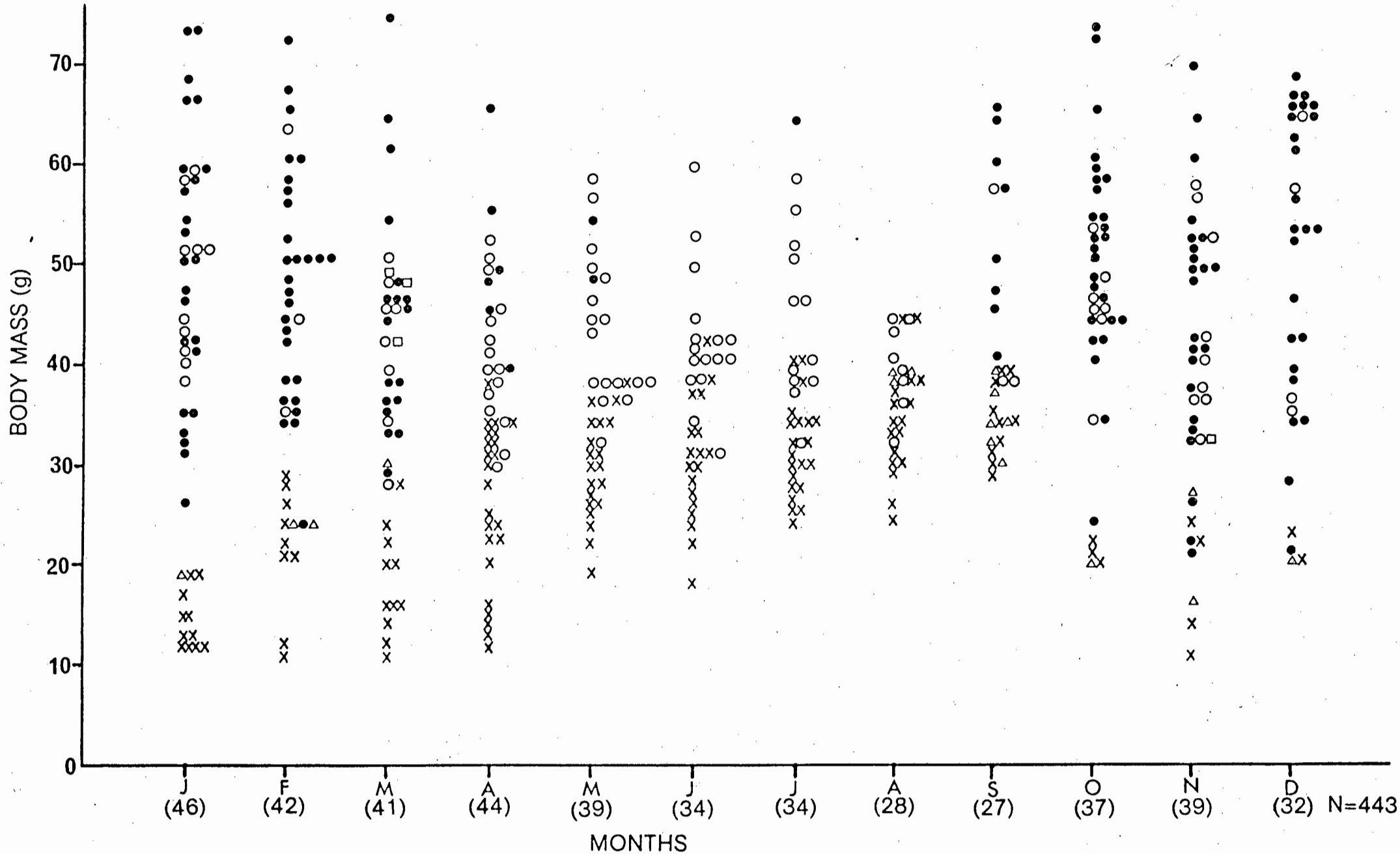
The initial field growth rate (AB) was established by pooling the data (sexes separately) for mice weighing under 10g at first capture in the period October to March, which were recaptured one month later. Thereafter, from point **B** onward a mean growth rate was calculated by pooling the data from all mice which weighed under 20g at first capture and were recaptured at one month intervals. It is evident that growth is rapid and uniform for both sexes up to a mass of about 30g and that thereafter growth tapers off very significantly. The mean initial summer growth rates of males and females (AC in Fig. 9) were compared using Student's 't'. For DF = 175, $t = 3,6$ $p = < 0,01$. Thus, the growth rate of females is very significantly faster than that of males in the initial stages.

However, growth then evens out to such a degree that both sexes reach a mass of 40g at about 122 - 124 days. It seems most likely that the initially faster growth of the females is due to them becoming sexually mature younger than the males. Evidence from live mice shows that in the summer young females have perforate vaginas and may, therefore, be sexually receptive, at a mass of about 21g. This is supported by post mortem data for the summer (Fig. 10) which show females oestrus and pregnant in the range 20 - 26g. Thus, the initially faster growth of the females is probably due to the onset of pregnancy.

FIG. 10

Analysis of breeding condition vs. body mass of 443 killtrapped female R.pumilio. Data pooled for each month for the whole study 1972 - 1977. The breeding condition of each female was assessed from autopsy in the laboratory.

● = Pregnant or lactating
○ = Parous
□ = Oestrus, parous
△ = oestrus, non-parous
X = non-parous


BODY MASS (g)
0
10
20
30
40
50
60
70
J (46)
F (42)
M (41)
A (44)
M (39)
J (34)
J (34)
A (28)
S (27)
O (37)
N (39)
D (32)
N=443
MONTHS

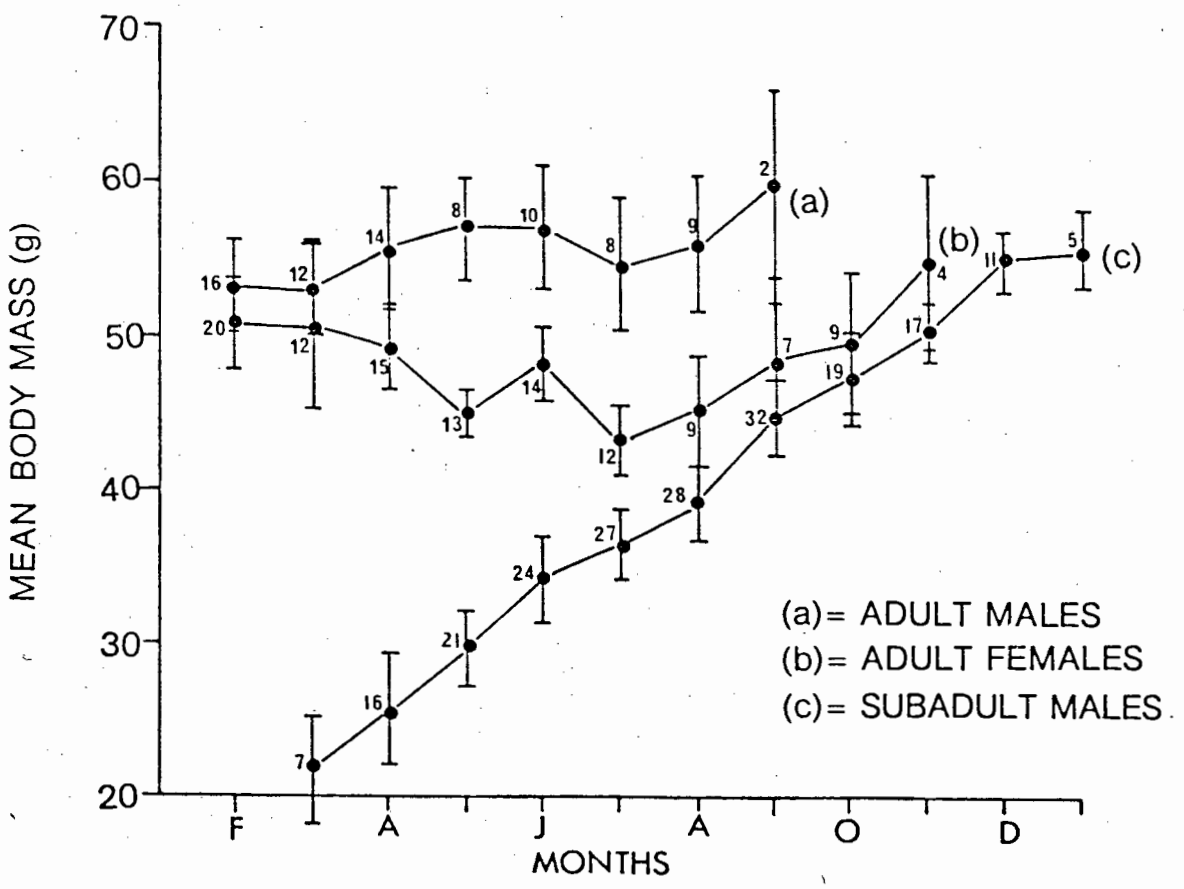
VII.3 Seasonal variations in body mass of adults and juveniles

The extreme flattening of the growth curve of both sexes at around 40g is noteworthy. This is probably due to the fact that, at a mean period of four months after birth, the mice have entered the winter season, which is much less favourable for growth than the summer. Unfavourable seasons for growth have been found in a number of small mammals. For example, Zejda (1971) reported absence of growth in certain cohorts of Clethrionomys glareolus during the European winter. Sheppe (1972) and Neal (1977) reported a decline of 25% and 20% in mean body mass of Mastomys natalensis and Lemniscomys striatus during the dry season in Zambia and Uganda respectively. Brooks (1974) reported that, for Rhabdomys in the dry Highveld winter of the Transvaal, a sample of 3 males maintained more or less constant mean body mass but that a sample of 4 females showed a drop of 8,6% in mean body mass between May and September.

In the case of Rhabdomys on the Cape Flats, Fig. 11 shows the fluctuations in mean body mass of adults (> 43g) which were recaptured throughout winter. The choice of 43g at first capture as a criterion is somewhat arbitrary, but the aim was to include only mice that were clearly adult and which had passed the initial phase of growth. The mean initial mass of adult males, Fig. 11(a), was 53,5g. From the body mass/age class analysis of all killtrapped males presented in Fig. 6, it can be seen that the mean body mass of males

FIG. 11

Fluctuations in mean body mass of adult and juvenile R.pumilio during winter 1972 - 1977. Winter months May to August are relatively unfavourable for growth. Curves for adults based on animals livetrapped before winter as adults (>43g) and recaptured throughout winter. Curve (c) is based on juvenile males first caught at a body mass of less than 35g and recaptured throughout winter. Two standard errors are given.



in class 5 was only 47,4g. Thus, it seems likely that the majority of the males in Fig. 11(a) were in class 5 or older and hence more than four months old. Between April and August the mean mass of males remained more or less constant (Fig. 11 a) with a slight decline in July whereas the mass of females declined (Fig. 11 b). However, analysis of the reproductive condition of females (Fig. 10) shows that prior to May significant numbers of females were pregnant. This would undoubtedly have affected the mean masses of females prior to May in Fig. 11(b). If one considers female mass between May and August only, then it remained approximately constant, showing a rise in June and a decline in July. Hence, during the period May to August, the months of highest rainfall and lowest temperatures, the masses of adults of both sexes remained constant, though July appeared to be the least favourable month in both sexes. The analysis cannot be carried beyond September for males because none were recaptured for so long a period. In females, the growth between August and November was probably due to the onset of a new breeding season and resultant pregnancy.

Fig. 11(c), by way of contrast, shows the mean winter growth of young males first captured in March (up to 31g at first capture) or later (up to 35g) and including only individuals which were recaptured at least until September. This demonstrates that growth during winter was steady for young males although much slower than summer growth (cf. Fig. 9). There was a reduction in growth rate during July and August and a spurt during September. Thus, since adults are able

to maintain their body masses and young males grow slowly but steadily, the winter period, although less favourable than the summer, does not appear to be limiting as far as the survival of the mice is concerned.

VII.4 Maximum body mass of individuals

An interesting point is to consider at what age growth ceases and how heavy these old mice may become. Females in spring are coming into breeding condition and hence their body mass increases are complicated by the onset of pregnancy in some mice. To avoid this problem, if one considers only males in the oldest age classes in Fig. 6, then it is clear that old mice have a mean mass around 55g. Males in classes 5, 6, 7 and 8 have mean body masses of 47,4g, 49,4g, 55,2g and 57,3g respectively. The heaviest male ever killtrapped weighed 76g and one of 78g was livetrapped. The evidence suggests the somewhat surprising conclusion that some mice may continue to grow until they enter class 7 at about nine months of age.

VII.5 Mean body mass of the winter population

The population mean mass is much less than that of these old animals, since it involves mice of various age classes and it also varies seasonally. To avoid the complicating factors of pregnancy, and the presence of very young mice, the

mean masses of livetrapped males and females were computed and compared by means of Student's 't' for July month 1972 - 75, when no females were pregnant. Thus, Table 15 shows that the mean mass of males in July was only 39,5g and of females 33,6g. Males were very significantly heavier than females ($t = 5,49$, $DF = 169$, $p < 0,001$).

TABLE 15

COMPARISON OF MEAN BODY MASSES OF LIVETRAPPED MALE AND FEMALE R.PUMILIO IN JULY MONTH 1972 - 1975.

BODY MASS OF FEMALES IS NOT COMPLICATED BY PREGNANCY IN JULY

	MALES	FEMALES	
N	83	88	t = 5,49
Mean Body Mass (g)	39,52	33,59	DF = 169
S.D.	8,33	5,60	P < 0,001
S.E.	0,91	0,60	
Range (g)	23 - 59	22 - 52	

factors as the length and timing of the breeding season, the

proportion of breeding females, the age at reproductive maturity, the gestation period, litter size and number of litters produced per season per female assume vital importance in the future of the population.

VIII.2 Breeding season

The seasonal changes in reproductive activity of Rhabdomys in relation to rainfall are shown in Fig. 13. The duration and timing of the breeding season has been gauged from the proportion of adult females (excluding age classes 1 and 2) which were pregnant or lactating in each month (Fig. 13 c). There was a long breeding season which commenced in September (spring) and ran through to April (fall). However, the most important breeding months were October to March, as shown by the high proportion of pregnant females. From October to February about 75% of mature females were pregnant or lactating. This figure dropped to about 65% in March and was down to 15% in April. As this was based on embryos visible during dissection and it takes several days for an embryo to grow to visible size, the true pregnancy rate was probably higher. The months when the greatest proportion of females were pregnant corresponded with the months having the greatest numbers of males with sperm (Fig. 13 a).

From Fig. 13 (d) it can be seen that the rainfall pattern was one of wet winters (May to August) and dry summers. Thus, breeding took place in the dry summer months and, in

FIG. 13

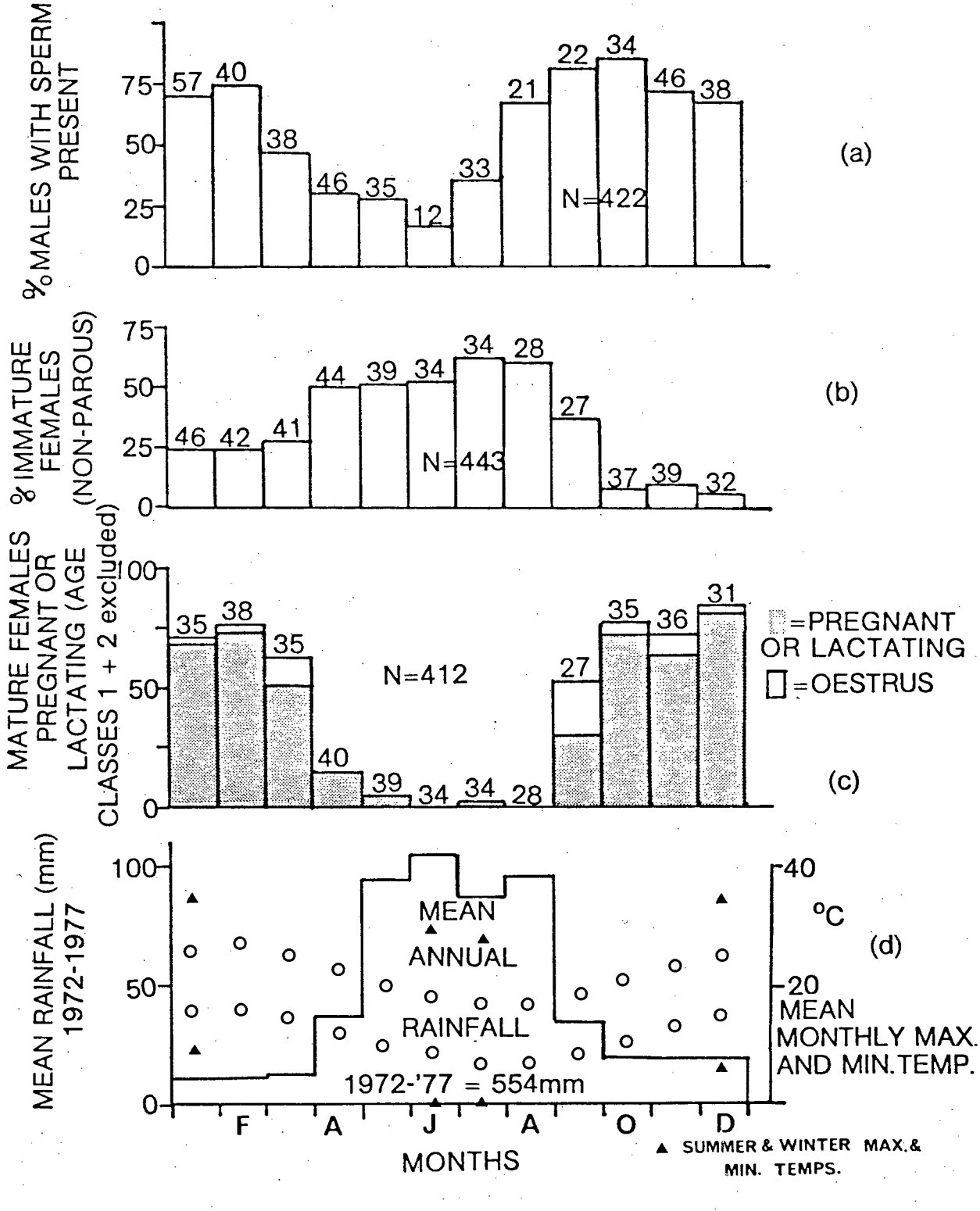
Seasonal changes in reproductive activity of R.pumilio in relation to rainfall. Data pooled for each month 1972 - 1977. Based on 422 killtrapped males and 443 killtrapped females autopsied in the laboratory.

a) = monthly proportion of males with sperm

b) = monthly proportion of immature females

c) = monthly proportion of pregnant, lactating or oestrus females

d) = mean monthly rainfall and maximum and minimum temperatures



fact, was remarkably correlated with low rainfall since virtually no breeding took place in the four winter months with high rainfall. As might be expected from this breeding pattern, the proportion of immature females (non-parous, non-oestrus) increased during the second half of the breeding season and rose to a maximum during the winter (Fig. 13 b). The fact that breeding intensity was inversely correlated with rainfall is interesting and contrary to what has been found for rodents in other parts of Africa. On the Transvaal Highveld, where there is summer rainfall from October to March, Brooks (1974) found that R.pumilio bred throughout the summer and Coetzee (1965) found the same for the multimammate mouse Praomys natalensis. In the tropics, where there are normally one or two rainy seasons per year, breeding is correlated with the rains, e.g. Neal (1977) for the grass mouse, Lemniscomys striatus, in Uganda and Delany (1972) for Lophuromys and Praomys jacksoni in the Congo, Uganda and Malawi. However, Delany (p. 30) points out that this correlation is not identical for each species. He says that the reasons for this are not known with certainty, but suggests that diet is involved and that high rainfall is associated with maximum food supply for each species. In the Western Cape, with its Mediterranean type climate, the winter rainfall is not correlated with an increased food supply (unlike summer rainfall regions) since the main time of seedfall of the Acacia trees, which provide the bulk of the food for the mice, is in summer (December to April, Table 38). Hence Rhabdomys has retained its summer breeding pattern in a winter rainfall region, presumably because of increased

summer food supply.

The temperature regime in the winter (Fig.13 d) may also not be favourable to breeding since in addition to being wet it is also rather cold with mean daily minimum temperatures around 7 - 10°C, falling as low as -1°C occasionally.

The breeding season described above occurred in the study area of primarily alien vegetation. It is necessary to enquire whether the same seasonal pattern of reproduction occurred in the areas of indigenous fynbos vegetation in the western Cape. In Cape Point Reserve, about 50 km south of the study area, in mid-November 1975 several juvenile Rhabdomys males weighing less than 26g and both pregnant females and females with large teats were found (Jarvis unpub. data). On the Cape Flats in an area of indigenous vegetation about 5km south of the study area, during December and January 1975/76, although no pregnant females were found, four juvenile females weighing 13g, 23g, 23g, 28g and three juvenile males weighing 21g, 28g and 31g were found in a total sample of 14 animals (David & Jarvis, unpub. data). At De Hoop, near Cape Agulhas, 180km ESE of the study area at the end of March 1975, six females were killtrapped of which three were pregnant, one was in oestrus and one was a juvenile (Jarvis & David, unpub.). All this evidence is consistent with a summer breeding season coinciding with what was found in the study area. Conversely, at De Hoop during the first week of July 1972, a sample of seven killtrapped females showed none breeding (Jarvis, unpub.), and in the Bontebok

National Park, near Swellendam 220km east of Cape Town, between 29 June and 3 July 1973, 24 Rhabdomys were caught none of which were breeding (Jarvis & David, unpub.). This is supporting evidence that breeding ceases during winter in indigenous fynbos areas, as in the study area.

VIII.3 Age at sexual maturity

The age at which mice attain sexual maturity is of considerable importance to the population as it marks the time at which females are potentially able to breed. Changes in this age may have a profound influence on population growth each year. Smith (1966, p. 357) selects age of sexual maturity, mean litter size and longevity as the three factors which affect the rate of increase (r). Of these, Smith says that a reduction in the age at which a female produces her first young has the most influence on r. In the laboratory sexual maturity may be ascertained by methods such as that used by Leslie et al (1945) who plotted the log of body mass of female Rattus norvegicus against the percentage of animals with corpora lutea in the ovary. Their criterion for maturity was the mass at which 50% of females had corpora lutea. In this study during autopsy of killtrapped animals no corpora lutea could be seen macroscopically on the ovaries of young non-parous females. Most mature females were either parous or heavily pregnant when caught and hence, since unfortunately a 'clean' body mass was not taken during this study - that is, the body mass minus the weight of the gravid uterus, it was difficult to arrive at an estimate of the body mass at which sexual maturity occurred. It is very useful to have some criterion which can be used in the field when dealing with live mice. One is normally reliant on external signs such as a perforate vagina or large teats and failing these one has only the body mass as a guide.

VIII.3.1 Females

Pregnancy was the criterion used to establish sexual maturity in this study. When dissecting killtrapped females, the minimum age of sexual maturity was assessed from the youngest animals which were either pregnant or in oestrus. From Fig. 10 it can be seen that the youngest females in oestrus were in the range 16 - 24g and the youngest pregnant females weighed from 21 - 24g. A mean age of sexual maturity for the population was more difficult to obtain. Fig. 14 shows an analysis of the breeding condition of killtrapped females by age class and month, using data pooled for the whole study 1972 - 77. In a sample of 210 females from the breeding season October - March, whose age class was determined, only 15 were class 2 (up to 6 weeks old). None of these were parous and only one in oestrus. However, in the case of class 3 females 45 out of 53 (85%) were breeding or had bred during the season and the same was true for 49 out of 50 (98%) of class 4 females. Whereas, of class 3 females killed between April and June only three out of 21 (14%) had bred. Class 3 females were in the age range 6 - 12 weeks (Table 10.) The fact that 85% of class 3 females were breeding combined with the evidence from Fig. 10 that practically all females over 25g body mass were sexually mature from October to March, suggests that sexual maturity was attained early in the age class - perhaps in the range 6 - 7 weeks (see Fig. 9). Fig. 14 shows that 100% of females in all the older age classes were pregnant or parous from October to March. If the 15 very young class 2 animals are excluded,

FIG. 14

Analysis of breeding condition of 383 livetrapped females by age class. See TABLE 10 for chronological ages. Data pooled for each month 1972 - 1977. Monthly sample sizes in brackets.

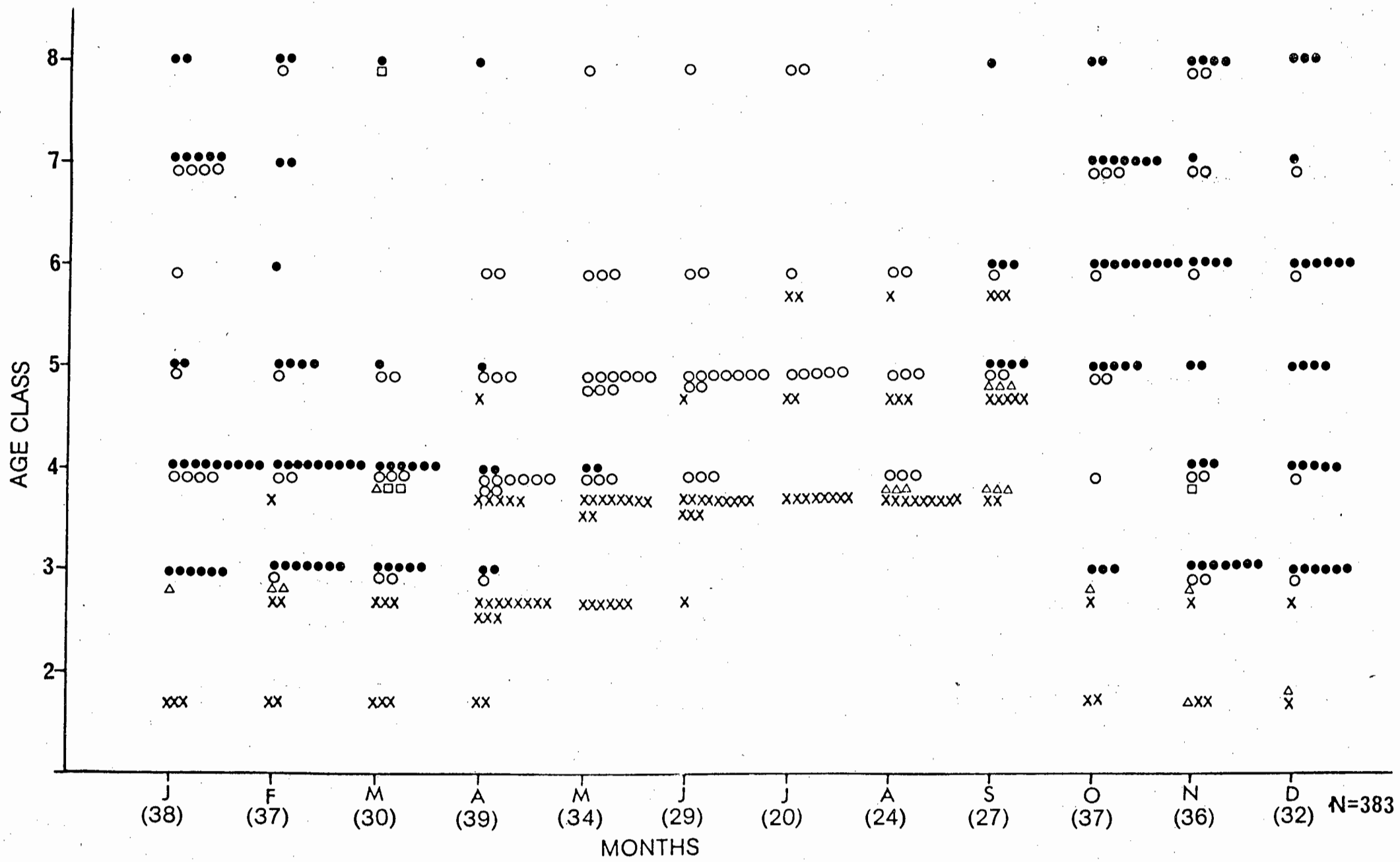
● = Pregnant or lactating

○ = Parous

□ = Oestrus, parous

△ = Oestrus, non-parous

X = Non-parous

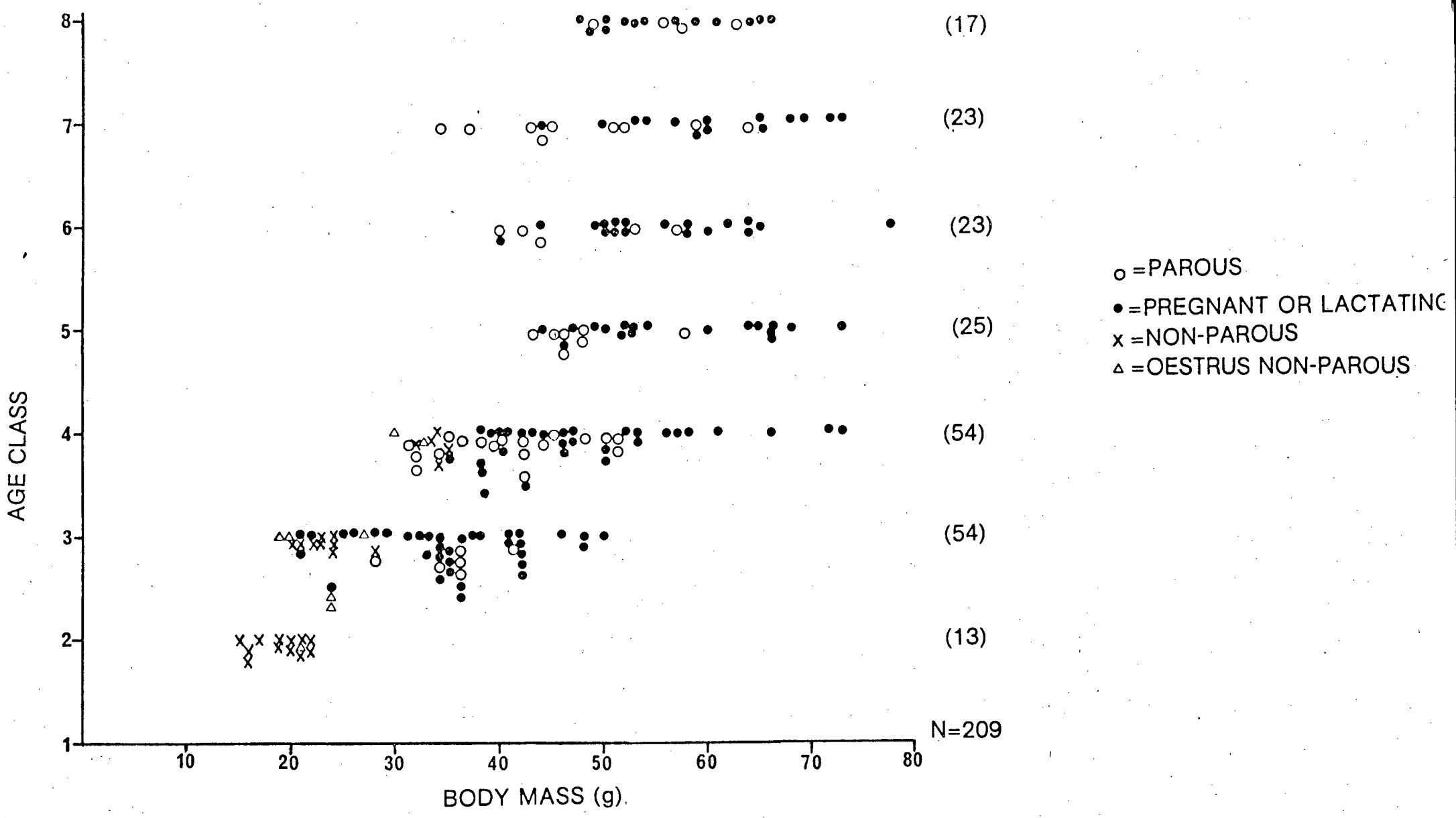

AGE CLASS
8
7
6
5
4
3
2
J (38)
F (37)
M (30)
A (39)
M (34)
J (29)
J (20)
A (24)
S (27)
O (37)
N (36)
D (32)
MONTHS
N=383

then 186 out of 195 mice (95%) over the age of 6 weeks were in breeding condition - which is a remarkably high proportion. Fig. 15 is an analysis of breeding condition of females for the whole study period by age class and body mass and shows the range of body masses of breeding females in each age class. The degree of overlap between age classes is so great as to effectively preclude the possibility of determining the age of a mouse of over 30g during the breeding season.

It was difficult to obtain the approximate body mass at which females were sexually mature because corpora lutea were not normally seen macroscopically on the ovaries of non-parous mice. In the case of pregnant females, their body masses were heavily influenced by the masses of the gravid uteri. Unfortunately, a clean body mass (body mass minus the mass of the uterus) of females was not taken during this study. The nearest approach was to take the mean mass of all class 3 females which showed no evidence of sexual maturity and to compare this with the mean mass of all class 3 females which were in the very early stages of pregnancy and in which the embryos were recorded as being too small for a crown-rump length measurement. In this latter case, the assumption was that the mass of the uterus would not be significant in relation to the body mass and that this would thus approximate the mean mass at sexual maturity. Analysis of the killtrap records revealed that the mean body mass of a sample of 26 class 3 females which were apparently not mature, was 24,5g and SE = 0,90.

FIG. 15

Analysis of breeding condition of 209 killtrapped females by age class and body mass during the breeding season October to March. Data from the autopsy of females for the summer months October through March pooled for the whole study 1972 - 1977.


AGE CLASS
8
7
6
5
4
3
2
1
10
20
30
40
50
60
70
80
BODY MASS (g)
(17)
(23)
(23)
(25)
(54)
(54)
(13)
N=209
o =PAROUS
• =PREGNANT OR LACTATING
x =NON-PAROUS
Δ =OESTRUS NON-PAROUS

This sample was judged as immature because no corpora lutea could be seen macroscopically on the ovaries of any of the females, but it included five females which the condition of the uterus indicated were in oestrus. The mean body mass of a sample of 12 class 3 females in very early pregnancy was 28,6g and SE = 1,87. Thus, at the 95% confidence interval the mean body mass at sexual maturity was 28,6 ± 3,7g (i.e. 25 - 32g). The distribution of body masses of these 12 females was somewhat skewed and the median value was 27,5g which may give a better estimate of central tendency.

From the field growth curve (Fig. 9) it appears that females aged 6 - 7 weeks weigh 26 - 31g at sexual maturity. This indicates a high degree of correlation between the two methods of estimation.

The finding that, during the breeding season, female Rhabdomys became sexually mature soon after 6 weeks of age differs considerably from that of Brooks (1974) who, on the basis of 11 litters born to captive females, stated that the mean age of reproductive maturity of females was 65 days (range 32 - 82 days). However, in the case of wild females, Brooks states that 9% of one month old mice and 56% of two month old mice were reproductively active. According to his classification, one month old mice were aged from 2 - 6 weeks and weighed 11 - 26g and two month olds were aged from 6 - 10 weeks and weighed 27 - 36g. Fig. 10 shows that on the Cape Flats 13 out of 50 females (26%) in the range 11 - 26g

were pregnant or in oestrus and 35 out of 38 (92%) in the range 27 - 36g were pregnant, parous or in oestrus. Hence, using a classification by mass, mice on the Cape Flats appear to mature earlier than those in the Transvaal.

VIII.3.1.1 Comparison of livetrapping with killtrapping estimates

In the field, when handling livetrapped animals, the only external sign that a female is coming into breeding condition is the occurrence of a perforate vagina, which is sealed in non-breeding females. This may be useful in detecting the minimum breeding age of the mice. The youngest perforate female ever livetrapped weighed only 13g - but this was unique. The minimum breeding age appeared to fall in the range 15 - 19g, since in the summer months October to March, 12 out of 65 mice (18½%) in that mass range were perforate. There was some evidence that early in the 1974 and 1975 seasons, mice matured younger than in other years since, of 11 mice recorded as perforate in the category 15 - 24g from October to December, six were from 1974 and four from 1975. From January to March young perforate mice were found in 1973, 1976 and also 1977. Generally, however, the breeding age appeared to be somewhat older. From October to March, 27 out of 97 mice (28%) in the category 20 - 24g were perforate, and in the category 25 - 29g, 26 out of 63 (41%) were perforate. No livetrapped mice were found to be perforate in the months May to August.

Table 16 shows the proportion of livetrapped mice which were perforate each month. With the exception of a few months when the sample sizes were rather small, the proportion of perforate females was well below 80%, though the killtrap sample showed that 95% of females in age classes 3 - 8 were breeding during the season. In addition, examination of the killtrap data showed that in a sample of 112 mice found pregnant by dissection, 35 (31%) were imperforate. The evidence suggests, therefore, that the condition of the vagina by itself is not reliable as a quantitative measure of the number of breeding females, since it may re-seal after copulation. Hamilton (1941) found the same situation in Microtus pennsylvanicus - the vagina could be perforate or imperforate at all stages of pregnancy and non-parous perforate females were not necessarily impregnated.

The minimum breeding ages of livetrapped mice with perforate vaginas in the body mass range 19 - 29g were somewhat lower than the mean age of sexual maturity as revealed by the killtrap sample. Thus, the age of the livetrapped perforate females derived from the growth curve (Fig. 9) would be in the range 32 - 48 days, compared with a suggested age of 42 - 50 days derived from the killtrap data. The probable explanation for this is that the perforate females may not necessarily have been in breeding condition. For instance, Johnston & Oliff (1954) found that in a sample of 12 captive Mastomys natalensis, the mean age of perforation of the vagina was 76 days, while the first oestrus did not occur until

TABLE 16

NUMBER AND PERCENTAGE OF LIVETRAPPED PERFORATE FEMALES DURING THE BREEDING SEASON (MINIMUM BODY MASS 15g)

N = Sample size P = Number with perforate vagina

	SEP			OCT			NOV			DEC			JAN			FEB			MAR			APR			MAY		
	N	P	%P	N	P	%P	N	P	%P	N	P	%P	N	P	%P	N	P	%P	N	P	%P	N	P	%P	N	P	%P
1972/73	13	12	92	14	14	100	16	12	75	17	14	82	24	14	58	48	28	58	39	11	28	39	1	3	22	0	0
1973/74	7	0	0	10	5	50	6	2	33	5	2	40	10	6	60	6	4	67	10	3	30	16	4	25	11	0	0
1974/75	10	8	80	10	8	80	13	9	69	12	8	67	35	22	63	55	33	60	75	29	39	71	17	24	80	0	0
1975/76	47	12	26	37	20	54	41	15	37	34	16	47	38	5	13	47	13	28	32	11	34	30	0	0	0	-	-
1976/77	3	2	67	10	4	40	12	5	42	20	8	40	17	12	71	29	21	72	29	17	59	23	1	4	26	0	0

a mean age of 104 days. In captive R.pumilio, Brooks (1974) states that spontaneous perforation of the vagina occurs at 5 - 8 weeks - well before his mean age of 65 days for reproductive maturity. In this study there were at least five females in the killtrap records which were perforate but whose reproductive tract showed no signs at all of breeding. Hence, evidence of breeding based on numbers of females with perforate vaginas in the field is probably not reliable but it may serve as a useful guide to the start of the breeding season.

The problem of interpreting the breeding condition of live females is underscored by the fact that pregnancy of mice may be difficult or impossible to detect in the field. Palpation of the abdomen of live mice in order to detect pregnancy was not used in this study, and in any case this method cannot detect early stages of pregnancy. Sometimes the condition of the teats was informative, when it was obvious that a female was suckling young or had recently suckled. However, it was seldom found possible in the field to detect lactation by expressing milk from the nipples and this criterion was dropped as being too unreliable. Indeed it was often found impossible to obtain milk from dissected animals whose mammary glands indicated lactation. Measroch (1954) found the same difficulty in obtaining milk from female Tatera. Brooks (1974) states that: "In Rhabdomys, lactation detected approximately 43% of recent pregnancies ...".

Useful field criteria for female Rhabdomys can be obtained from Fig. 10, which shows that the lightest female found to be in oestrus weighed 19g and the lightest pregnant one weighed 21g. Fifteen out of 37 females in the range 19 - 29g (41%) were in breeding condition between October and March and practically 100% of females of 30g or more were pregnant or parous. Thus, useful criteria to apply in the field during the breeding season (at least on the Cape Flats) would be that 19g was minimum breeding age and females of 30g or more were almost certain to be sexually mature.

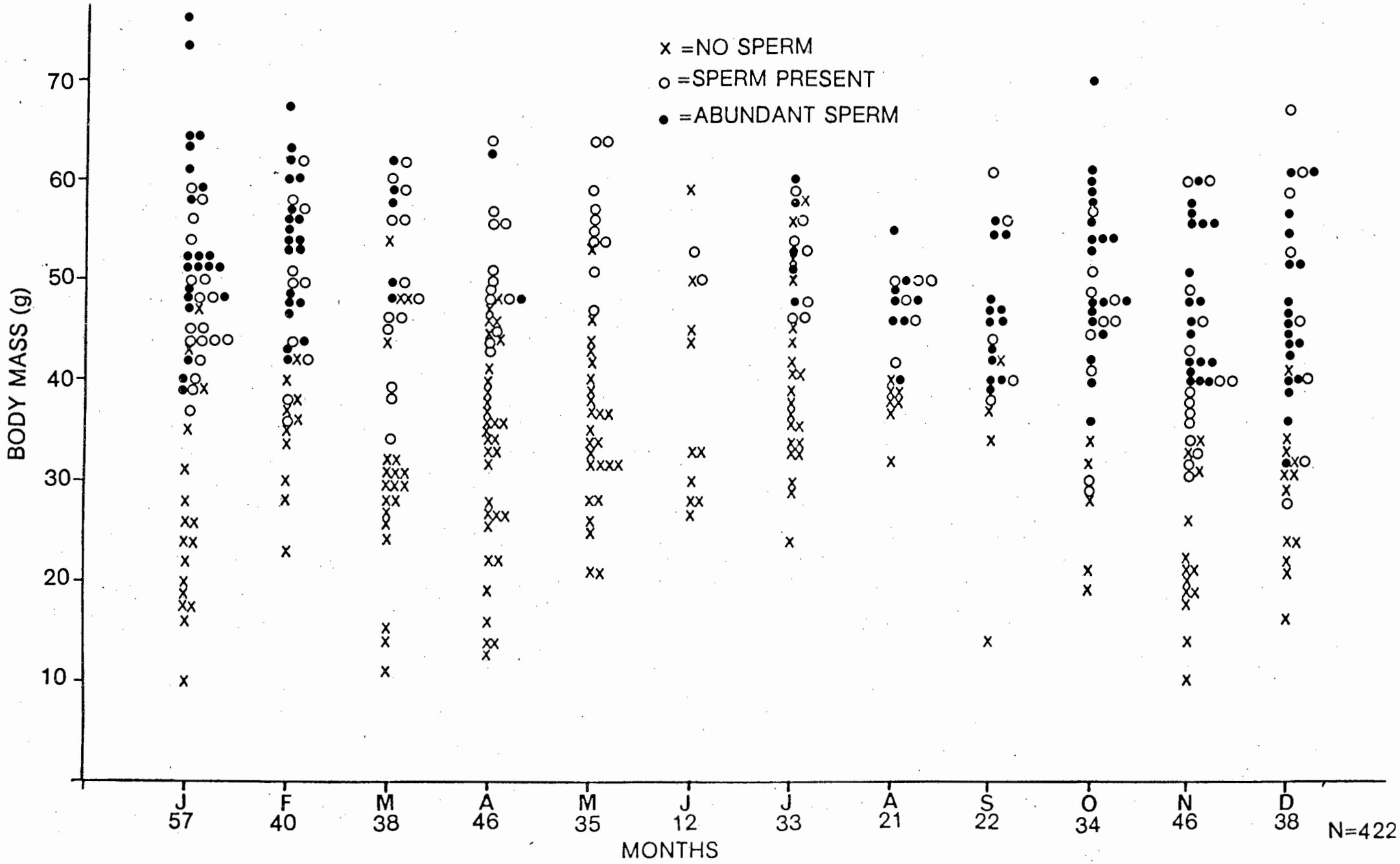
VIII.3.2 Males

In the case of males, the only external character in live animals which indicates the breeding status is the presence of descended (scrotal) testes. However, examination of the killtrap data showed a number of small mice in summer which had no sperm but had descended testes. Hence, this criterion was unreliable and the one used to determine the sexual maturity of males was the presence of visible semen in the vas deferens of dissected animals. Other workers such as Keller and Krebs (1970) and Brooks (1974) used the presence of visible coiling in the epididymis to determine sexual maturity.

Fig. 16 shows the occurrence of sperm versus body mass in killtrapped males. It is evident that, with only two exceptions, no male under 30g had sperm. In the breeding

FIG. 16

Analysis of breeding condition of 422 killtrapped males : occurrence of sperm vs body mass. Data pooled for each month 1972 - 1977. Monthly sample sizes in brackets.


x =NO SPERM
o =SPERM PRESENT
• =ABUNDANT SPERM
BODY MASS (g)
70
60
50
40
30
20
10
J 57
F 40
M 38
A 46
M 35
J 12
J 33
A 21
S 22
O 34
N 46
D 38
MONTHS
N=422

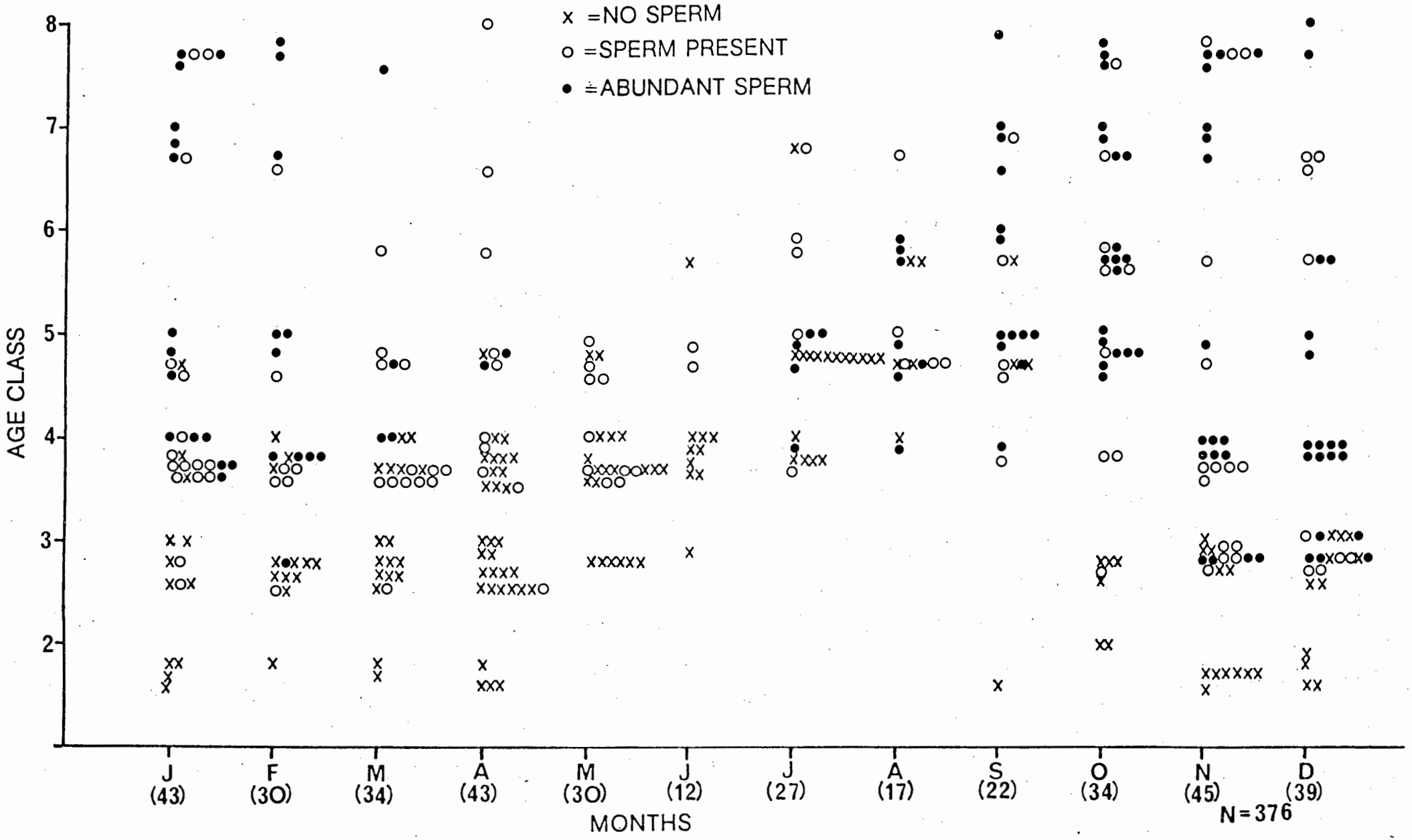
months October to March, most males over 35g had sperm but only five males weighing under 40g were classed as having abundant sperm. In the non-breeding season no male of under 40g had any sperm.

Brooks (1974) reports that about 20% of one month old (11 - 26g) and 53% of two month old (27 - 36g) Rhabdomys in the Transvaal were reproductively active. Examination of Fig. 16 shows that, on the Cape Flats, no males between 11 - 26g had any sperm (N = 45) and only 14 out of 45 mice (31%) between 27 - 36g had sperm present. In general, one can say that, during the breeding season on the Cape Flats, only males over 35g were sexually mature and these were aged from about 80 days old upwards (Fig. 9), which indicates that males matured towards the end of age class 3, about 4 - 5 weeks later than females.

Fig. 17 is an analysis of the occurrence of sperm for different age classes of killtrapped males. It shows that in class 3 males, aged from 6 - 12 weeks, only 25 out of 63 (40%) had sperm from October to March, but 54 out of 65 class 4 males (83%) had sperm during the same period. This, therefore, tends to support the above evidence from body mass data and also demonstrates that males tend to come to maturity later than females, since 85% of class 3 females were reproductively active. My results seem to be at variance with those of Choate (1971), who says: "Males usually become sexually mature first, but not always", and Brooks (1974)

FIG. 17

Analysis of breeding condition of 376 killtrapped males : occurrence of sperm vs. age class. Data pooled for each month 1972 - 1977. See TABLE 10 for chronological ages.
Monthly sample sizes in brackets.


x =NO SPERM
o =SPERM PRESENT
• =ABUNDANT SPERM
AGE CLASS
8
7
6
5
4
3
2
J (43)
F (30)
M (34)
A (43)
M (30)
J (12)
J (27)
A (17)
S (22)
O (34)
N (45)
D (39)
MONTHS
N=376

who states that roughly equal percentages of two month old males and females were mature.

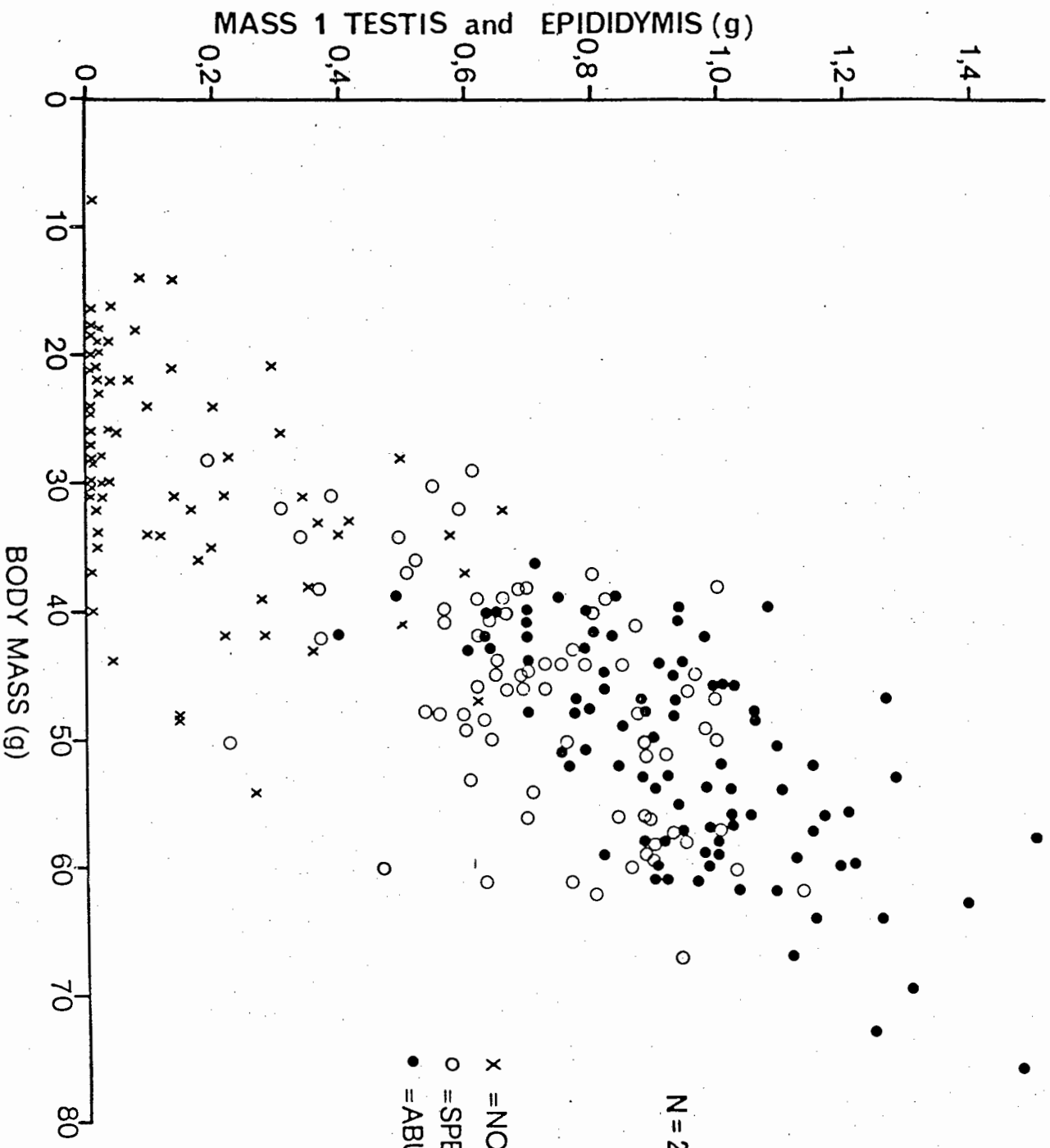
VIII.4 Reproductive status of the male

The seasonal changes in reproductive activity of males, as gauged by the percentage of males with sperm, are shown in Fig. 13(a). There was a distinct seasonal pattern which correlated fairly well with that of the females (Fig. 13 c). It was noticeable that there was a sharp rise in the percentage of males with sperm during August, about a month before the first pregnant females were found. Thereafter, the proportion of active males remained high until March when there was a distinct drop in the number of animals breeding, of both sexes. Activity remained low for the following four months, but it appears that there were some males able to breed at any time of year.

One of the most difficult questions to answer concerns the age at which males begin to take an active part in breeding. This must be contrasted with the age of sexual maturity which indicates only the average age at which sperm is being produced. This is because a very young male, although having sperm present, may take little or no part in breeding. Workers such as Neal (1977) assessed the abundance of sperm in the epididymis of males microscopically and considered that only males with abundant sperm took an active part in breeding. In the present study, the quantity of semen in the vas deferens was assessed subjectively by eye, during dissection. Fig. 18 shows the correlation of testis mass and the occurrence of sperm with body mass during the

FIG. 18

Analysis of breeding condition of 241 killtrapped males : body mass vs. the mass of one testis plus epididymis, according to relative sperm abundance. Data pooled for the breeding season September to March only, 1973 - 1977.

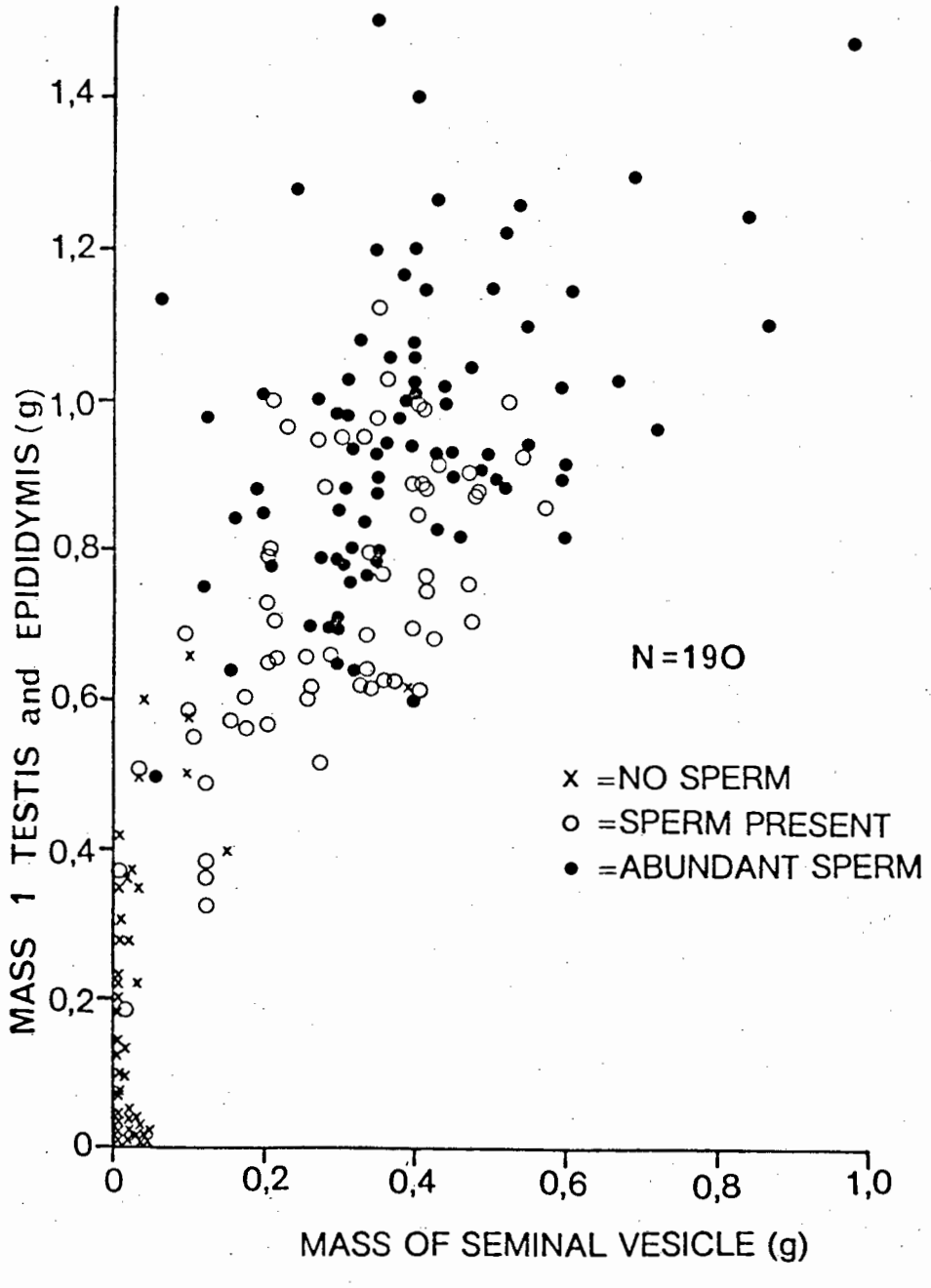

MASS 1 TESTIS and EPIDIDYMIS (g)
0
0,2
0,4
0,6
0,8
1,0
1,2
1,4
BODY MASS (g)
0
10
20
30
40
50
60
70
80
× =NO SPERM
o =SPERM PRESENT
• =ABUNDANT SPERM
N = 241

breeding season September to March. This demonstrates that, although practically all males with a single testis plus epididymis mass above 0,5g had sperm, there seems to be no clear distinction between males having abundant sperm and those classified as 'sperm present'. Thus, many males having large testes (single testis mass > 0,8g) were classified only as 'sperm present'. If one assumes that such males were active breeders, this may throw some doubt on the validity of the subjective assessment of sperm.

This problem was investigated as follows : the single testis plus epididymis mass of each male was plotted against the mass of one seminal vesicle for the breeding season (Fig. 19). For this analysis, the breeding season was taken to end in February because of the evidence of a drop in reproductive index (see below) in March, shown in Fig. 21. Fig. 19 shows that males with small testes had small seminal vesicles. The masses of the latter were very significantly greater during the breeding season than in the winter (mean mass one seminal vesicle : September to February = 0,267g N = 195, March to August = 0,06924g N = 171; DF = 364, t = 11,17, p = < ,001). It is also evident that, with only one exception, males with a single testis mass below 0,6g had a single seminal vesicle mass below 0,2g. In fact, with only two exceptions, males with a single testis mass below 0,55g did not have a seminal vesicle mass above 0,15g. With regard to the occurrence of sperm, the situation is somewhat unclear in that although practically all males with a seminal vesicle mass over 0,15g

FIG. 19

Analysis of breeding condition of 190 killtrapped males : mass of one testis plus epididymis vs. the mass of one seminal vesicle, according to relative sperm abundance. Data pooled for the breeding season September to February only, 1973 - 1977.



had sperm, some males with smaller seminal vesicles and a testis mass below 0,6g also had sperm. However, males with a single testis mass above 0,6g showed a dramatic increase in the range of seminal vesicle masses, with many males having a seminal vesicle mass of well over 0,4g (Fig. 19). The assumption is made here that this increase in seminal vesicle mass was significant and marked a change in the reproductive status of the male. I would suggest, therefore, that males with small seminal vesicles below 0,15g and a single testis of less than 0,55 - 0,60g probably did not take an active part in breeding.

The status of each male during the breeding season has been illustrated by constructing a reproductive index (RI) comprising the mass of a single testis and epididymis plus the mass of a single seminal vesicle. This has been plotted against body mass and sperm abundance in Fig. 20 and against month and age class in Fig. 21. Applying the criterion devised above, males with a reproductive index of 0,7 - 0,8g or more are considered to be fecund and at least potentially reproductively active. This criterion seems to correlate reasonably well with the evidence as presented in Fig. 20. From this it can be seen that males with a small RI below 0,8g mostly had a body mass of 40g or less. Only 10 males heavier than 40g had a RI below 0,8g. Conversely, only two males of body mass less than 38g had a RI greater than 0,8g. Most males with a body mass of 40g or more, had a RI greater than 0,8g. From this evidence it is suggested that 38 - 40g marks the body mass range at which most males

FIG. 20

Analysis of breeding condition of 203 killtrapped males : reproductive index vs. body mass, according to relative sperm abundance. The reproductive index of each male comprised the mass of one testis plus epididymis plus the mass of one seminal vesicle. Data pooled for the breeding season September to March only, 1973 - 1977.

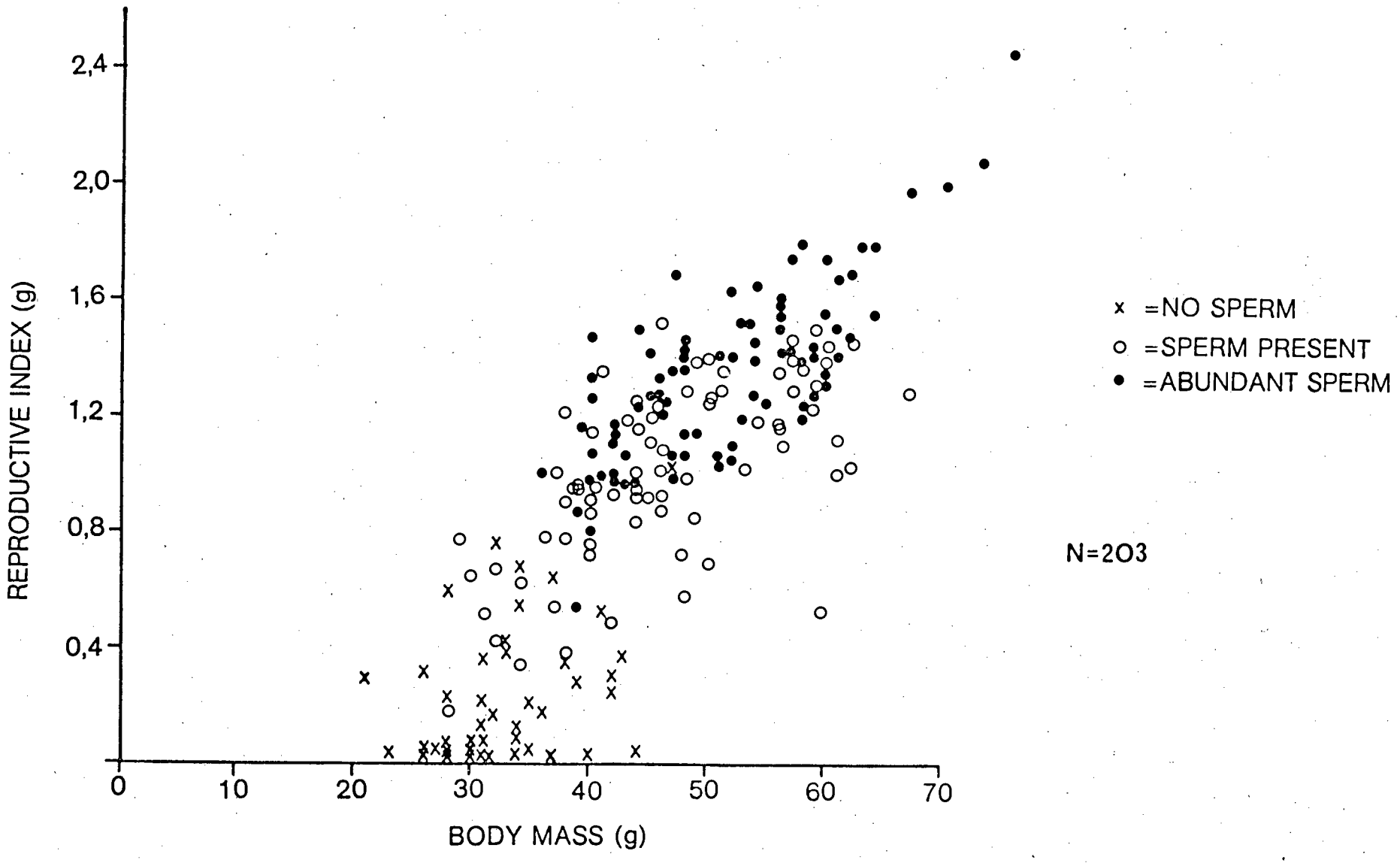
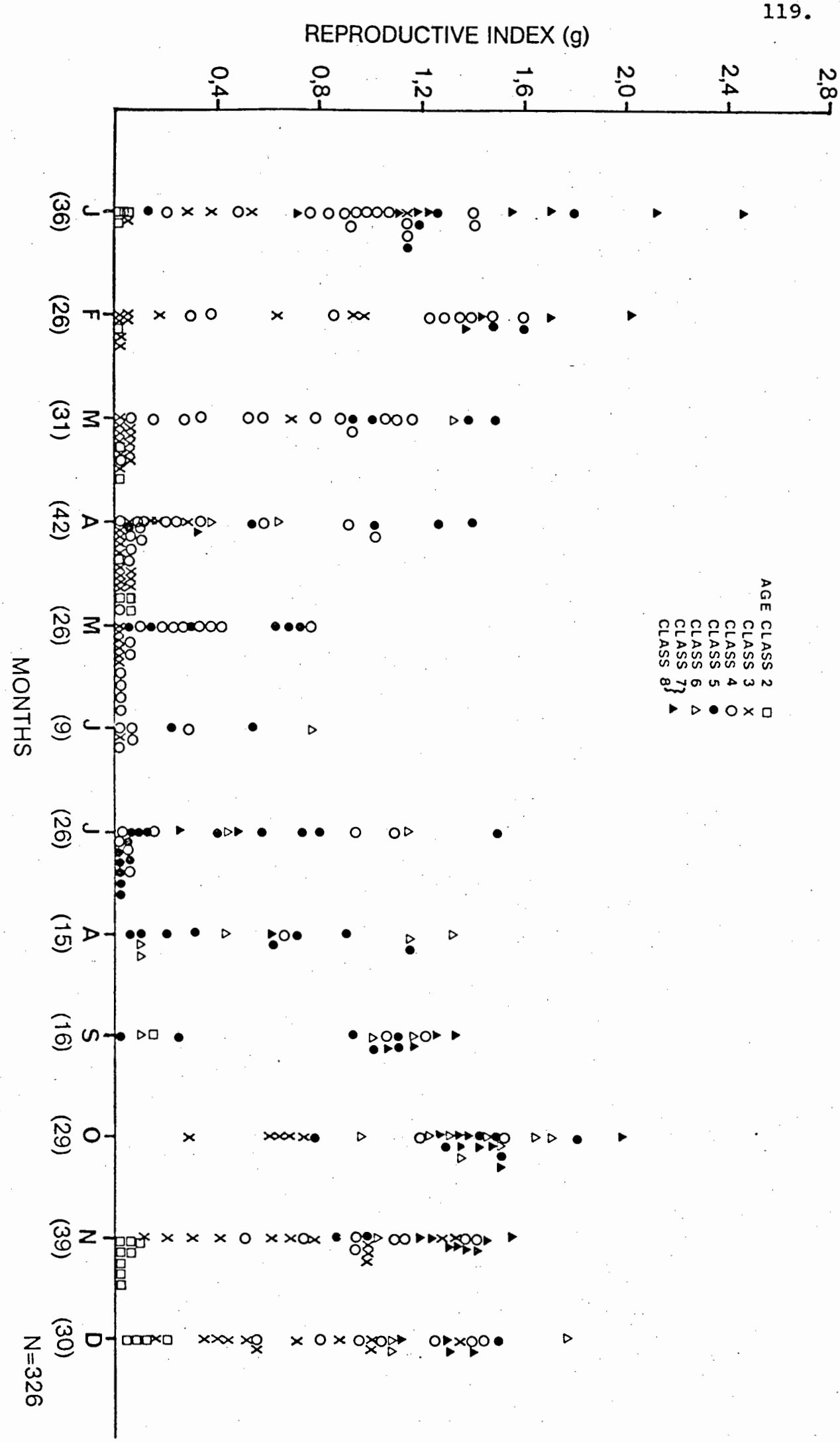

REPRODUCTIVE INDEX (g)
2,4
2,0
1,6
1,2
0,8
0,4
0
10
20
30
40
50
60
70
BODY MASS (g)
x =NO SPERM
o =SPERM PRESENT
• =ABUNDANT SPERM
N=203

FIG. 21

Analysis of breeding condition of 326 killtrapped males : reproductive index vs. age class. Data pooled for each month 1973 - 1977. The reproductive index of each male comprised the mass of one testis plus epididymis plus the mass of one seminal vesicle. See TABLE 10 for chronological ages. Monthly sample sizes in brackets.


REPRODUCTIVE INDEX (g)
0,4
0,8
1,2
1,6
2,0
2,4
2,8
AGE CLASS 2
CLASS 3
CLASS 4
CLASS 5
CLASS 6
CLASS 7
CLASS 8
J (36)
F (26)
M (31)
A (42)
M (26)
J (9)
J (26)
A (15)
S (16)
O (29)
N (39)
D (30)
MONTHS
N=326

become reproductively active in the summer.

From Fig. 21 it appears that males were least active in May and June and that there was a sharp rise in the reproductive index in September, just before the start of the main breeding season in October. Males retained high reproductive indices until February but there was a distinct decline in the index in March and April. This pattern of activity is confirmed by Table 17, which shows the percentage of adult males (age classes 3 - 8) which had a RI of > 0,7g each month.

If we look at the age structure of the males in Fig. 21, with only one exception all males of age class 5 or older were active (RI > 0,7), as were the majority of class 4 males, some of class 3 but none of class 2. There seems to be good evidence that young males have a greater chance of becoming sexually active in the season of their birth if born in the first half of the breeding season, than if born later. For example, in the case of class 3 males aged 6 - 12 weeks, 12 out of 28 (43%) had a RI greater than 0,7g in October to December, but this applied to only 3 out of 25 (12%) in January to March. Thus an overall figure of 15 out of 53 class 3 males (28%) had a RI greater than 0,7g from October to March and are considered capable of having taken an active part in breeding. This compares with the figure of 40% of class 3 males which were recorded as having sperm (Fig. 17) during the breeding season.

TABLE 17

PROPORTION OF BREEDING MALES EACH MONTH 1973 - 1977

Males with Reproductive Index > 0,7g were considered to be able to take an active part in breeding. Sample (N = 301) contains only age classes 3 - 8 (adults). See also Fig. 21

MONTH	MALES WITH RI > 0,7g	
	N	%
JAN	32	78
FEB	25	60
MAR	29	38
APR	38	13
MAY	26	8
JUN	9	11
JUL	26	23
AUG	15	33
SEP	15	80
OCT	29	86
NOV	31	77
DEC	26	73

RI = Reproductive Index = Mass (g) of one testis plus one seminal vesicle

The evidence as presented in Fig. 21, with high reproductive indices during the breeding months, declining to a minimum in the winter months of June and July, suggests the possibility of a reproductive cycle in the male during which testes and seminal vesicles might regress in the non-breeding season. Sheppe (1973) believed that the testes of some old Praomys (mastomys) natalensis regressed after the breeding season. Coetzee (1965) did not find clear evidence of a seasonal cycle in male Praomys natalensis in the Transvaal. Most big males seemed to have abundant sperm throughout the year. Delany (1972) citing Neal (1967) states that Neal found no evidence of testicular regression in rodents in Uganda. However, Neal (1977) himself says that in the case of Lemniscomys striatus there was a pronounced seasonal variation in the mass of the adult testes and vesiculae seminales which reached a maximum mass towards the end of the rains and then regressed to a minimum at the end of the dry seasons. Brooks (1974) states that there was regression in the testes of adult Rhabdomys in the winter months in the Transvaal. Both these assessments were based on the mean masses of the testes of adults in different months of the year.

However, it seems to me that care must be exercised in the interpretation of such data. For example, in Fig. 21 it is clear that the mean reproductive index in May and June is considerably lower than in the months October to February. However, this does not necessarily imply regression of the testes and seminal vesicles. This is because the age of the mice is critical. Thus, the sample might be composed

primarily of relatively young mice which were born in the second half of the breeding season and never developed adult size reproductive organs. This would be true, for example, of all the class 3 and 4 mice in May and June (Fig. 21) and could be true of some of the class 5 mice, the youngest of which might be only 5 months old (Table 10). These mice would have entered the winter period of slower growth before developing adult reproductive organs.

To demonstrate that regression has occurred, therefore, it is necessary to find older mice (e.g. classes 6, 7 and 8) with low reproductive indices outside the breeding season, since these invariably have a high index during the breeding season (Fig. 21). There are only a few mice which fulfil these requirements - notably one class 5, two class 6 and one class 7 in April; one class 6 in June, one class 6 and two class 7 in July and one class 7 in August, all of which had a RI below 0,8g. By August the class 6 mice are no longer reliable indicators since they could have been born at the end of the previous breeding season. In the mice just listed, therefore, it appears that regression of the reproductive organs did occur. However, these represent only a small proportion of tht total winter sample which consisted mainly of young mice in which full development of the testes and seminal vesicles had not taken place by the time the breeding season came to an end.

VIII.5 Variations in age of sexual maturity : proportions of young which bred in the year of their birth

In view of the claim of Krebs & Myers (1974 : 297) that "changes in the rate of sexual maturation of young voles and lemmings are a major driving force behind population cycles", we must now consider whether there were variations in the age of sexual maturity of young Rhabdomys from year to year. The evidence of Krebs & Myers (1974) tends to show that in some species of microtines there was some delay in maturation in years of peak density. In many published accounts, the ages of the young are derived from body masses but, as has already been pointed out for Rhabdomys, for animals over about 8 weeks old, this can be a highly unreliable procedure. This could be especially true if growth rates differed from one year to another. Krebs (1964, p. 26) claimed that the median weight at sexual maturity of summer-born young Lemmus was higher in the year of peak numbers than in the other years of the study. The implications of this are not stated by Krebs - but presumably they are that the lemmings were older at maturity in the peak year. This need not have been the case, however, since if the growth rate in the peak summer had been faster than in other years, then the age of the heavier lemmings could have been the same as in other years of slower growth.

Kalela (1957) studied Clethrionomys rufocanus in Finland and found that the number of summer-born young which matured the

same season varied from year to year. In particular, he showed that the number of early-born young males which matured in the summer of 1954 was far greater than that of 1955. In the case of females many early-born young matured in 1955, although fewer than in 1954. He claimed that this was due to the depressive influence of population density which was higher in 1955 than in 1954, though only trap indices are available for density estimation (Kalela, Fig. 6). It is not explained why there should have been such a discrepancy between the rates of maturation of males and females, nor is any connection demonstrated between population density per se and rate of maturation. The connection is merely assumed. The point can also be made that the breeding season in 1955 was two weeks later than in 1954 (Kalela, Figs. 7 & 8) and this could have influenced the maturation of young.

In the case of Rhabdomys, the pregnancy rates and numbers of sexually mature mice are shown in Table 18 for each year of the study. Mice have been divided into age categories on the basis of molar tooth wear; namely old overwintered animals and young of the year. Age at sexual maturity can be obtained only from the latter group. Since it has already been demonstrated that class 2 mice were never mature the analysis includes only class 3 and older animals and hence only mice that were born early in the season (i.e. they reached at least class 3 by March). It is plain from the figures in brackets in Table 18 that 80 - 90% of young females born early in the breeding season, bred in the same season. Among young males the proportions were lower and

TABLE 18

Comparison of reproductive performance of old (overwintered) and young mice.

Pregnancy rates of females and numbers of males sexually mature during each year of the study in breeding season September - March. Males were considered sexually mature if they had a Reproductive Index (RI) > 0,7g.

The RI = mass (g) of one testis plus one seminal vesicle.

		FEMALES				MALES				VALUE OF CHISQUARE			
		N	% of sample	No. pregnant	% pregnant	N	% of sample	No. with RI > 0,7	% mature	Females	Males	P	
1972/73	Overwintered	15	41	9	60,0	13	32	No	-	2,81		NS	1972/73
	Young of year	22	59	13 (+4)*	59,1 (77,3)	27	68	Data	-	0,001	-	NS	VS1973/74
1973/74	Overwintered	13	59	5	38,5	8	25	8	100	7,45		< ,01	1973/74
	Young of year	9	41	6 (+1)	66,7 (77,8)	24	75	18	75,0	1,10	,435	NS	VS1974/75
1974/75	Overwintered	7	19	6	85,7	16	27	16	100	8,04		<,01	1974/75
	Young of year	29	81	20 (+7)	69,0 (93,1)	44	73	30	68,2	1,09	9,735	<,01	VS1975/76
1975/76	Overwintered	42	53	21	50,0	36	49	33	91,7	2,94		NS	1975/76
	Young of year	37	47	21 (+9)	56,8 (81,1)	37	51	16	43,2	0,383	2,88	NS	VS1976/77
1976/77	Overwintered	29	47	19	65,5	13	35	13	100				
	Young of year	33	53	19 (+10)	57,6 (87,9)	24	65	14	58,3				

Young of the year were age classes 3 or 4, plus class 5 if caught in January or later and class 6 if caught in February or later.

* Females in brackets were parous or lactating, hence they DID BREED in the year of their birth.

also more variable. Since it is not possible, with the current techniques, to state precisely the age at maturity of the mice we must rely on the fact that differences in the age of maturity in different years would show up as a higher or lower percentage of young mice breeding each year. As already explained, mature mice were mostly already pregnant or parous when captured and hence it was impossible to say precisely when they became mature.

The proportions of young mice breeding in consecutive years have been compared by means of chisquare in Table 18. There were no significant differences between years in the numbers of young females breeding, but it was interesting that the highest proportion of young females found breeding (93,1%) was in 1974/75 which was the year of peak numbers. It has already been shown that males matured more slowly than females and this shows up in Table 18 as lower proportions of young males with reproductive index greater than 0,7g. The only significant difference in the proportion of young males breeding was between 1974/75 and 1975/76 when the proportion breeding in the latter year (43,2%) was significantly lower (X^2 = 9,735) than in the former. The breeding season of 1975/76 commenced in October 1975 with an exceptionally dense population for that time of year and was followed by the swiftest decline of the study in winter 1976.

In summary, one can say that at least 80% of the early-born young females bred in the season of their birth and this

did not appear to vary significantly from year to year. The proportion of young males becoming sexually mature in the same season was lower and more variable. There was no obvious correlation with population density since in 1974/75, when the highest density of the study was recorded, the proportion of young females breeding was the highest on record and of young males was the second highest. However, the following breeding season, which commenced with an unusually high population, the proportion of young females breeding remained high (Table 18) but the proportion of young males maturing dropped to the lowest of the study.

VIII.6 Summary of findings on sexual maturity

In general, young females attained sexual maturity when they entered age class 3 at about 6 weeks of age during the breeding season. The criterion used was pregnancy. Their body mass at sexual maturity was around 30g. At least 78 - 90% of young females (age class 3 and above) born early in the breeding season were found to breed in the season of their birth but animals born too late to reach age class 3 before the end of March overwintered in the non-parous state.

Young males grew more slowly and attained sexual maturity later than females as judged both from the occurrence of sperm and a reproductive index equal to the mass of one testis plus the mass of one seminal vesicle. This was achieved at about 11 - 12 weeks old during the breeding season when the

males weighed around 40g. The proportion of young males born early in the breeding season which attained maturity in the same season varied from 43 - 75% in this study. This was lower than that of females due mainly to the fact that far fewer age class 3 males became mature than females.

VIII.7 Litter size

The number of surviving offspring produced per female clearly has a major influence on population growth and hence one way to increase population growth would be to increase litter size, provided the female can rear the young. According to Krebs & Myers (1974 : 291) litter size may be affected by season of year, age and body mass of the female and by whether or not she is parous. There may also be changes in litter size from year to year.

The frequency distribution of all the litters counted during the dissection of killtrapped mice (145 litters, 711 embryos excluding resorbed embryos) is shown in Fig. 31 (a). This is an overall mean of 4,90 $\pm$0,11 healthy embryos per litter (range 2 - 9). This agrees fairly well with the figures quoted in the literature, e.g. mean 4,5 N = 6, Hanney (1965); mean 5,0 N = 11, Smithers (1971); mean 4,6 N = 5, Hubbard (1972); mean 5,9 N = 18, Brooks (1974); though Brooks' figure appears to be significantly higher than the others.

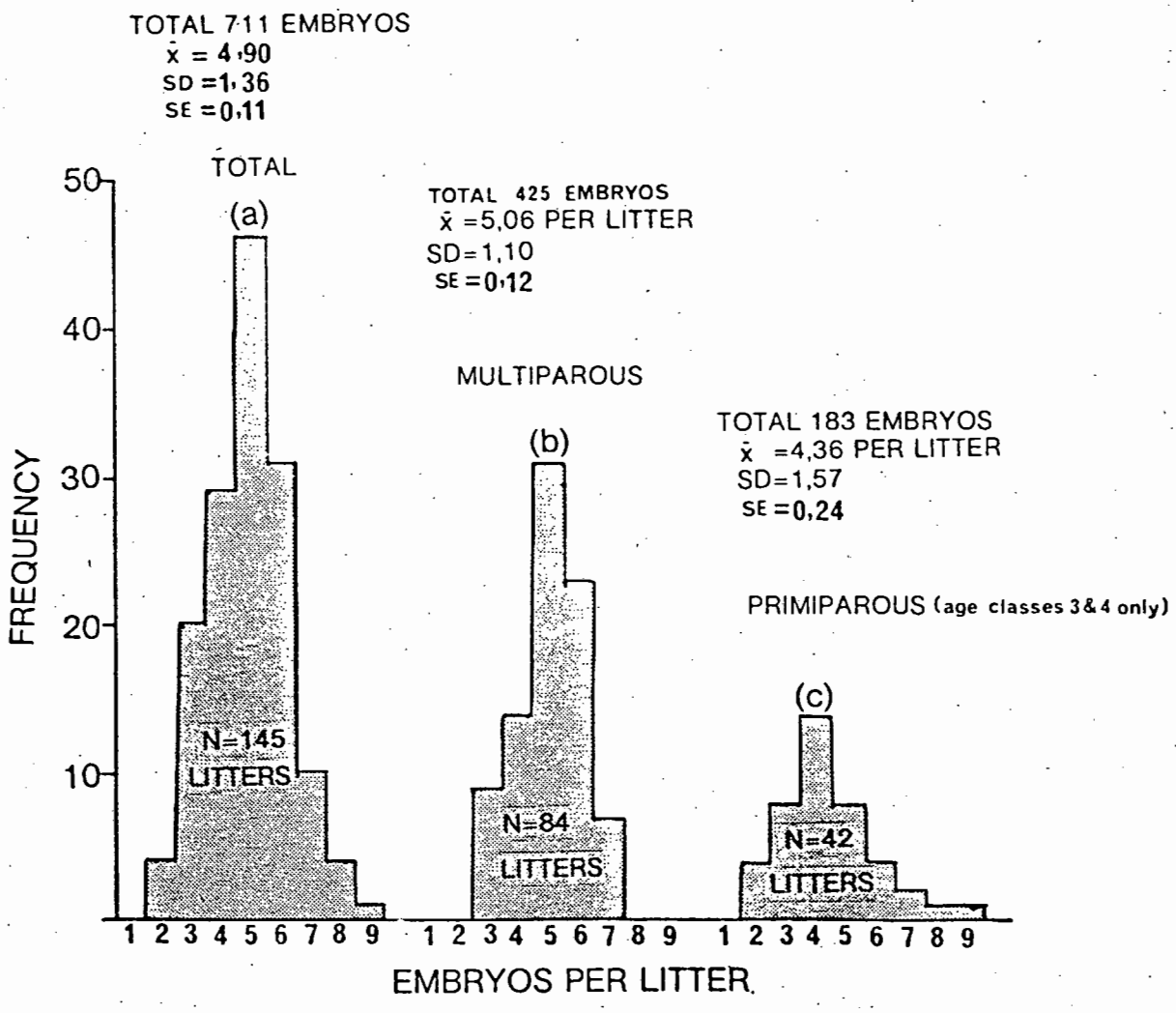
We must now examine the data, controlling for some of the variables mentioned above. Firstly, the age of the female, which Delany (1974) also says may influence litter size. The females were divided into multiparous and primiparous on the basis of whether placental scars were present or absent on the uterus; the object being to segregate young from older females. The distribution of embryos is shown in Fig. 31 (b, c). Further analysis of the ages of the primiparous females showed that in the early part of the breeding season many of them were old females of age class 5 or more which had been born at the end of the previous season, but too late to come into breeding condition. They had thus passed the winter in the non-parous state. These were, therefore, excluded from the sample of primiparous females in Fig. 31 (c) which includes only young females of age classes 3 or 4. The litter sizes of these older primiparous females were then compared with the litters of multiparous females of the same age, to test for significant differences. The result of this was that a sample of 13 primiparous females in age classes 5, 6, 7 and 8 had a mean litter size of 5,38 whereas 44 multiparous females in the same age classes had a mean litter size of 5,30 ($t = 0,25$ NS). These older primiparous females were, therefore, included in the sample of multiparous females in Fig. 31 (b), since there was no difference in the mean litter size.

There were 425 embryos in 84 litters of multiparous females or $5,06 \pm 0,12$ embryos per litter (range 3 to 7) compared with 183 embryos in 42 litters of primiparous females or

FIG. 31

Frequency distribution of litter sizes of pregnant killtrapped females. Litter sizes of primiparous and multiparous females analysed separately.

Total sample = 145 litters.



4,36 ± 0,24 embryos per litter (range 2 to 9). Comparing these values by means of Student's "t" yields t = 2,90 for DF = 124, p < ,01. Thus the first litter of young females up to about 4 months old is significantly smaller than the mean value for older females.

Another factor which could influence litter size is the body mass of the female, as reported for voles (Microtus spp.) for example, by Keller & Krebs (1970). Fig. 22 shows an analysis of female body mass versus litter size. Since the gravid females were not weighed minus uterus at the time of dissection, only those females were used in the analysis whose embryos were too small to measure and which were in the earliest stages of pregnancy. Hence, the assumption is made that the small mass of the uterus in these cases will not significantly affect the result of the analysis. Fig. 22 shows that although there is a considerable scatter of points, there is a significant correlation of litter size with body mass (t = 3,21 DF = 48 p< ,01). For example, females carrying four embryos were in the mass range 24 - 49g whereas females carrying six embryos were in the range 36 - 68g. Thus, heavier females did tend to have larger litters.

The next question to consider is whether litter size varied from year to year. The litter sizes of pregnant females for each year of the study, primiparous and multiparous separately, have been analysed in Table 19. The mean litter size of multiparous females did not vary much through-

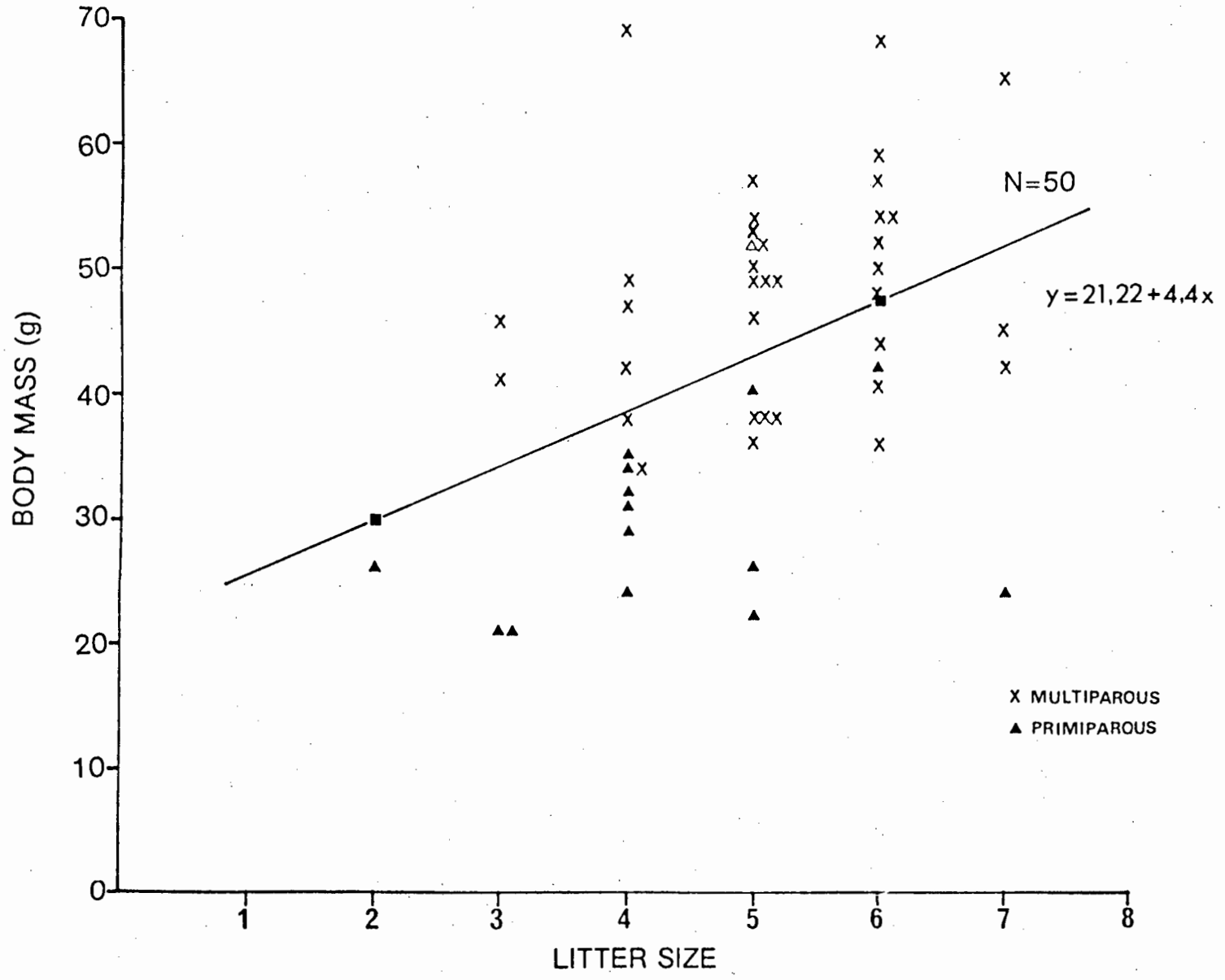


FIG. 22

Analysis of body mass vs. litter size of 50 kill-trapped females. Only females in very early pregnancy (embryos recorded as crown-rump length = zero) included in the analysis. Regression shows that there was a significant correlation of litter size with body mass.

TABLE 19

MEAN LITTER SIZES EACH YEAR AND STATISTICAL COMPARISONS

	MULTIPAROUS FEMALES					PRIMIPAROUS FEMALES (UP TO 4 MONTHS OLD - AGE CLASSES 3 & 4)				
	1972/3	1973/74*	1974/75	1975/76	1976/77	1972/73	1973/74	1974/75	1975/76	1976/77
No. of litters	15	6	11	35	29	7	4	15	9	11
Mean Litter Size	4,9	5,2	5,6	5,0	5,1	4,0	5,0	5,7	3,8	3,5
S D	1,407	0,687	1,206	0,98	1,187	1,732	0,816	1,632	0,666	1,214
S E	,376	,307	,381	0,166	0,220	0,707	0,471	0,436	0,235	0,384
t	0,4936	0,742	1,676	0,3692		1,070	0,818	3,308	0,662	
P	NS	NS	<0,10	NS		NS	NS	<0.01	NS	
TOTAL EMBRYOS RESORBED	0	1	0	1	23	0	0	0	1	9

*Litter born in July excluded

out the study but it did rise steadily to its highest level during the peak density year of 1974/75, before declining in the two following years. There were no significant differences between consecutive years as shown by 't' test. The mean litter sizes of primiparous females varied more than those of multiparous females, but they showed precisely the same trends as those of the older females. Mean litter sizes rose steadily during the first three years of the study, reaching a peak in the breeding season of 1975/75 when population density was the highest that we recorded. The only significant difference in litter size was in 1975/76 which was significantly lower than 1974/75 ($t = 3,3$ $p < ,01$; Table 19).

The possible significance of these changes in mean litter size must remain in doubt. One can note that both categories of female produced their largest litters in the year of peak population density and that the young females appeared to be far more affected by changing environmental conditions, as expressed in the litter size, than were older females.

Krebs & Myers (1974) review the literature on changes in litter size of various species during different phases of a microtine cycle. They report that most authors did not find any significant changes from year to year. Krebs & Myers (1974 : 293) suggest that "if the changes in litter size are to be an important driving force in the population cycle, litter size should be depressed in the decline phase and enhanced in the increase phase". Some authors have, apparently, found some evidence of a decreased litter size

in the peak year. Krebs & Myers (1974 : 293) cite Hoffmann (1958) as reporting a 10 - 25% drop in litter size during the peak summer for a Microtus montanus population. However, this conclusion is not consistent with the evidence presented in Hoffmann's Table 1. It can only be reached by considering just the September sample and ignoring the June and July samples. If one takes only the July sample, then the decline year of 1954 had the lowest litter size. If one calculates a mean for the whole breeding season for each of the three years of his study, then one obtains the following mean litter sizes: 6,18 (N = 16) in 1952 (increase); 6,54 (N = 62) in 1953 (peak); 6,46 (N = 30) in 1954 (decline). These results do not seem to be consistent with a drop in litter size in the peak summer.

Keller & Krebs (1970) found that the litter size of M.ochrogaster was depressed 25% in the peak summer of 1966, but similar in the increase and decline summers of 1965 and 1967, but they found no differences in M.pennsylvanicus over the same period. Hoffmann (1958) found no change in litter size in a population of M.californicus. Krebs (1964) found no significant differences in litter size of two species of lemming over a four year period.

Hamilton (1937, Fig. 2) working on M.pennsylvanicus found considerable variation in litter size from month to month in the same season, but it appears that his largest litters occurred in his year of highest density (1935), though he does not give a mean size for each year.

VIII.8 Pregnancy rate

The mean pregnancy rate for the whole study is presented in Fig. 13 (c). It is now necessary to consider whether there were changes from year to year. The numbers and percentages of mature females that were pregnant during the breeding season for each year of the study are presented in Table 18. The crude pregnancy rates are presented for overwintered females and young of the year separately. In addition, figures in brackets for young females are the additional number that were parous or lactating, indicating that they had bred. This figure gives a better estimate of the total young females that bred in the year of their birth. There were no significant differences in the numbers of young females that had bred in consecutive years of the study. It was not possible to calculate the total numbers of overwintered females that had bred each year because uterine scars indicating that the female had bred could, in some cases, have persisted from the previous breeding season and it was not possible to distinguish them with certainty. One is, therefore, dependent on crude pregnancy rates for these older females, which could be liable to random sampling errors. Testing pairs of consecutive years by means of chi-square showed that the pregnancy rate in 1974/75 was significantly higher than in either the previous or the following year ($p < ,01$).

It is interesting to note that in both overwintered and young females the highest pregnancy rates were recorded in

1974/75, the year of peak population density. The fact that litter size was also highest that year suggests the possibility that nutrition may have been a factor and that an unusually abundant food supply may have contributed to good reproduction. Food supply is discussed in Chapter XII, but unfortunately variations in food supply during the study are unknown. In microtines, Krebs & Myers (1974 : 293) say that a review of the literature shows that most workers agree that pregnancy rate does not vary in relation to the population cycle.

VIII.9 Length of breeding season

The mean length of the breeding season for the whole study can be gauged from the distribution of breeding females in Fig. 13 (c). We must now consider whether this varied from year to year. The number of breeding and non-breeding adult females is shown for each month for each year of the study in Table 20. It is apparent that breeding normally commenced in September (no pregnant females were found in August) and ended in March or April each year. Only in 1975/76 were pregnant females found as late as May and this extension of the breeding season was coupled with a late start to it (October before breeding got under way). There appear to have been no major differences in length of breeding season from year to year, but the sample sizes in some months in Table 20 are very small. This information should, therefore, be augmented by examining the number of new juve-

TABLE 20

Analysis of breeding condition of adult female Rhabdomys from killtrap data for each year of the study. (Age classes 3 - 8 only).

B = Breeding = females on autopsy found to be pregnant, lactating, oestrus or showing recent uterine scars. Number pregnant in brackets.

NB = Non-breeding = includes parous animals which did not show recent signs of activity.

		AUG	SEPT	OCT	NOV	DEC	JAN	FEB	MAR	APR	MAY
1972/73	B	0	6 (4)	7 (4)	5 (4)	5 (4)	4 (2)	2 (1)	3 (3)	0	0
	NB	5	0	0	0	0	0	3	2	5	5
1973/74	B	2 (0)	3 (1?)	1 (0)	4 (4)	1 (1)	2 (2)	2 (1)	3 (2)	3 (0)	0
	NB	2	4	1	1	0	0	0	0	0	6
1974/75	B	0	1 (0)	5 (5)	4 (4)	6 (6)	4 (4)	5 (5)	4 (2)	0	0
	NB	1	0	0	1	0	2	2	2	5	9
1975/76	B	0	1 (0)	10 (7)	9 (6)	8 (6)	15 (10)	12 (10)	5 (3)	3 (3)	2 (2)
	NB	10	6	2	1	2	3	0	5	10	11
1976/77	B	1 (0)	4 (4)	7 (7)	6 (3)	8 (6)	4 (4)	9 (8)	10 (6)	3 (2)	0
	NB	7	3	2	4	0	1	3	1	11	6
TOTAL	B	3 (0)	15 (8)	30 (23)	28 (21)	28 (23)	29 (22)	30 (25)	25 (16)	9 (5)	2 (2)
	NB	25	13	5	7	2	6	8	10	31	37

niles livetrapped during the breeding season each year (Fig. 3). In the first two years of the study no juveniles were caught until November, but in the last three years juveniles appeared in October. In every year, some juveniles were caught in May, indicating pregnancies in April. One interesting anomaly was the complete absence of juveniles in February 1974.

Although it appears that breeding may start later in some years than in others, the length of the breeding season was in general fairly constant and cannot be compared with the great variability in the breeding season of some microtines. Krebs & Myers (1974 : 294) say that the breeding season of many microtines is very elastic and that changes in the length of the season are a major driving force in causing the population cycle. Winter breeding has quite often been noted in various species of vole and lemming.

VIII.10 Gestation period and the number of litters produced per season

The next important parameter to consider is how many litters a female has in the course of a breeding season. In this connection the gestation period is of some importance. Mitchell (1973) recorded gestation periods of 27, 26, 26, 25, 25 and 24 days (mean 25,5 days) in 6 litters born in captivity whose dates of mating were known. Four of these in-

volved a post-partum oestrus and hence in four cases a second litter arrived 27, 26, 25 and 25 days after the first one. Brooks (1974) gives the mean gestation period of 14 litters as 25,4 days and also confirms a post-partum oestrus. In his captive colony the mean interval between 17 'successive' litters was also 25,4 days. Choate (1971) gives a gestation period of 22 days, but this must be a minimum figure and the figure of 14 days of Meester and Hallett (1970) must be erroneous. One can theorise, therefore, that if the gestation period is about 25 days, the breeding season is at least 180 days long and a post-partum oestrus occurs then a female should be able to produce around 7 litters per season, provided she survived for the whole season.

An attempt to arrive at a reasonable estimate of the actual production was made by analysing the data from killtrapped females at the <u>end</u> of each breeding season. Thus, the data from all pregnant or parous females (with the exception of very old females, age class 8) collected from March to July were pooled for each season. The number of uterine scars plus embryos was summed for each breeding female and this was considered to reflect the breeding performance of each female over the preceding season. The results are presented in Table 21. The total scars plus embryos for all killtrapped females each year was divided by the number of females to give mean number of young born to each female. This was then divided by the mean litter size each year to yield the mean number of litters born per breeding female. It should, perhaps, be stressed that these results apply to females that

TABLE 21

ESTIMATED NO. YOUNG BORN PER PAROUS FEMALE OVER THE WHOLE BREEDING SEASON FOR EACH YEAR OF THE STUDY. FEMALES COLLECTED BETWEEN MARCH AND JULY EACH YEAR (END OF BREEDING SEASON). TOTAL UTERINE SCARS PLUS EMBRYOS FOR EACH FEMALE ACCUMULATED FOR EACH YEAR.

	1972/73	1973/74	1974/75	1975/76	1976/77*	TOTAL
NO. FEMALES	11	9	19	27	21	87
TOTAL UTERINE SCARS & EMBRYOS	111	108	215	269	131	834
MEAN NO. OFFSPRING (SCARS & EMBRYOS)	10,1	12,0	11,3	10,0	6,2	9,6
RANGE PER FEMALE	3 - 16	6 - 17	3 - 25	3 - 25	2 - 14	3 - 25
S D	4,70	4,24	6,45	5,35	3,05	-
+MEAN LITTER SIZE	4,59	5,20	5,65	4,80	4,68	4,92
MEAN NO. LITTERS PER FEMALE	2,2	2,3	2,0	2,1	1,3	2,0
RANGE	1 - 3	1 - 3	1 - 5	1 - 5	1 - 3	

* Females collected March - May only in 1977.

+Mean litter size is a mean for all females collected (See also Table 19)

had had at least one litter. Non-breeding females were not included, nor were old females, age class 8, which might conceivably have taken part in two breeding seasons.

The accuracy of this analysis depends largely on the reliability of uterine scars as a record of embryos. Uterine scars are believed to persist for the life of the animal. Brooks (1974) examined the uteri of 15 parous captive females and reported no loss of scars in the first 6 months. Evidence from three of his females seemed to show some loss of scars more than 6 months after the birth of a litter. Superimposition of scars of later litters on those of earlier sometimes rendered counting difficult and may have introduced errors. There would also have been some errors due to the precise number of scars being difficult to count in very gravid females - hence these would have been minimum values. Since there were no very old females in the sample, it is believed that counting and persistence of scars were sufficiently reliable for the results to give a good indication of at least the minimum number of young born to females during a breeding season.

The maximum number of litters actually produced by one female appears to be five (Table 21) and the mean litter production of 1,3 to 2,3 litters per season is surprisingly low. Choate (1971) reported a captive female which produced 21 litters before dying at the age of 29 months. An attempt to assess the possible lifetime production of female Rhabdomys was made by analysing the scar plus embryo counts of old (classes 7 and

8) females at the end of the breeding season between March and August. There were 8 females with a total of 158 scars and embryos (range 11 - 28) - a mean of 19,8 offspring per female. As this sample was rather small, a further sample of 12 class 7 and 8 females was taken from the second half of the season (January and February). These yielded a total of 237 scars and embryos (range 8 - 28) - also a mean of 19,8 offspring per female. Hence it would appear that a female who survives to old age may expect to produce on average about four litters during her life. This, again, is surprisingly few when one considers the potential productivity of an animal able to produce a litter every 25 days. The animals of age class 7 and 8 would be in the age range 9 - 18 months and could thus partake in a maximum of two breeding seasons. A lifetime production for females which survive to old age, of four litters, therefore is more or less consistent with the above finding of little more than two litters per season.

One of the possible reasons for this relatively low number of litters could be related to the age structure of the females, which can be seen in Table 18, from the percentage of young of the year in each year's sample, for the breeding season September to March.

The Table illustrates the fact that a large proportion were young of the year - up to 75% of males and 81% of females. Since females are not sexually mature until the age of 6 weeks or older, most of them will not be mature until the

second half of the season. It, therefore, follows that many of them will only have time to bear one or two litters before the breeding season ends. This, then, could be a factor influencing the apparently low number of litters produced.

The mean number of offspring (scars plus embryos) per female for pairs of consecutive years are compared statistically in Table 22. The only significant difference was between 1975/76 and 1976/77, when the number of offspring produced per female dropped significantly (DF = 46, $t = 2,90$, $p < ,01$). As the age structure of the females in the latter year did not appear to differ markedly from previous years (with the exception of 1974/75), the explanation must apparently be sought elsewhere. Table 19 shows the total number of resorbing embryos counted each year in the course of dissecting pregnant females. Resorbing embryos could be recognized because they were smaller than healthy embryos. It is clear that, in general, it was rare to find resorbing embryos in Rhabdomys uteri, only three being counted during the first four years of the study. However, in 1976/77 there was a dramatic rise in the number of resorbing embryos counted, to a total of 32 in 40 litters. This suggests that some unusual factor must have been operating that year which interfered with reproduction and caused fewer young per female to be produced. The possible reasons for the resorption of embryos are unknown.

This drop in reproduction is also reflected in Table 4, which

TABLE 22

Statistical comparison of mean number offspring per female (from Table 21) for pairs of consecutive years.

	1972/73 vs 1973/74	1973/74 vs 1974/75	1974/75 vs 1975/76	1975/76 vs 1976/77
DF	18	26	44	46
t	0,94	0,30	0,74	2,90
P	NS	NS	NS	< 0,01

shows that both the number of juveniles livetrapped and the population peak was lower in 1976/77 than in the previous two years. However, the drop in the number of juveniles captured, from 155 in 1975/76 to 114 in 1976/77 (26% drop) was not as great as might have been expected from the 40% drop in mean number of young born per female from 10,0 to 6,2 (Table 21). Furthermore, the breeding season of 1975/76 began with 48 females on the control grid whereas that of 1976/77 began with only 3 females yet subsequent population growth was the fastest of the whole study (Table 5). This does not appear to be consistent with a low production of young by females. Conversely, the drop in number of juveniles captured from 201 in 1974/75 to 155 in 1975/76 (23%) is far greater than might have been expected from the drop in mean number of young born per female from 11,3 in 1974/75 to 10,0 in 1975/76 and also from the fact that the 1974/75 breeding season began in September, with far fewer females (10) than did 1975/76 (48 females, Table 4). The relationship between the number of young produced per female and the number of juveniles livetrapped is thus far from clear. This suggests that the mortality of the young between birth and entering the trappable population may have played an important role.

VIII.11 Survival from birth

The survival of nestlings from birth has, therefore, been calculated for each year of the study and results displayed

in Table 31 (for explanation of the method and further discussion, see p.181). This shows that the lowest nestling survival was recorded in 1972/73 and 1975/76. The poor survival in the latter year (only 1,7 young weaned per pregnancy) probably explains the lower number of juveniles livetrapped compared with 1974/75, which had the second best nestling survival and the relatively high number of 2,9 young weaned per pregnancy, which would have contributed to the high population peak recorded that year. Survival of nestlings in 1976/77 was intermediate and the data show that only just more than two young per pregnancy were weaned. This shows a 20% increase over the number weaned the previous year (1,7). The drop in overall number of juveniles livetrapped (Table 4) in 1976/77 was presumably due to the much smaller number of breeding females that year (Table 31). It is not clear what the precise significance is of the far fewer mean number of young born per female per breeding season in 1976/77 (Table 21) - but presumably some of this loss was compensated for by the improved survival in 1976/77 compared with the previous year.

IX. SEX RATIO

IX.1 Estimation of sex ratio of wild populations

The sex ratio of most mammal populations is approximately 1:1. Myers & Krebs (1971a) quote the hypothesis of Fisher (1958) that "because each sex contributes equally to the genetic composition of future generations, selection will act to equalize the expenditure of energy in producing offspring of each sex. The population sex ratio should thus tend to equality if the cost of producing males and females is equal".

Examination of sex ratios in wild populations of small rodents reveals some interesting results obtained by livetrapping. Krebs & Myers (1974 : 299) say that in microtines "males are typically less abundant than females". It is necessary to examine rather carefully whether the results obtained reflect the true situation in the population or whether they are mere artifacts of trapping. For example, Smith (1968) estimated the size of a population of Mus musculus and one of Peromyscus polionotus in the same field first by marking and releasing all animals captured and then by digging out the complete burrow system. The sex ratios of adults obtained by live-trapping were as follows : for M.musculus, 60% males (N = 34); for P.polionotus in autumn, 83% males (N = 18) and in summer 65% males (N = 20). However, when he dug out the burrow system he obtained the following : for M.musculus, 45% males (N = 36) and for P.polionotus in autumn 45% males (N = 29) and in summer also 45% males (N = 31). Thus, although these

samples are very small, it appeared that livetrapping was not successful in capturing all the animals and that females of both species were avoiding the traps. In the case of P.polionotus it appeared that pregnant and lactating females in particular were avoiding the traps as most of these were caught only in the burrow system. Smith (1968) also maintains that the greater range of movement of males will expose them to capture in traps more frequently and this may partially explain the greater proportion of males caught. If it is true that part of a small mammal population is untrappable (for example pregnant and lactating females) then this must throw doubt on population estimates based on livetrapping.

Myers & Krebs (1971a) state that sex ratios of mammals may be estimated in two ways by livetrapping:

1. Residents: from resident animals known to be living in the trapping area at any instant, and
2. Recruits: from all animals recruited into the population over an extended time period.

The former sex ratio of residents is the effective sex ratio of the population. It can be calculated simply from the number of males and females caught in any month of trapping or, since this is liable to be highly variable, a better estimate may be obtained by accumulating the number of males and females caught each month (including recaptures) over the whole study period. The latter (i.e. recruits) is cal-

culated from the sex ratio of new (unmarked) recruits pooled over the entire study period.

Myers & Krebs (1971a) studied the vole species Microtus pennsylvanicus and M.ochrogaster in Indiana and analysis of sex ratios revealed some interesting anomalies. Live-trapping was conducted at 14 day intervals over a two year period. The sex ratio at birth favoured males in both species, although this was not statistically significant in either (M.pennsylvanicus: 281 young, 53,0% males; M.ochrogaster: 1469 young, 51,6% males). Among resident animals of both species caught during 2-day trapping periods there was a significant deficiency of males. On the average, about 45% of the trappable M.pennsylvanicus (N = 10317) and about 47% of the M.ochrogaster (N = 3445) were males. This was in contrast to several populations of both species in which new recruits pooled over the whole study period showed a significant excess of males (53,9% males for M.pennsylvanicus N = 1522 and 55,6% males for M.ochrogaster, N = 907). Myers & Krebs have drawn attention to the existence of this discrepancy in the presence of excess male recruits but a deficiency of male residents in these populations.

Southern (1973) carried out six-monthly index trappings over a 20 year period, between 1952 and 1972, on Apodemus sylvaticus and Clethrionomys glareolus, near Oxford. His results show a significant excess of males in both species when pooled over the whole study period (Apodemus 55,2% males, N = 968; Clethrionomys 53,1% males, N = 2494). Southern

does not give statistical tests of these results and claims that, if an equal sex ratio is assumed in nature, then "any bias in the trap catches is slight compared with the results of Smith" (1968). However, if one performs a chisquare test on Southern's results, it is clear that there is a very significant departure from the expected 1:1 ratio. For Apodemus X^2 = 10,33 and for Clethrionomys X^2 = 9,75; in both cases $p < ,01$.

These results all require explanation and it is necessary to examine whether similar anomalies may have occurred in the livetrapping of Rhabdomys. Fig. 23 illustrates the sex ratio in the control grid during each month of the study. It is evident that it was quite variable and in general that there was a deficiency of males. The overall ratio for the whole study period (the sum of the individuals captured each month) which is shown under residents in Table 23, was 48,3% males. This just falls short of significance at the 95% level. The results of the 13 months trapping in grid K are also shown. In this grid the proportion of only 45,1% males was even lower and was highly significant at the 95% level (X^2 = 19,1, $p < ,001$). The rest of Table 23 shows the total number of recruits (new mice) caught throughout the study, adults and juveniles separately. It is evident that, in contrast to the residents, there were significantly more males among the recruits than females. This was true especially of the adults, but not of the juveniles. Although the excess of males in grid K did not reach statis-

FIG. 23

Fluctuations in sex ratio of R.pumilio livetrapped on the control grid each month from 1972 - 1977. Sample size given for each point.

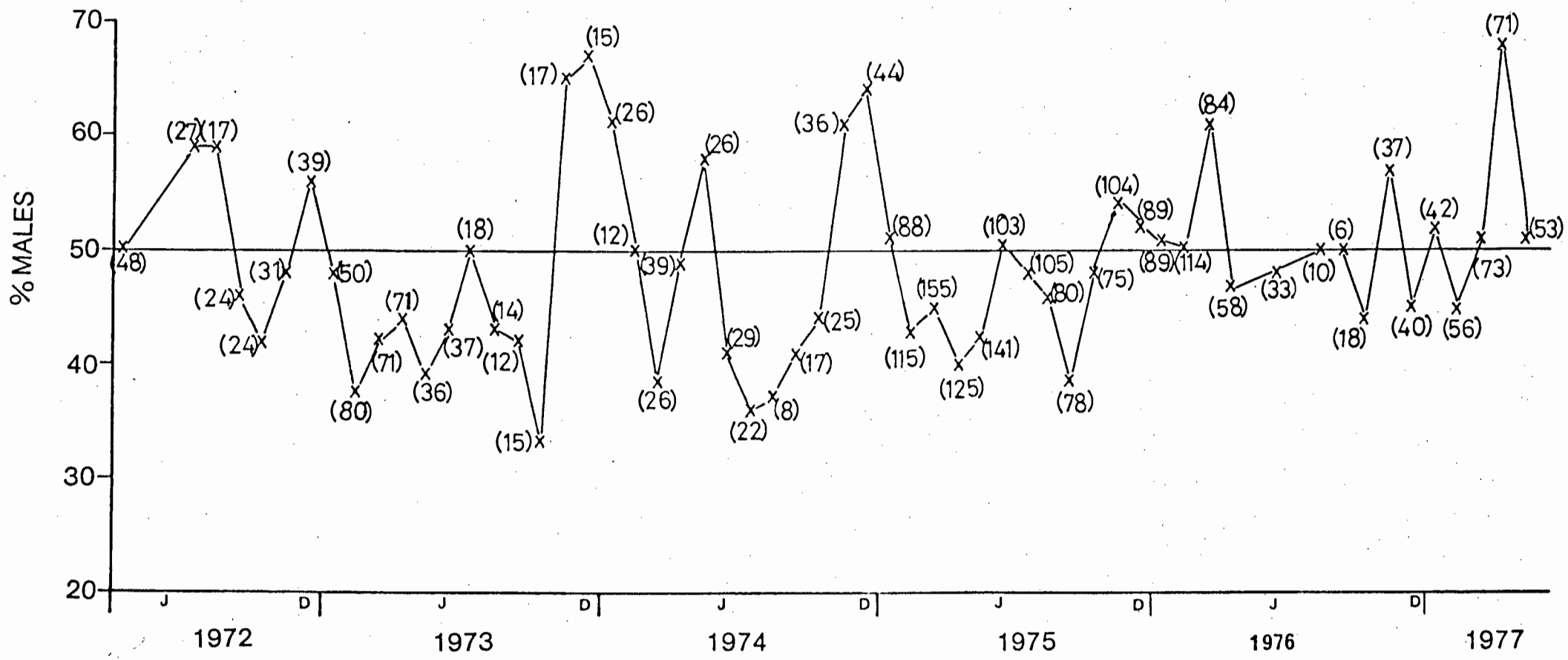


TABLE 23

Observed sex ratios of livetrapped mice on control grid and grid K.

Numbers of livetrapped mice (recruits and residents) showing proportion of males.

Juveniles = mice < 30g body mass at first capture.

	¤ RECRUITS									*RESIDENTS CUMULATIVE TOTAL	
	CONTROL			CONTROL			GRID K **			1972-77	Feb. 75-76
	All	Adults 1972-1977	Juveniles	All	Adults	Juveniles	All	Adults	Juveniles	CONTROL	GRID K
				FEBRUARY 1975 - FEBRUARY 1976							
Males	676	370	306	273	138	135	476	340	136	1447(771)	908(432)
Females	581	261	320	240	104	136	474	322	152	1551(970)	1104(630)
% Males	53,8	58,6	48,9	53,2	57,0	49,8	50,1	51,4	47,2	48,3	45,1
Chisquare	7,18	18,8	0,31	2,12	4,78	0,004	0,004	0,49	0,9	3,61	19,1
P	<0,01	< 0,001	NS	<0,2	< 0,05	NS	NS	NS	NS	< 0,10	< 0,001
				>0,1	> 0,02					> 0,05	

N.B. Observed sex ratios tested by means of chisquare.

* Residents are all mice caught each month accumulated over the study period. In brackets are recaptures.

¤ Recruits are NEW (unmarked) mice each month pooled over the study period.

** Grid K was livetrapped only from February 1975 - February 1976

tical significance, there were still markedly more males among the recruits than among the residents (50,1% against 45,1%). Brooks (1974) found a sex ratio of 54,8% males among 341 Rhabdomys recruits in the Transvaal, which fell just short of statistical significance. These results show a similar discrepancy to that described by Myers & Krebs (1971a) for Microtus and we must attempt to examine the possible causes.

IX.2 Factors influencing observed sex ratios

Myers & Krebs state that the sex ratio observed in a population at any instant will be affected by five factors : 1. the sex ratio at birth; 2. differential survival of both sexes of all age groups; 3. differential trappability of males and females: different responses of the sexes to livetraps; 4. differential movement: if males have larger home ranges than females the effective size of the trapping area will be larger for males provided they remain within the trapping area. Thus males may be more likely to encounter a trap and hence more males than females will be caught; 5. differential growth: the recruitment of both sexes into the adult age class will be influenced by the rate of growth. In this study, for practical reasons, live Rhabdomys were divided into only two age classes, juvenile and adult.

IX.2.1 Sex ratio at birth

If there were a preponderance of males at birth, one might expect the observed excess of males among the recruits. However, examination of 27 litters of full-term wild Rhabdomys embryos (Table 24) gave a sex ratio of 47,1% males, which was not statistically significant ($p > ,50$). In a sample of 271 young born in captivity, Brooks (1974) found a ratio of 44,3% males, which fell just short of significance ($X^2 = 3,54$ $p < 0,10 > 0,05$). It is clear that there was no excess of males at birth.

IX.2.2 Differential survival

Differential survival of either sex prior to reaching trappable age will influence the sex ratio of new recruits being trapped. Thereafter, differential survival will influence the sex ratio of residents, since the longer an animal lives the more frequently it will be trapped and so counted in the population.

Various means of expressing the mortality rates of mice are discussed and presented below in Chapter X. These are: the number of months for which mice of each sex were live-trapped (Table 26), survivorship curves (Figs. 25, 26 and 28) mean expectation of further life (Table 27) and the probability of survival per month (Table 28). It should be noted that these are all measures of residency in the study area.

TABLE 24

Sex ratios of embryos. Analysis of 27 wild litters; either from autopsy of full-term pregnant females or from litters born in livetraps.

No. litters	No. Embryos	Males	Females	% Male	Chisquare	P
27	121	57	64	47,1	0,40	NS

Emigrants are thus included under mortality. All this evidence shows that survivorship after first capture was higher for females than for males and that the mean expectation of further life was about 0,6 of a month longer for females, which in percentage terms was about 31% longer than males. The survivorship of juveniles was slightly greater than that of adults. The probability of survival per month was also higher for females. Thus, the evidence shows that females survive longer than males and it would appear that this differential in survival is the single most important factor in explaining the preponderance of females found among the residents.

However, it is not so clear why there should be an excess of males among the recruits. One might postulate that there was differential survival among nestlings such that there might have been more males leaving the nest and hence being recruited into the population. On reaching trappable age this could have changed to survival favouring the females. However, Table 23 shows that this was not the case since the excess of males among the recruits is evident only among the adults and not among the juveniles. In fact, the juveniles show an excess of females similar in proportion to the sex ratio at birth (Table 24). We now investigate whether differential trappability could explain the excess of adult males among the recruits.

IX.2.3 Differential trappability

In view of the findings of Smith (1968) already alluded to, the possibility exists that the deficiency of adult females among the recruits was due to pregnant and lactating females tending to avoid the traps. Thus, a segment of the population may, by its very nature, have been untrappable. This is very difficult to test for in practice. Trap-shy animals are possibly the group contributing the most serious errors to capture-recapture studies and they are normally an unknown quantity. Myers & Krebs (1971a) attempted to analyse differential trappability by determining the percentage of voles known to be alive which were actually caught at each trapping period. However, this does not seem to me to be a satisfactory method since it can never account for animals which are never caught at all - and it is the existence of such an untrappable group of females which could account for the observed discrepancy among the recruits.

The possibility that such a group of untrappable females might exist was investigated by analysing the capture of new adults during the breeding and non-breeding seasons, separately. If female Rhabdomys were behaving in a way similar to the Peromyscus studied by Smith (1968) then one would expect the pregnant and lactating females to be the ones most likely to avoid the traps. This should show up as a relatively reduced number of new adult females being captured during the breeding season (summer) when compared with

the males and with the non-breeding season (winter). The analysis is presented in Table 25 which shows that of the 308 adults captured during four complete breeding seasons, 39,3% were female and of 215 adults captured during the same four non-breeding seasons, 43,7% were female. There were thus 4,4% fewer females during the breeding season, assuming males were equally catchable at all seasons.

If one makes this assumption and also that there were roughly equal numbers of males and females available to be caught, then it is possible to calculate the expected number of adult females in the breeding season as follows: the number of adult males trapped in summer (October - March) showed a 54,5% increase over the winter catch (187:121, Table 25). If females were equally catchable they should also have shown the same proportional increase, namely 54,5% of 94. Hence the expected number of females was 145,3. The observed number was only 121, (X^2 = 4,06 $p < 0,05$). Hence the number of adult females captured during the breeding season was significantly less than expected. This is, therefore, consistent with the hypothesis that some breeding females were avoiding the traps.

This possibility is also suggested by Table 23, which shows that among juvenile recruits there was an excess of females similar to the ratio at birth (Table 24) but that among adults there was an excess of males which on the control grid was highly significant ($p < 0,001$), though not on grid K.

TABLE 25

Analysis of trappability of new adult males and females livetrapped in the control grid during breeding and non-breeding seasons.

Adults = mice >30g at first capture.

	No. New Adult Males Caught		No. New Adult Females Caught		TOTAL		% Females	
	Breeding Oct-Mar	Non-breeding Apr-Sept	Breeding Oct-Mar	Non-breeding Apr-Sept	B	N-B	B	N-B
1972/73	23	22	23	15	46	37	50,0	40,5
1973/74	37	16	13	9	50	25	26,0	36,0
1974/75	77	62	52	50	129	112	40,3	44,6
1975/76	50	21	33	20	83	41	39,8	48,8
TOTAL	187	121	121	94	308	215	39,3	43,7

Since trapping on the latter grid was conducted only between February 1975 and February 1976, the adult sex ratio on the control grid was compared for the same time period. This showed that the excess of males was still significant ($p < 0,05$ Table 23) although much less so than for the whole study period.

Since it has already been shown that survival of females was greater than that of males, the failure to catch adult females could not have been due to their failing to survive. This seems to me to be fairly persuasive, if circumstantial, evidence that some adult females must have been avoiding the traps, leading to an apparent deficiency of females among the recruits. Among the residents this deficiency was reversed and became an excess of females due to their longer survival and also to the paradoxically greater readiness of those females that <u>were</u> captured to re-enter the traps. This is shown by the greater proportion of recaptures among female residents when compared with males in both the control grid and grid K (Table 23). The trapping intensity on grid K was lower than that on the control grid as there was only one trap per station and trap rows were 20m apart. This fact, combined with the apparent greater readiness on the part of some females to re-enter traps, may explain the lower proportion of males among the residents on grid K (45,1%) when compared with those on the control grid (48,3%) since on grid K the trap-addicted females would tend to occupy most available traps and hence prevent the males from being caught.

IX.2.4 Differential movement

If one sex moves greater distances than the other, this would increase the probability of encountering traps and hence might influence the sex ratio of new recruits. The mean distance moved between successive recaptures (av. D of Brant, 1962) was determined for a sample of males and females on the control grid and grid K. The results are presented in Table 9. The mean distance moved on the control grid between successive recaptures was 9,3m for males and 7,9m for females. This difference was not statistically significant ($t = 1,798$ $p < 0,1 > 0,05$). Thus, though males had a slightly greater movement pattern than females, it seems unlikely that this could have had a significant effect on observed sex ratios.

IX.2.5 Differential growth

As already pointed out, Table 23 shows that among new recruits the sex ratio of juveniles favours females, whereas the sex ratio of adults favours males. Myers & Krebs (1971a) found a similar situation in the populations of the two species of Microtus that they were studying. Their suggestion for at least a partial explanation of this phenomenon was that it might be due to accelerated growth by the males so that they reached adult weights faster and were, therefore, exposed to being trapped as juveniles or sub-adults

for a shorter time. They computed instantaneous relative growth rates of males and females and found that the juvenile and sub-adult males of both species did have faster growth rates than the females.

Fig. 9 shows the mean field growth rates of male and female Rhabdomys from birth during the summer peak growth season. It is clear that females under 30g body mass (which was the criterion used to separate adults from juveniles in this study) grew faster than males. As this was a field growth curve, based on the weights at recapture of young animals, it was not possible to make allowance for early pregnancy of females. From evidence already presented it would seem that the body masses of some females from about 25g upwards would be influenced by pregnancy. If one could allow for this it would tend to bring the female growth curve closer to that of the male. However, since Fig. 9 shows that the faster growth of females began from an early age, the unbalanced adult sex ratio could not have been due to the faster growth of males. It is, therefore, my belief that the most likely factor which might have caused the excess of males among the new recruits was the trap-shyness of a proportion of the adult females which were avoiding the traps and hence not being sampled.

IX.3 Nestling survival and energy cost

As pointed out by Myers & Krebs (1971a) the only factors which may influence the selection of sex ratios are those which affect survival prior to weaning. All the factors examined above are operative post-weaning. Evidence presented in Chapter X under "survival from birth" shows that the proportion of nestlings of each sex surviving to weaning was identical to the sex ratio of the embryos. Hence there were no differences in survival of nestlings of either sex. One is, therefore, led to assume that the energy cost of producing a male or a female to reproductive age is about the same, in accord with the hypothesis of Fisher, already quoted (p.148).

IX.4 Summary

Sex ratios of mammal populations may be estimated in two ways from livetrapping, namely: (1) from the proportions of males and females alive in the population at any instant (the residents), and (2) from accumulating the numbers of new recruits (unmarked mice) each trapping session over a long period. Analysis of results in this study showed that among residents there was a deficiency of males (45 - 48% males, Table 23) whereas among new recruits there was a significant excess of adult males, but approximate equality among the juveniles. Five factors were examined which might have had a bearing on the explanation of these

unequal sex ratios. These were sex ratio at birth; differential survival; differential trappability; differential movement and differential growth.

It was found that there was differential survival of females as measured by residency in the study area. Analysis of the capture frequencies, in months, of all livetrapped mice showed that females were captured for significantly longer periods than males (Table 26). These data were equated with ecological longevity and when translated into survivorship curves (Fig. 25) revealed a longer expectation of life after first capture for females than for males. It is believed that the greater survival of females was the most important factor explaining the excess of females among the residents.

The excess of adult males among the recruits, on the other hand, was believed to be caused by differential trappability of adult males. This was, apparently, due to one segment of the female population, namely the pregnant and lactating females, tending to be rather trap-shy. This led to more adult male recruits than females being trapped during the breeding season.

X. MORTALITY

X.1 Introduction

Mortality rates are one of the most difficult parameters of wild populations on which to obtain accurate information. A prolonged mark-recapture livetrapping study is essential for this purpose. Even then, the study is liable to be plagued by sampling problems, as has already been mentioned. Perhaps the most important two of these are: (1) that livetrapping cannot distinguish death from dispersal and, therefore, equates the two. In other words, an animal which is no longer recaptured is assumed to be dead, whereas it may merely have moved elsewhere. (2) Unequal trappability may lead to a biased sample, since not all members of the population may enter the traps equally readily. For example, in R.pumilio it has already been shown that some pregnant and lactating females were, apparently, avoiding the traps. Again, in some species, young animals below a certain age may not enter traps, leading to serious under-representation of juveniles in the sample. In the case of Rhabdomys we captured during the course of the study, 50 juveniles as small as 6 - 9g which had just left the nest, and many of 10g or more. It thus appeared that juveniles were readily captured. However, it may still have been the case that they were being under-represented in the catch - that fewer of these very young mice were being caught in relation to the proportion they formed of the population.

X.2 Survival after first capture

In the present study estimates of mortality were divided into two categories, namely: (1) survival after first capture, and (2) survival from birth; survival being the complement of mortality. The former was obtained from analysis of the recapture histories of all individual mice captured during the study (i.e. the number of months for which all individuals were captured). Mice were analysed into one of the categories : 'mice caught for one month only; mice caught for two months only ....', etc. The data are presented in Table 26 and Fig. 24. These data were equated with the ecological longevity of the mice and survivorship curves were derived from them. It is evident that the biggest single category was that of mice caught for one month only, which comprised about 42% of females and 47% of males. Females were apparently longer lived than males. Our longest record was for a female which was caught for 15 months, whereas the longest record for a male was for 13 months (Table 26). Only three males were caught for longer than 9 months, whereas 22 females were caught for longer than that. Testing the mean number of months for which the two sexes were captured by means of student's 't', shows that females were caught for significantly longer than males ($t = 5,9$ $p<0,001$ Table 26).

Mean 'survivorship' curves for both sexes on the control grid for the duration of the study are presented in Fig. 25. It

TABLE 26

Table of residency on the control grid.

Analysis of number of months for which individual mice were livetrapped on the control grid from 1972 - 1977. This is equated with ecological longevity and the data have been used to construct survivorship curves (Fig 25).

See also Fig 24.

NO. OF MONTHS FOR WHICH CAPTURED

NO. OF MONTHS	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	TOTAL MICE	(MONTHS) MEAN	SD	t	p
N MALES	311	118	75	73	40	18	9	6	6	0	2	0	1	0	0	659	2,39	1,85	5,9	< ,001
N FEMALES	238	78	83	52	44	21	20	8	5	8	7	3	2	1	1	571	2,97	2,54		

FIG. 24

Frequency of capture (number of months) of livetrapped individual R.pumilio on the control grid from 1972 - 1977. Sexes and age groups separately.

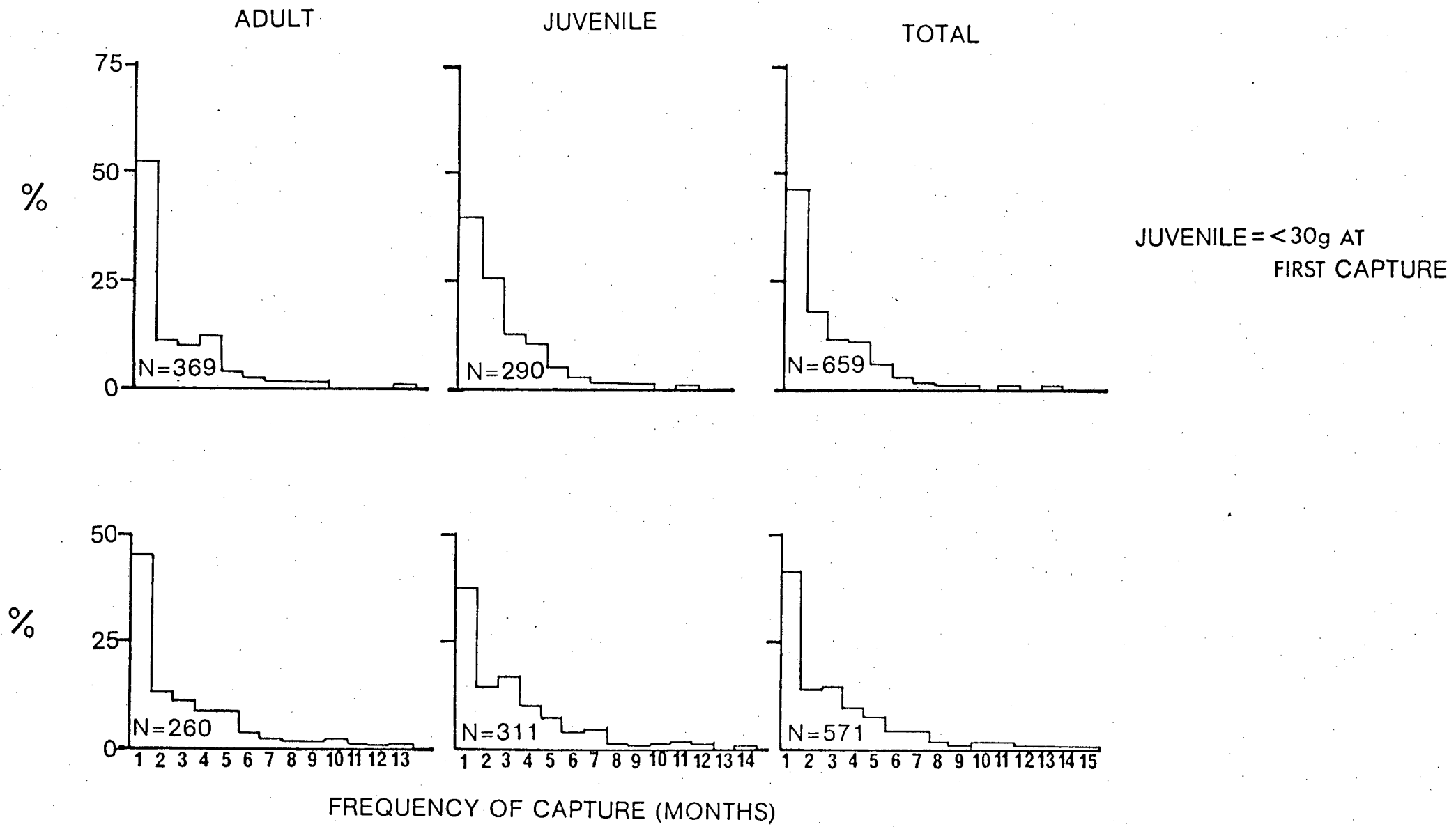
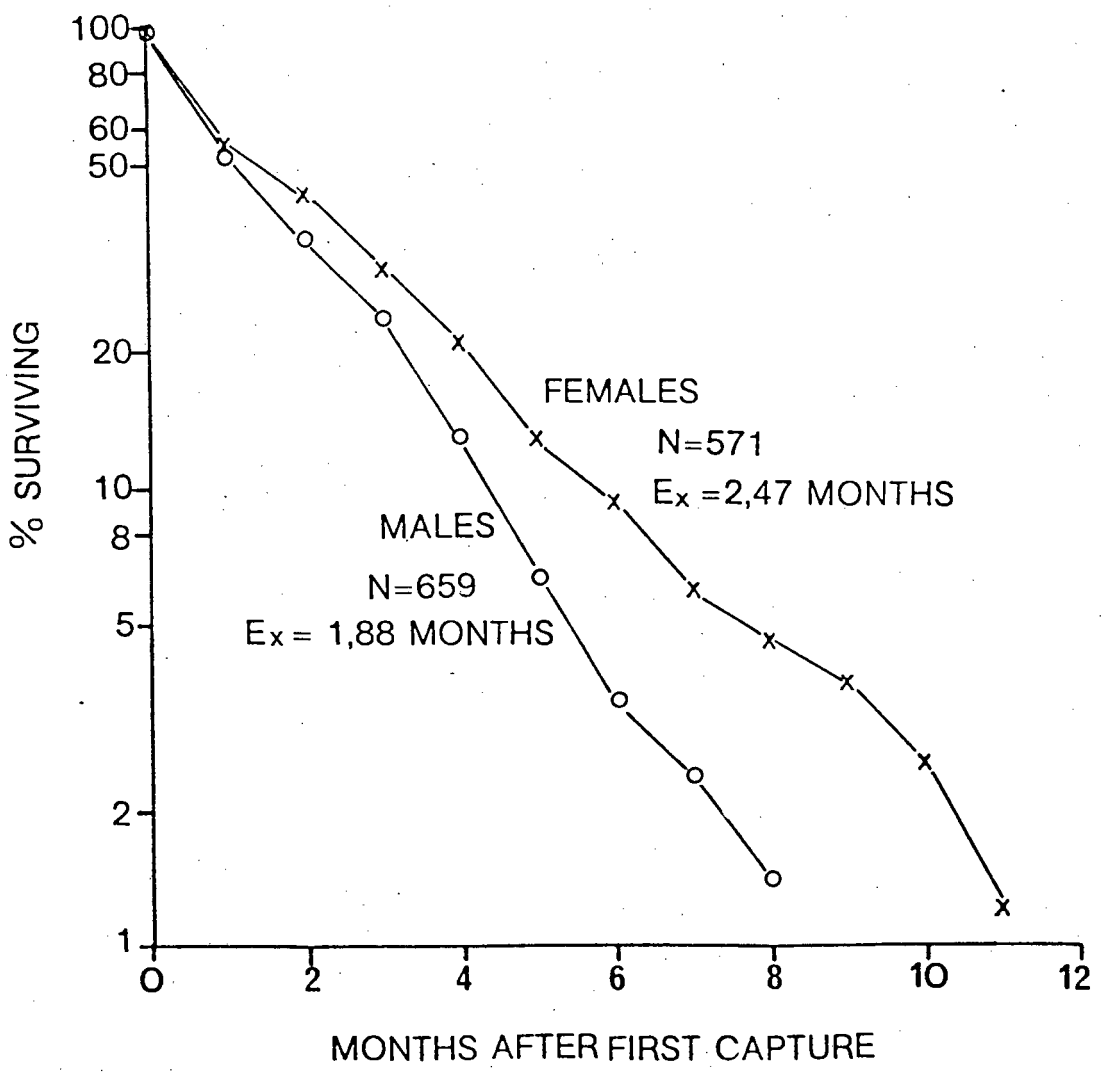

ADULT
JUVENILE
TOTAL
75
50
25
0
%
N=369
N=290
N=659
JUVENILE = <30g AT FIRST CAPTURE
50
25
0
%
N=260
N=311
N=571
1 2 3 4 5 6 7 8 9 10 11 12 13
1 2 3 4 5 6 7 8 9 10 11 12 13 14
1 2 3 4 5 6 7 8 9 10 11 12 13 14 15
FREQUENCY OF CAPTURE (MONTHS)

FIG. 25

Mean 'survivorship' curve from first capture for all male and female R.pumilio livetrapped on the control grid. Data pooled for whole study 1972 - 1977. 'Survivorship' was computed from the number of months that mice were resident in the control grid.

Ex = mean life expectancy (months) from first capture. This is the same as the mean number of months for which mice were resident in the control grid and assumes that mice which disappeared from the control grid were dead.



should be noted that these survivorship curves do not measure true survivorship from birth, but record the mean proportion of each sex which were captured for successive months after first capture. This type of survivorship curve is really a 'residency' curve, but evidence presented in Chapter XI shows that dispersal was believed to be at a low level and hence the curve measures the mean survival from the time of first capture. It thus summarises the mortality experience of a group of animals over a period of time and obscures variations in mortality that may occur within that period. The greatest mortality occurs in the first month. Survival improves in month 2 for females and in months 2 and 3 for males. Thereafter, mortality rate is more or less constant for both sexes (the curve is more or less a straight line) which shows that there is no evidence of senescence, as pointed out by Getz (1960) for M.pennsylvanicus.

It is clear that mean survivorship at all stages after first capture was higher for females than males. This is confirmed by the mean expectation of further life, which was calculated by the formula of Southwood (1966, p.286). Table 27 shows the mean expectation of further life for adults and juveniles of both sexes. On the control grid, whereas females could expect to live for a further 2,47 months after first capture, males could expect only 1,88 more months of life. On grid K the values were 2,74 and 2,08 months respectively. The superior survivorship of females over males may be due to greater mortality of males or to a greater tendency of males

TABLE 27

Survival (residency) on the livetrapped grids in months after first capture, averaged for the whole study period.

Ex = mean expectation of further life (months) from first capture measured from number of months of residency on the grids (see Table 26). Sample sizes in brackets (number of mice).

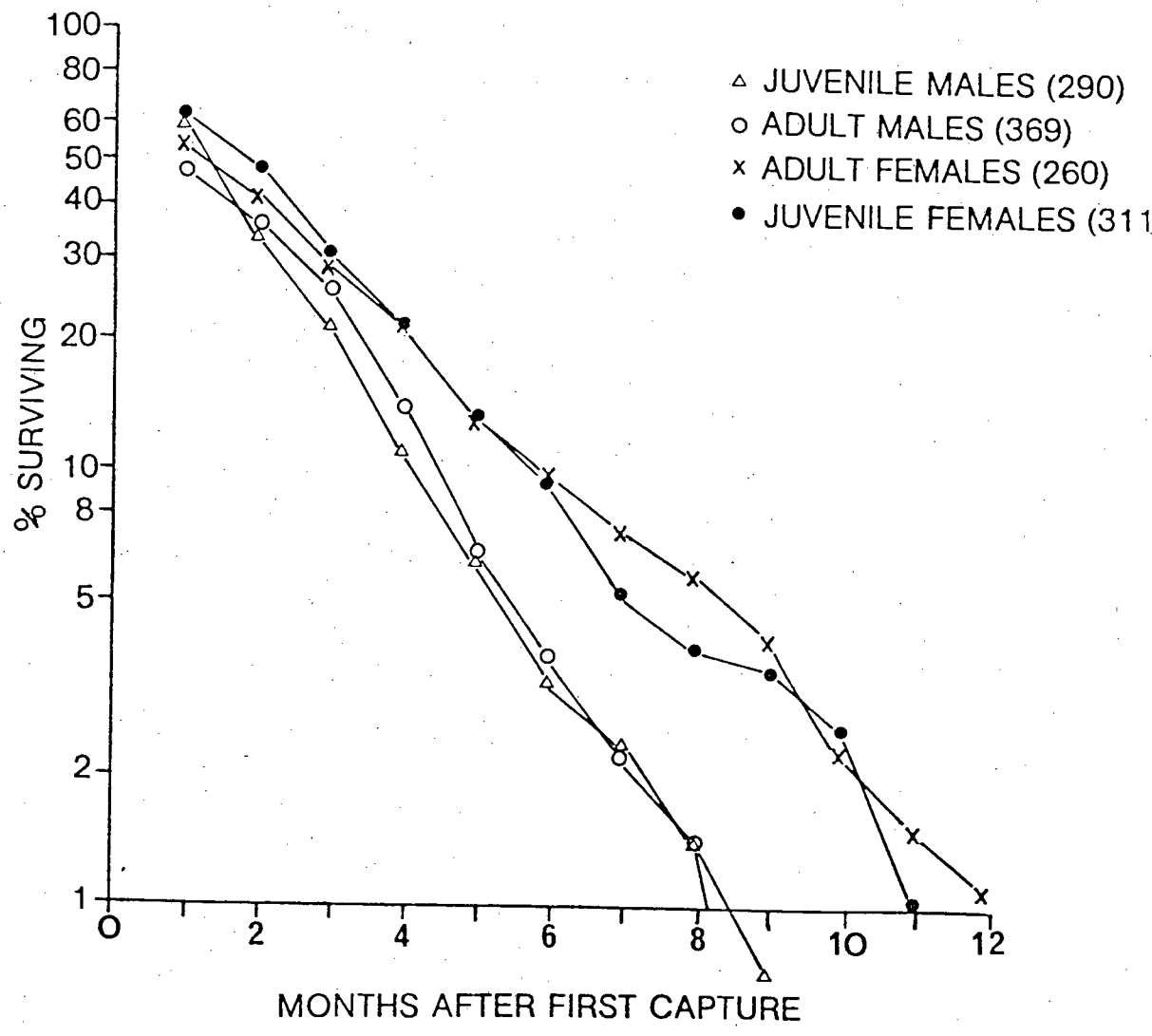
Juveniles = mice < 30g at first capture.

	CONTROL 1972 - 1977 Ex months Males	Ex months Females	GRID K FEBRUARY 1975 - FEBRUARY 1976 Ex months Males	Ex months Females
ALL	1,88 (659)	2,47 (571)	2,08 (372)	2,74 (381)
ADULT	1,87 (369)	2,41 (260)	2,05 (282)	2,52 (267)
JUVENILE	1,91 (290)	2,51 (311)	2,16 (90)	3,25 (114)

to disperse from the study area. This question cannot be answered with confidence on the available data, but evidence presented in Chapter XI shows that though there were twice as many identified male dispersers as females, the overall level of dispersal appeared to be low. In Fig. 26 the separate survivorship curves for adults and juveniles are presented. It is evident that survivorship was very similar for the two age groups. The mean expectation of further life was slightly higher for juveniles than for adults - the biggest difference recorded being only about three weeks longer for juvenile females on grid K (Table 27). This very small difference as well as the great similarity in the pattern of recaptures between adults and juveniles as shown in Fig. 24 suggests that, once having left the nest, mortality was independent of age in the population. Once an animal reached trappable age it was subject to the same mortality factors as the rest of the population. The mean longevity in the field of only two to three months after first capture is remarkably short. The mean expectation of life from birth was even shorter at 1,5 - 1,6 months (see below and Fig. 28). This contrasts strongly with the lifespan in the laboratory, which may be over two years (Choate, 1971; Brooks, 1974). However, this seems to be comparable with what has been found in voles, since Getz (1960) gives a mean survival of 2,1 - 2,2 months for adult male and female M.pennsylvanicus in a marsh habitat and 1,6 - 1,9 months in an abandoned field and Krebs (1966) gives life expectancies of adult M.californicus of 8 - 13 weeks in expanding populations and 2 - 7 weeks in declining ones.

FIG. 26

Mean 'survivorship' curve from first capture for adult and juvenile (<30g at first capture) R.pumilio live-trapped on the control grid. Data pooled for whole study 1972 - 1977. 'Survivorship' computed as in FIG. 25. Sample sizes in brackets.



Another means of illustrating mortality patterns is the average probability of survival from one month (trapping period) to the next. These are calculated from the observed recaptures of marked mice each month. They are minimum survival values and they are not the same as ϕ_i of Jolly (1965) whose formula for survival uses estimates of population size. The mean probabilities of survival per month for the whole study are presented in Table 28. These confirm the results shown by the survivorship curves, namely that the probability of survival per month was higher for both adult and juvenile female groups than for males and that the probability of juveniles surviving was slightly higher than for adults. The monthly time-specific probabilities of survival of adults are shown in Fig. 27 (density data shown in Fig. 4). These data illustrate the changes through time. Some of the values show wide fluctuations which may be due largely to very small samples some months.

Seasonal changes in mortality can be gauged from the mean figures given in Fig. 27 and Table 29 for each six month period comprising the main summer breeding season, October through March, and a 'winter' period April through September. The mean figures for breeding and non-breeding periods in Fig. 27 show that adult female survival was consistently higher than that of males during the breeding season, but less so during the winter. In 1973 and 1975, female survival in winter remained higher than males, but in 1974 and 1976 it declined to below that of males. Krebs (1966) during a study of M.californicus, which covered two breeding seasons

TABLE 28

Pm = Probability of survival per month (from one trapping period to the next) averaged for the whole study. Total mice caught (including recaptures) in brackets.

Juveniles = mice < 30g at first capture.

Grid K was livetrapped only from February 1975 - February 1976.

Pm = Probability of survival per month.

	CONTROL 1972 - 1977		GRID K Feb. 1975-Feb. 1976	
	Males Pm	Females Pm	Males Pm	Females Pm
ADULT	(792) 0,553	(687) 0,618	(670) 0,557	(732) 0,630
JUVENILE	(655) 0,581	(864) 0,702	(238) 0,600	(372) 0,695

FIG. 27

Minimum monthly probabilities of survival of adults (>29g at first capture) livetrapped on the control grid. Density data presented in FIG. 4.

P = probability of survival to next (monthly) trapping period. Vertical lines divide each year into six months summer breeding (October to March) and six months 'winter' (April to September). Mean probabilities of survival for each six months are given for males and females.

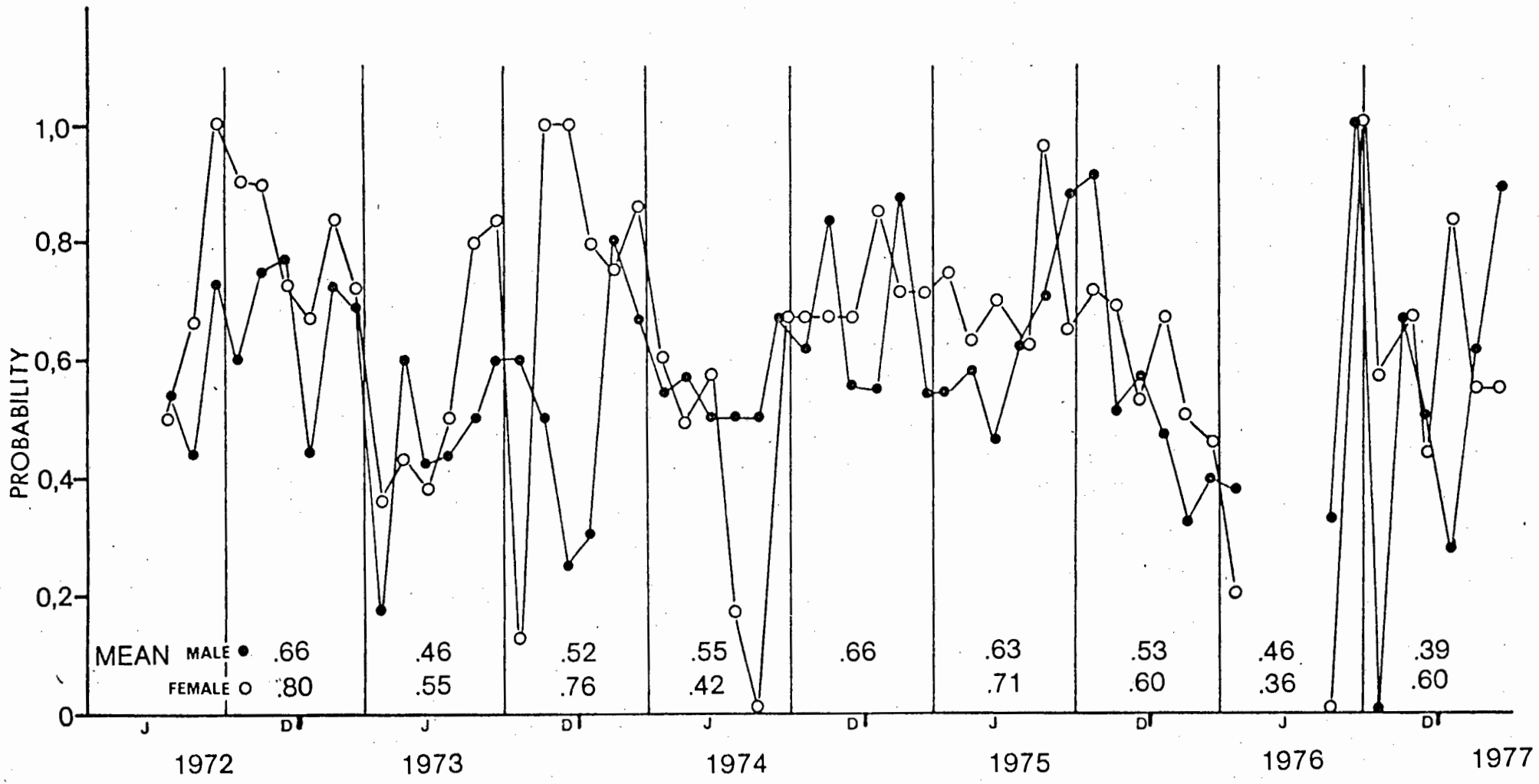

PROBABILITY
1,0
0,8
0,6
0,4
0,2
0
MEAN MALE ● .66 .46 .52 .55 .66 .63 .53 .46 .39
FEMALE ○ .80 .55 .76 .42 .71 .60 .36 .60
J D J D J D J D J D J
1972 1973 1974 1975 1976 1977

TABLE 29

Pm : PROBABILITY OF SURVIVAL PER MONTH (FROM ONE TRAPPING PERIOD TO THE NEXT) COMPARING MAIN BREEDING SEASON (OCTOBER TO MARCH) WITH NON-BREEDING SEASON (APRIL TO SEPTEMBER)

CONTROL GRID

PERIOD	Pm: Probability of survival per month			
	Pm ADULT MALES	Pm JUVENILE MALES	Pm ADULT FEMALES	Pm JUVENILE FEMALES
OCT 1972 - MAR 1973	0,663	0,616	0,795	0,875
APR 1973 - SEP 1973	0,455	0,271	0,549	0,633
OCT 1973 - MAR 1974	0,519	0,620	0,755	0,771
APR 1974 - SEP 1974	0,547	0,604	0,417	0,794
OCT 1974 - MAR 1975	0,663	0,646	0,711	0,666
APR 1975 - SEP 1975	0,634	0,666	0,714	0,748
OCT 1975 - MAR 1976	0,529	0,559	0,595	0,646
APR 1976 - SEP 1976	0,463	0,600	0,363	0,179
OCT 1976 - MAR 1977	0,388	0,636	0,601	0,667

and one non-breeding season, also found that during the former, female voles survived considerably better than males, but during the latter there was no difference in survival between the sexes. In general, winter survival was lower than summer survival, particularly in 1973 and 1976, but not in 1975 when population density remained unusually high throughout winter (see Fig. 3). Thus, survival was usually better during the breeding season when the population was increasing. This pattern is consistent with the findings of Krebs (1966) who recorded improved survival in expanding populations of M.californicus, as mentioned above.

In order to assess whether there were differences in survival between one year and another, the mean life expectancy from first capture has been tabulated for each year from the beginning of the breeding season in Table 30. It appears that the worst survival occurred in 1975 - 76 which was the year of a very sharp decline in numbers from February 1976 (Fig. 3). For three of the four groups the best survival occurred in 1974 - 75 which was the peak year of the study when numbers were unusually high throughout the winter period. It is interesting that 1973 - 74, which was the year of lowest numbers, had quite good survival. In fact, juvenile females survived better than in any other year and juvenile males and adult females had survival second only to 1974 - 75. In general, it can be seen that there were some relatively big changes in survival from year to year - for example, adult females had 100% and males had 46 - 80% greater mean expec-

TABLE 30

Survival (Residency) on the control grid : number of months after first capture for each year of the study. Adults and Juveniles separately.

Ex : Mean expectation of further life (months) from first capture, measured from number of months of residency on the control grid. Sample sizes in brackets.

Juveniles = mice < 30g at first capture.

Period	Ex (months) Adult Males		Ex (months) Juvenile Males		Ex (months) Adult Females		Ex (months) Juvenile Female	
Sep 1972 - Aug 1973	1,98	(54)	1,71	(42)	2,34	(44)	2,72	(45)
Sep 1973 - Aug 1974	1,61	(37)	2,17	(24)	2,50	(22)	3,70	(25)
Sep 1974 - Aug 1975	2,33	(128)	2,33	(90)	3,13	(91)	2,74	(119)
Sep 1975 - Aug 1976	1,29	(81)	1,60	(83)	1,50	(47)	1,83	(72)

tation of further life in 1974 - 75, compared with 1975 - 76 (see Discussion below).

X.3 Survival of young from birth to post-weaning

The biggest sample of the data, which involves measurement of survival after first capture, has been presented; but a serious problem is the possible confusion of death with emigration. The survival of the young from birth to trappable age (post-weaning) is a most important parameter since it is at this stage of their development that they are believed to be especially vulnerable - and there is no possibility of emigration. However, it is difficult to obtain information on this as it is almost impossible to find nests of young in the field. One is, therefore, obliged to rely on indirect methods of estimating the survival from birth. The method adopted here is that used by Getz (1960) and Chitty & Phipps (1966). The number of heavily pregnant females was observed at month t and the number of new juveniles was then counted at month t + 1. The assumption made is that the number of new juveniles will be the offspring of the females which were heavily pregnant in the previous month. From the growth curve (Fig. 9) it can be seen that young leave the nest at about 14 days of age, when they weigh about 8g. By 30 days of age they grow to about 19g. Hence, juveniles weighing 19g or less would have been born some time within the previous month. The analysis presented in Table 31,

TABLE 31

Infant survival from birth on the control grid.

Number of heavily pregnant females (>54g) at month t compared with number of juveniles (up to 30 days old <20g) caught in month t + 1.
Pregnant females include females identified as pregnant in the field, even though below 55g body mass.

Juvenile males in brackets.

Month t	1972/73		1973/74		1974/75		1975/76		1976/77		T O T A L	
	No. heavy pregnant females	Month t+1 number juveniles	No. heavy pregnant females	Month t+1 number juveniles	No. heavy pregnant females	Month t+1 number juveniles	No. heavy pregnant females	Month t+1 number juveniles	No. heavy pregnant females	Month t+1 number juveniles	No. heavy pregnant females	Month t+1 number juveniles
SEPT	0	0	0	0	0	7 (2)	0	3 (2)	0	4 (2)	0	14
OCT	0	0	1	6 (3)	3	4 (1)	9	24 (14)	6	15 (7)	19	49
NOV	2	1 (1)	0	1 (0)	3	5 (2)	17	12 (5)	5	5 (3)	27	24
DEC	7	3 (1)	1	4 (3)	3	23 (10)	10	23 (12)	2	6 (2)	23	59
JAN	7	16 (7)	0	0	2	16 (6)	5	25 (13)	6	7 (3)	20	64
FEB	3	5 (3)	1	6 (1)	9	24 (11)	9	3 (1)	4	15 (8)	26	53
MAR	0	4 (3)	3	7 (3)	14	20 (10)	4	2 (0)	5	5 (4)	26	38
TOTAL	19	29 (15)	6	24 (10)	34	99 (42)	54	92 (47)	28	57 (29)	141	301 (143)
Survived % males	51,7		41,7		42		51		50,9		47,5	
Mean no. young weaned per pregnancy	1,53		4,00		2,91		1,70		2,04		2,13	
* Mean litter size	4,59		5,20		5,65		4,80		4,68		4,97 +	
% Survival from birth	33,3		76,9		51,5		35,4		43,6		42,9	

* See Table 19.

\+ = overall mean litter size calculated from total number of offspring born to all females in this Table.

therefore, includes only juveniles of under 20g captured in month t + 1.

The problem of counting the number of pregnant females at month t was slightly more difficult. Females in the hand are only certainly identifiable as pregnant a very few days before parturition. To count only those females would be a gross underestimate, since the young are weaned as early as 14 days and we could livetrap young as small as 6 - 8g hence it would be possible for a female to produce a litter up to 14 days after the trapping period in month t and still be in time to contribute weaned young to trapping period t + 1. It was, therefore, necessary to determine whether it could be established that females of a certain body mass during the breeding season were in an advanced stage of pregnancy. From the autopsies of killtrapped females, it was determined that the crown-rump length of a full-term foetus was about 30mm. Gestation period was about 25 days. The body masses of pregnant killtrapped females were, therefore, analysed into two categories as in Table 32 - namely females carrying advanced embryos of crown-rump length 16 - 30 mm (at which size the embryos could be sexed), and those in early pregnancy having embryos too small to measure. It is assumed that the former group would have given birth within 14 days. From Table 32 it can be seen that 48% of pregnant females carrying embryos with a crown-rump length of 16 - 30mm weighed at least 55g compared with only 12% of females in early pregnancy. It was, therefore, decided to count all livetrapped females of 55g or more during the

TABLE 32

Identification of heavily pregnant females in the field from body mass. Analysis of pregnant killtrapped females by body mass and crown-rump (CR) length of embryos.

Full term embryos have a CR length = 30mm
Embryos can be sexed at CR length = 16mm

Body mass of pregnant females (g)	Embryo CR length 16-30mm No. Females	%	Embryo CR length 0 - 5mm No. females	%
> 70	5	48	0	12
60 - 69	12		3	
55 - 59	3		3	
50 - 54	11		8	
40 - 49	8		16	
< 40	3		19	
TOTAL	42		49	

breeding season, September to March, as being pregnant and likely to produce young within two weeks.

The resulting analysis of pregnant females compared with the number of juveniles of less than 20g caught one month later is presented in Table 31. This is similar to the index of early juvenile survival of Krebs & Delong (1965). It can be seen that the apparent survival from month to month was very variable ranging from very good when practically all young apparently survived, to very poor. The small sample sizes involved in some months should probably be treated with caution. There are some anomalies, such as in September when no pregnant females were recorded and yet juveniles were recorded in October in three of the five years of the study. It is hoped that the total number of young per year gives a reasonably accurate picture of survival for that particular breeding season.

Survival was worst in 1972/73 and 1975/76 when about 35% of young born survived to trappable age and was best in 1973/74 and 1974/75 when from 51 - 77% of young survived. The overall figure of 43% survival from birth (57% mortality) confirms the expectation of high mortality between birth and weaning, though survival of R.pumilio appears to be considerably better than that of M.pennsylvanicus, since Getz (1960) recorded only 12% survival from birth. Chitty & Phipps (1966) also recorded variable survival from birth for M.agrestis, but over a complete breeding season from March to November 1960, they recorded 53 pregnant females and 128

juvenile recruits. Since litter size was 4,6 overall survival was 52,5%. Krebs & Myers (1974 : 310) recorded an infant survival of only 0,88 - 1,31 M.pennsylvanicus per lactating female. Since litter size was 4,54 this represented survival of only 19 - 29%.

The year to year pattern of survival in Table 31 is more or less in agreement with the mean expectation of life as shown in Table 30. Thus the best two years for survival in both Tables were 1973/74 and 1974/75. The latter year was the year of high population growth and highest density on the study area (Fig. 3) and this would have been impossible without good infant survival. It is noticeable that reproduction began early that year with small juveniles appearing in October (Table 31) and was maintained steadily throughout the season with 20 juveniles of under 20g being caught as late as April. It may seem strange that 1973/74 should be the year with the best infant survival, since it was also the year of low numbers and the lowest summer breeding peak (Fig. 3). The explanation appears to be that there were extraordinarily few breeding females that year - in fact only two were recorded up to February. This accounts for the very small number of young that were captured - but, evidently, those young that were born survived very well. The year of worst survival was 1975/76 (as also in Table 30) when, although it appears that large numbers of young were born, the population suffered a very severe decline.

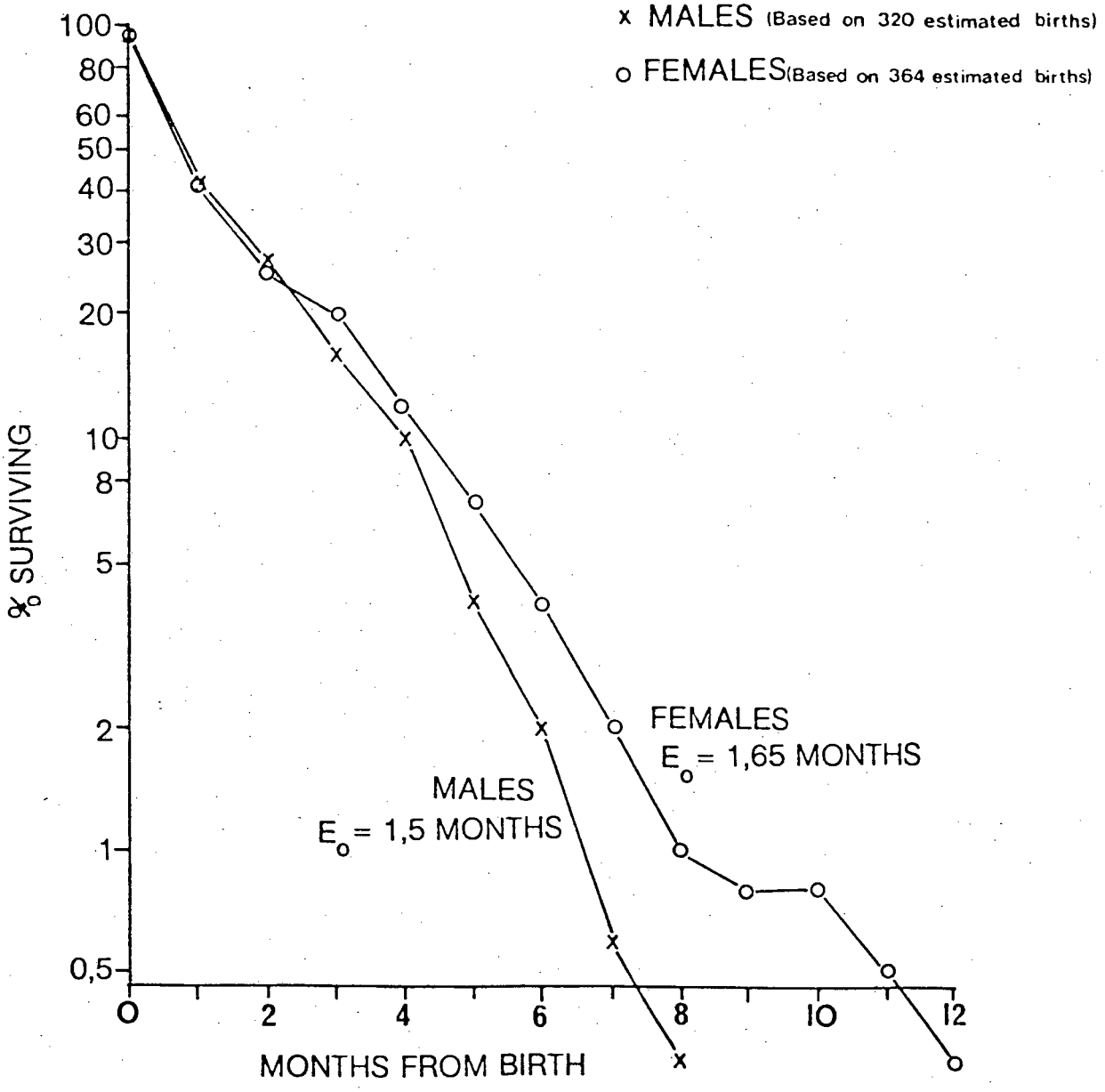
The recapture histories of all the juveniles in Table 31 were analysed. From these data survivorship curves from birth for males and females were obtained (Fig. 28). These can be compared with Figs. 25 and 26 which show 'survivorship' after first capture. The estimated number of young born was the number of pregnant females times the mean litter size (141 x 4,966 = 700). The expected number of males was the percentage of males in newborn litters from Table 24. Hence the expected number of males born was 700 x 47,1% = 330 and the expected number of females at birth was 370. From these figures the number of mice found dead in traps was subtracted.

It is interesting that in Table 31, of the sample of juveniles which survived to trappable age, 47,5% were males - which is almost identical to the percentage of males in a sample of 121 embryos (Table 24). Hence, the survival of males and females was the same from birth to trappable age. The mean expectation of life at birth was only 1,65 months for females and 1,52 months for males (calculated by the formula of Southwood, 1966). Although females still enjoy a marginally greater expectation of life than males, it is much less than the difference that appears in Table 27 and is also less in absolute terms than the mean expectation of life from first capture. The reason for this is probably that by far the largest slice of mortality occurred in the nest before the infants reached trappable age and since this portion of the overall survival was the same for the two sexes, it tended to obscure later differences in survival

FIG. 28

Mean survivorship curve from birth of R.pumilio on the control grid. Total estimated births was the cumulative number of heavily pregnant females livetrapped in the field multiplied by the mean litter size. These females were assumed to have given birth within 14 days of capture (gestation period = 25 days). Young are weaned at 14 days. Survivors to weaning age were, therefore, livetrapped at month 1 when they weighed under 20g (juveniles < 20g at first capture are up to 30 days old). Thereafter, the period of residency of the survivors in the control grid was computed from their livetrapping history.

Eo = mean life expectancy (months) from birth.



which emerged after the mice reached trappable age.

X.4 Discussion

As with mean survival from first capture, there were relatively large changes in the mean number of young weaned per pregnancy and the percentage survival from birth between years. If one compares the years of worst survival, 1972/73 and 1975/76, with the years of best survival, 1973/74 and 1974/75, it is clear that the number of young weaned per pregnancy improved by 90 - 160% in the best years. Krebs & Myers (1974 : 310) recorded an improvement of about 50% in infants weaned per pregnancy between the decline and the increase phase (0,88 - 1,31) of M.pennsylvanicus.

This suggests that changes in survival from year to year might have a pronounced effect on population growth rate and the size of the population peak. However, it is not obvious how these factors are related in practice. Good infant survival of R.pumilio in 1974/75 was correlated with a population increase of 8,7 times in a standard six month period (Table 5), contrasted with poor infant survival and a population increase of only 2,4 times in the following year. On the other hand, it is not clear, using infant survival as a yardstick, how the population increase in 1976/77 could have been as high as 11,6 times when infant survival was little better than the previous year and the actual number of young juveniles caught (57) was far less than the number in

1974/75 (99 - Table 31). It must also be explained why the population growth rate in 1975/76 was so low when 92 young juveniles were caught - only seven fewer than the previous year. In this case the explanation appears to be that survival from first capture for all groups was considerably lower in 1975/76 than for any other year (Table 30). In 1973/74, although survival of young was good, the poor growth rate seems to have been due to the very small number of pregnant females (only six) and, hence very few young. In 1972/73, the survival of young was poor, but the absolute number of young captured was slightly higher than in 1973/74 due to a larger number of pregnant females.

Immigration does not appear to have been an important factor influencing population growth since Table 33 shows that it remained fairly constant throughout the study.

Krebs & Myers (1974 : 308) performed a multiple regression analysis of mean rate of population growth in M.californicus on male survival rate, female survival rate, percentage of lactating females and index of early juvenile survival. They found that female survival rate had the highest relative importance with juvenile survival second most important. Gaines & Rose (1976) performed the same analysis on M.ochrogaster and found that early juvenile survival had the highest relative importance with female survival next.

In the present study, while the above two factors are consistent with high population growth in 1974/75 and low growth in

TABLE 33

Immigration on the control grid. Measured as proportion of new heavy adults (>40g at first capture) each month. These heavy mice are assumed to have immigrated from elsewhere and not merely to have avoided capture in situ.

Month	1972 - 1973							1973 - 1974						
	New heavy adults			Total new mice			Immig.	New heavy adults			Total new mice			Immig.
	M	F	T	M	F	T	%	M	F	T	M	F	T	%
*SEP	7	8	15	7	8	15	100	2	1	3	2	1	3	100
OCT	2	1	3	2	1	3	100	2	3	5	2	4	6	83
NOV	2	0	2	9	5	14	14	3	1	4	8	4	12	33
DEC	6	1	7	13	5	18	39	1	0	1	5	2	7	14
JAN	4	3	7	16	13	29	24	8	2	10	14	6	20	50
FEB	2	4	6	16	29	45	13	2	0	2	3	1	4	50
MAR	3	0	3	8	6	14	21	1	1	2	6	10	16	13
APR	0	0	0	6	6	12	0	5	0	5	11	7	18	28
MAY	1	2	3	4	5	9	33	0	2	2	4	4	8	25
JUNE	0	0	0	9	5	14	0	1	1	2	5	7	12	17
JUL	2	0	2	4	4	8	25	1	0	1	1	1	2	50
AUG	1	0	1	2	2	4	25	0	0	0	0	0	0	0
TOTAL	30	19	49	96	89	185	26	26	11	37	61	47	108	34

* In SEPTEMBER new mice of 30g or more were considered to be immigrants.

continued/...

TABLE 33 continued ....

Month	1974 - 1975 New heavy adults M	F	T	Total new mice M	F	T	Immig. %	1975 - 1976 New heavy adults M	F	T	Total new mice M	F	T	Immig. %
SEP	5	1	6	5	1	6	100	8	6	14	8	7	15	93
OCT	3	2	5	5	7	12	42	8	2	10	12	5	17	59
NOV	4	1	5	14	9	23	22	12	3	15	29	18	47	32
DEC	6	2	8	15	9	24	33	3	1	4	14	12	26	15
JAN	15	8	23	33	32	65	35	5	4	9	28	22	50	18
FEB	8	7	15	22	28	50	30	4	2	6	36	24	60	10
MAR	9	6	15	37	40	77	19	3	2	5	20	9	29	17
APR	1	1	2	24	22	46	4	2	1	3	7	13	20	15
MAY	5	1	6	25	34	59	10		N O	T	R A	P P	I N G	
JUNE	3	0	3	13	10	23	13	2	0	2	7	8	15	13
JUL	7	1	8	18	11	29	28		N O	T	R A	P P	I N G	
AUG	7	3	10	7	7	14	71	3	0	3	3	1	4	75
TOTAL	73	33	106	218	210	428	25	50	21	71	164	119	283	25

continued/...

TABLE 33 continued ...

Month	1976 - 1977 New heavy adults M	F	T	Total new mice M	F	T	Immig. %	TOTAL New heavy adults	Total new mice	Immig. %
SEP	1	3	4	1	3	4	100	42	43	98
OCT	2	4	6	5	6	11	56	29	49	59
NOV	7	3	10	18	11	29	24	36	125	29
DEC	4	3	7	10	12	22	45	27	97	28
JAN	3	1	4	11	8	19	21	53	183	29
FEB	7	0	7	19	17	36	19	36	195	18
MAR	3	1	4	24	17	41	10	29	177	16
APR	0	0	0	16	4	20	0	10	116	9
MAY	1	0	1	1	6	7	14	12	83	14
JUNE								7	64	11
JUL								11	39	28
AUG								14	22	64
TOTAL	28	15	43	105	84	189	23	306	1193	25,6

1975/76, yet poor survival after first capture must also have been implicated in the low growth in the latter year. In contrast, these factors do not seem to explain the apparently high population growth in 1972/73 and 1976/77 and relatively low growth in 1973/74. The latter case seems to have been due to the presence of very few breeding females, but in the former two years it is not obvious why population growth was as high as it was. Hence, the results do not apparently reveal any of the above factors as being dominant in determining the population growth rate. It is likely that different factors may assume major importance at different times. This suggests that the factors governing population growth are highly complex and that the relations between them are not yet understood.

X.5 Summary of mortality

Mortality was estimated in two ways : (1) survival after first capture and (2) survival from birth. Survival after first capture was measured from the number of months that mice were captured in livetraps. The majority of mice (42 - 47%) were caught for only one month. From these data mean 'survivorship' curves were prepared and probabilities of survival per month were calculated. Mean % surviving after first capture was higher at all stages for females than for males. Females were caught for significantly longer ($p < 0,001$) than males. Only three males, compared with 22 females, were caught for longer than 9 months - maximum 15 months for one

female and 13 months for one male (see p.72 for total lifespans). The mean expectation of life from first capture was 1,9 months for males and 2,5 months for females, taken over the whole study. There were relatively big changes in this parameter in different years of the study. Seasonal changes in probabilities of survival per month showed that, in general, survival during the breeding season was higher than during winter.

Survival of young from birth was assessed from the number of young weighing under 20g livetrapped each month, compared with the number of heavily pregnant females one month previously. Results presented in Table 31 show that overall survival from birth was about 43% - confirming high nestling mortality. There was considerable variation in nestling mortality from year to year (as expressed in the mean number of young weaned per pregnancy). This correlated well with high population growth rate in 1974/75 and low growth in 1975/76 but not in the other years of the study. In addition, low survival after first capture appeared to be important in reducing the growth rate in 1975/76 and a paucity of pregnant females had the same effect in 1973/74. The very high population growth rate in 1976/77 could not be readily explained on the basis of available parameters such as nestling survival, adult female survival or proportion of pregnant females (see Discussion above).

XI. IMMIGRATION AND DISPERSAL

XI.1 Introduction

Because livetrapping of small mammals is unable to distinguish death from emigration, animals which disappear from the livetrapping grid are assumed to be dead, whereas in reality they may merely have moved off the trapping area. Extensive emigration, therefore, could seriously invalidate estimates of mortality unless it were balanced by immigration. In practice, field workers are usually forced to the assumption that these two forces cancel one another because they have no way of investigating either practically. However, there is usually no proof that this is a valid assumption and it rests on the belief that immigration and emigration (or dispersal) are more or less random events involving the movement of animals in all directions.

XI.2 Immigration

Immigration is rather more difficult to measure than emigration because of the difficulty of knowing the origin of unmarked animals which may appear in the traps. One cannot distinguish mice which inhabit the grid but which have avoided capture on previous occasions from those which have moved into the grid from elsewhere. This problem may be eased slightly if there is a well-marked breeding season and provided that young juveniles are easily captured. In

that case one may be justified in assuming that the juveniles must have been born in situ and that at some season (for example, just before and during the first half of the breeding season) the appearance of new heavy adults is probably due to immigration.

In an attempt to identify immigrants in the Rhabdomys population, the numbers of unmarked heavy adults (> 40g) and the total number of unmarked mice captured each month are presented in Table 33. A body mass of 40g was used to distinguish immigrants because the growth curve (Fig. 9) shows that mice of both sexes take at least 14 weeks to reach a mass of 40g. It is, therefore, considered that very few mice resident in the control grid could have avoided capture for so long in view of the fairly intensive trapping routine (the traps were checked eight times per month) and the high trappability of R.pumilio (Table 7). Hence the majority of new heavy adults were believed to have been immigrants from elsewhere.

Table 33 shows that immigration occurred throughout the year but fell to a minimum in terms of number of individuals in the winter months May to August, though it often remained quite high in percentage terms since total new recruits were low in winter. There was normally an increase during the early breeding season both in absolute and percentage terms. It is difficult to prove that new heavy adults had immigrated from elsewhere, but it seems probable. If one takes a year such as 1974, for example, when numbers were very low,

only two males of over 40g were caught from May to August and yet 18 were caught from September to December (first half of the breeding season). It is hard to believe that so many big males had avoided capture for so long in a low density population and, since the first pregnant females were not caught until the end of September, it is hardly possible for young males to have reached body masses of over 40g before January. Hence one is led to assume that this is evidence of immigration due to movement associated with the start of a new breeding season. There is also additional evidence already mentioned (p. 38), obtained from trapping in grid K in winter 1975. This showed that of 125 new mice marked in the control grid from May to August 1975, 21% were immigrants which had already been marked in grid K. This seems fairly strong evidence that immigration was a continuous influence throughout the year.

That small mammals can avoid capture in the face of intensive trapping has been shown by Gentry et al (1971) who first tagged shrews (Blarina brevicauda) by prebaiting with radioactive bait and then trapped them in a 5ha central grid and in a 9ha peripheral grid during 36 days and 18 days of continuous trapping, respectively. It can be deduced from their data that of 50 shrews captured in the central grid, 42 were caught by day 7 and additional labelled animals were caught on days 16, 21, 25 and 30. Thus, in the extreme case, a shrew avoided capture for 30 days of continuous trapping. One must, therefore, be cautious in interpreting data on immigration. However, the best that can be done is

to accept the highest probability and in the case of R.pumilio this seems to favour immigration, rather than avoidance of capture.

XI.3 Dispersal

Krebs and his co-workers, building on the studies of earlier workers who kept various species of vole in artifical pens and found that they increased to densities many times those found in nature, took the view that dispersal was not a random process. They concluded that the reason for these abnormally high densities was the prevention of dispersal and that a study of the process of dispersal might reveal that it played an important role in normal population regulation of the mice. In several studies they, therefore, set about investigating the role of dispersal in Microtus population dynamics (e.g. Krebs et al 1969, Myers & Krebs 1971b, Krebs et al 1976 and Hilborn & Krebs 1976). Clearly, the provision of food and the absence of predators in artificial pens made it impossible to extrapolate the results of those studies to natural populations. One of their first experiments (Krebs et al, 1969) was, therefore, to enclose with 0,6m high vole-proof fencing, some 0,8ha (2 acres) natural areas, which were then monitored by regular live trapping. These areas showed great increases in density of voles to levels far above those of control grids, with ultimate destruction of the habitat due to overgrazing.

Gentry (1968) studied M.pinetorum also in 0,8ha enclosures in South Carolina. Densities inside the enclosures were higher than those in natural populations in the same area, which he ascribed to the prevention of dispersal and the provision of additional food in the form of trap bait. However, the maximum densities inside the enclosures reached only about 25 mice/ha (10 per acre) and recorded survival was low. He had proof that mice could both enter and leave the enclosures (via tunnels under the fence) and hence his conclusions about the absence of dispersal must remain suspect. Even if only erratic dispersal was occurring, it would have been important to establish which animals were finding their way out (perhaps by netting the exit tunnels?).

Krebs & Myers (1974 : 312) say that dispersal as a population process might act in two possible ways. It might either involve excess animals, possibly subordinate or juvenile, which were forced to emigrate when population density reached high levels. According to this view, most of the losses from a declining population would be due to dispersal. Alternatively, a dispersing vole might differ qualitatively from the residents and hence dispersal might selectively remove individuals of a certain kind from the resident population and so change the characteristics of the population left behind. In this case dispersal is seen as some kind of definite, selective mechanism and might have its most important influence during population increase, rather than population decline.

These two views appear to correspond with Lidicker's (1975) ideas on saturation and pre-saturation dispersal. He defines the former as "the outward movement of surplus individuals from a population living at or near its carrying capacity". Amongst these surplus individuals he includes social outcasts, juveniles, very old individuals and those in poor condition. With regard to pre-saturation dispersal, Lidicker (1975 : 106) says: "... it occurs during population growth and may even begin very soon after growth starts .... such emigrants .... will in general be in relatively good condition and may include any sex and age group, including pregnant females".

Dispersal in R.pumilio was studied by establishing a peripheral grid (grid K) which surrounded the control grid on three sides, the fourth side being the bank of the Kuils River (Fig. 2). Grid K consisted of three parallel rows of trap stations 20m apart, forming three sides of a rectangle; the inner row was 20m from the outer border of the control grid. Livetrapping was conducted in grid K from February 1975 through February 1976, usually in the middle of each month about two weeks after the month-end trapping in the control grid. For details and exceptions see Chapter II. All unmarked mice captured on grid K were marked and released using an identifying code for the grid. By surrounding the control grid with traps it was hoped to get positive evidence of any dispersal taking place. Marked mice from the control grid which were captured in grid K were recorded and released.

During the 13 months of trapping in grid K, 250 marked males and 227 marked females disappeared from the control grid. If dispersal accounted for a significant fraction of these, I hoped to catch many of them in grid K. This was based on the assumption that dispersing mice were 'trappable' and did not simply move straight through the surrounding area without stopping to investigate traps and also that, even if they did behave normally towards traps, they remained long enough in grid K to be captured. The results are presented in Table 34 which shows the number of marked mice from the control grid caught in grid K as well as what was believed to have been the number of 'true' dispersers.

In order to identify dispersing mice it would seem necessary to have a definition of what constitutes dispersal. Lidicker (1975 : 104) defines dispersal as movements of organisms "in which they leave their home area, sometimes establishing a new home area. This does not include short-term exploratory movements ....". I define 'true' dispersers as control grid mice, whose last recorded capture was in grid K and whose trapping history showed no home range overlap and hence appeared to have dispersed from the control grid. They constituted only 8,0% of the number of missing mice. This was considerably less than the total number of control grid mice caught in grid K, since analysis of the recapture records showed that most of these mice had home ranges overlapping both grids and hence were caught in both grids for several months. These were not classified as dispersers.

Myers & Krebs (1971b), Krebs et al (1976) and Hilborn & Krebs (1976) studied dispersal by maintaining vole-free areas through regular removal trapping. These areas acted as 'vole-sinks' in the neighbourhood of control populations. All voles captured in these vole-sinks every two weeks were removed. Some of these dispersers were tagged voles from the control populations and it was, therefore, possible to say at what stage of the control population cycle the greatest amount of dispersal occurred.

Myers & Krebs (1971b, Fig. 6) and Krebs & Myers (1974 : 313) have recorded the percentage of losses due to dispersal from two populations of M.pennsylvanicus (grids F & I) at different phases of the population cycle. They found that dispersal accounted for a far higher proportion of the losses in an expanding population (56% for males; 69% for females), than in a declining one (15% for males; 12% for females). Krebs et al (1976, Table 4) found a similar situation in two populations of M.townsendii and claimed that the percentage of loss explained by dispersal was positively related to the rate of increase of the control population. However, their results are not entirely convincing since the highest rate of loss due to dispersal (35%) was recorded during a decline period on grid C (winter 1971 - 72) and on grid E the losses due to dispersal during the two declines were only slightly less than the losses during the increase periods and were more than the losses during the approximately stable period in summer 1973. Hilborn & Krebs (1976, Table 5) studying two other populations of M. townsendii, also found that

losses due to dispersal were highest in the increase phase (24%). During the peak they were 18% and in the decline from 0 - 5%.

It can be seen from Table 34 that the proportion of 'true' dispersers identified during this study (8,0%) is far lower than that recorded in the above-mentioned studies. However, this is due mainly to the different method of studying dispersal which I employed. Instead of removing all tagged animals from the control populations as soon as they appeared outside the control grid, they were recorded and released. Thus, had the method of Myers & Krebs (1971b) been applied, I would immediately have removed all marked mice from the control grid the first time they were captured in grid K. Therefore, all the mice in column 3 of Table 34 (marked mice appearing for the first time in grid K) would have been removed by their method; namely 66 males and 35 females or 101 mice. Since 477 mice were lost from the control grid during the same period, it follows that 21,2% of overall losses would have been recorded as due to dispersal. This is comparable with the figures obtained by Krebs et al (1976, Table 4), since of 998 M.townsendii lost from control grids, 222 or 22% dispersed (Table 4 actually records 269 voles or 27% dispersal, but this appears to be the result of a casting error). My (hypothetical) figure of 21% is somewhat less than the overall figure of 29,5% dispersal out of 427 M.pennsylvanicus lost from controls, which can be calculated from Table X of Krebs & Myers (1974 : 313) but

TABLE 34

Dispersal from the control grid on to peripheral grid K from February 1975 to February 1976.

* = No. marked mice from control grid caught for the first time in grid K.

✱ = 'True' dispersers are marked mice from the control grid whose last recorded capture was in grid K and whose trapping history does not show home range overlap between the two grids.

	Minimum number alive on grid K	Total No. marked mice from control grid caught on grid K		*No. 'new' mice from control grid caught on grid K		No. lost from control grid		✱ No. 'true' dispersers		% loss due to dispersal
		M	F	M	F	M	F	M	F	
1975 FEBRUARY	173	22	8	22	8	15	17	9	5	43,8
MARCH	234	11	8	5	4	29	27	2	0	3,6
APRIL	253	16	9	4	4	17	23	4	1	12,5
MAY	227	9	5	2	1	21	31	1	1	3,8
JUNE	221	9	4	3	0	26	14	1	1	5,0
JULY	180	6	5	1	3	17	15	0	1	3,1
AUGUST	162	5	6	2	2	9	3	1	0	8,3
SEPTEMBER	153	1	2	0	0	9	14	0	0	0
OCTOBER	145	4	3	3	1	9	9	1	0	5,6
NOVEMBER	145	3	3	2	1	22	13	0	0	0
DECEMBER	165	4	4	4	3	29	20	3	1	8,2
1976 JANUARY	179	6	6	6	2	20	11	1	2	9,7
FEBRUARY	205	14	9	12	6	27	30	3	0	5,3
TOTAL		110	72	66	35	250	227	26	12	8,0 M 10,4% F 5,3%

considerably more than the overall figure of 7,2% losses due to dispersal out of 320 M.townsendii which disappeared from controls (calculated from Table 5 of Hilborn & Krebs, 1976).

The finding that the majority of animals from the control grid which were caught in grid K were, in fact, not dispersers but simply had overlapping home ranges, suggests that some of the voles removed by Myers & Krebs (1971b) and Krebs et al (1976) may have fallen into the same category. Their proportion of true dispersal may, therefore, have been less than it appeared. This seems possible since the removal grid in the former study was only about 27m (90ft) from control grids F & I and was situated between them. In the latter study the removal grid was 30m from the control grid. In the present study, the inner row of grid K was 20m from the outer border of the control grid, which was about double the mean distance Rhabdomys moved between successive captures (Table 9). The much lower proportion of 'dispersers' recovered (7,2%) by Hilborn & Krebs (1976) may have been due to their removal grid being situated much further from the control - about 80m, which would have effectively eliminated any possibility of overlapping home ranges. (According to Hilborn & Krebs, 1976, p.1509, removal grid Z was situated 40m from control grid Q, but from their scale in Fig. 1 it can be seen that at their closest points grids Z and Q were about 80m apart - 266ft).

The findings of Stickel (1946) concerning dispersal of the

wood mouse, Peromyscus leucopus, are relevant to this situation. Stickel clearly demonstrated the origin of mice moving on to a one acre removal grid by first livetrapping a 17 acre peripheral grid and marking and releasing all the mice on the area. The home ranges of all the livetrapped animals were recorded. She then killtrapped in the one acre removal grid in the centre of the area for 35 nights. She found that all the mice that invaded the removal grid were marked mice which had pre-established home ranges in the surrounding area. The first mice to move on to the removal area were those whose home range bordered it and as removal trapping continued, the mice removed on later nights were those whose home ranges were situated progressively further away. No unmarked adults moved on to the removal grid. Thus none of these mice would be classified as true dispersers according to my conception of dispersal - they had been on temporary foraging or exploratory expeditions, possibly seeking to enlarge their own home ranges, which became possible when their erstwhile neighbours (and competitors for space) were removed. Stickel's results emphasise the possibility that the Microtus entering the removal grids of Krebs et al, could have fallen into the same category - namely not true dispersers but mice on the move due to the artificial creation of the 'vole-sink'.

Gaines et al (1979), who found very high rates of dispersal of tagged voles from control grids to removal areas 50m away (a mean of 64% of losses in winter-spring and 42% in summer), also suggested that removal trapping was producing

a 'vacuum effect' - attracting voles from resident populations.

The findings of workers previously referred to that dispersal was greater during the increase phase of a population prompted the enquiry as to whether the same was true of R.pumilio. For this purpose the period February 1975 to 1976 was divided into increase and decline phases by reference to Fig. 3. The very high dispersal rate of 43,8% in February 1975, the initial month of trapping on grid K, is believed to be an artefact, due to the sudden identification of a 'backlog' of dispersers from the control grid; of the 14 dispersers identified in February 1975, eight had been missing from the control grid for periods of two months (three mice), three months, four months, five months (two mice) and 11 months. Only the balance of six mice were, therefore, included in the calculation for February. The months of expanding population were taken as being February through May 1975 and November 1975 through February 1976. The months of declining population were June through October 1975. The analysis is presented in Table 35 using figures from Table 34. This shows that marked mice from the control grid, caught for the first time in grid K (equivalent to tagged mice captured on the removal grids of Myers & Krebs, 1971b, and Krebs et al, 1976) were very significantly more numerous during the increase than during the decline ($p < 0,001$). 'True' dispersers were also significantly more common during the increase ($p < 0,01$). The higher level of significance for the first group (mice with overlapping

TABLE 35

(Figures from Table 34)

Analysis of dispersal from control grid into grid K in phases of expanding and declining population.

¤ only 6 mice have been counted as dispersers for February 1975 (see Text)

* Dispersers are marked mice from the control grid whose last recorded capture was in grid K and and whose trapping history showed no home range overlap with grid K.

Period	Status	From Control No. lost	Total No. from control caught in grid K	% Loss	* No. dispersers from control	Due to Dispersal % Loss
1975 Feb-May 1975 Nov-Dec 1976 Jan-Feb	Expanding	352	86	24,4	¤ 25	7,1
1975 Jun-Oct	Declining	125	15	12,0	5	4,0
CHISQUARE			53,13		10,16	
P			< 0,001		< 0,01	

home ranges) suggests that this could be evidence of increased movement in the breeding season but, nevertheless, it does seem that dispersal is more prevalent during the increase phase (breeding season) of Rhabdomys, which agrees with the findings of other workers on voles.

It is evident from Table 34 that the number of male dispersers was over twice that of females. This is a much higher ratio than that of total mice lost - namely 250 males; 227 females, suggesting that there may have been selective dispersal of males. Stickel (1946) found that twice as many adult male Peromyscus (36 males : 18 females) moved on to her removal grid. Myers & Krebs (1971b) found that more male M.pennsylvanicus dispersed from a control population than females and Krebs et al (1976) found that more male than female M.townsendii colonised a removal grid.

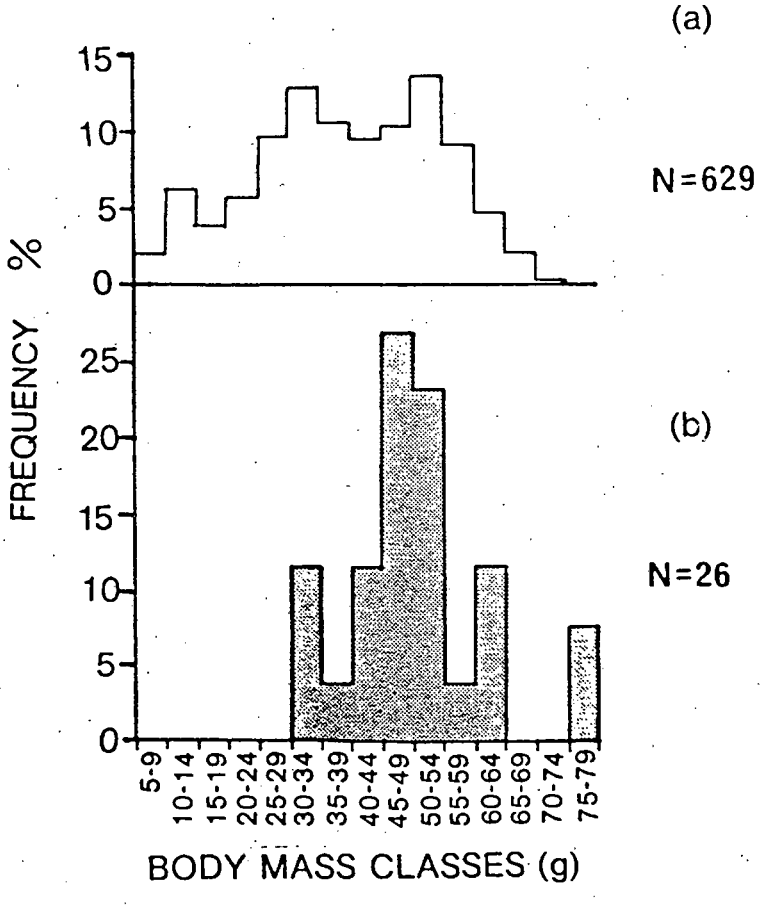
The distribution of body masses of the dispersing males and of males in the control grid during the same period is shown in Fig. 29. The body masses of the control grid males include all recaptured animals. Thus, if a male is caught more than once, its weight will be included each time. Female body masses have not been analysed because they are complicated by pregnancies. It is noticeable that the majority of the dispersers were large adults and not colonising juveniles, as might perhaps have been expected. Indeed, the two males of 75g and 78g were among the heaviest animals recorded in the whole study.

FIG. 29

Bodymass distribution of resident males on the control grid compared with dispersing males from February 1975 to February 1976.

(a) = all males caught, including recaptures

(b) = marked mice that dispersed from the control on to grid K



This is not in accord with the concept of Brown (1966) and Christian (1970). They suggested that the young maturing subordinate male would be the class of animal most likely to disperse from its birthplace in mammal populations due to the intolerance of dominant males, particularly in times of high population density. Christian (1970) particularly suggested that these young males would be responsible for colonising new habitats. Brown (1966) states the case dramatically when he cites Andrewartha & Birth (1954) as saying: "the plight of the young male is desperate". He must either oust a resident, find an empty space, or die.

It is not certain precisely where these ideas fit, in relation to those of Lidicker (1975, above), but presumably they would fall under his pre-saturation dispersal.

Estimates of mean expectation of life from first capture (Table 27) show a greater mean expectation of life for juvenile females of 0,6 months - which represents a 32% increase over that of males. This could support the idea of emigration of young males. These two lines of evidence are, therefore, in conflict. The significance of the finding of dispersal of large adults in R.pumilio is not clear from the available evidence. A sample of only 26 dispersing males is too small to justify firm conclusions and more experiments need to be done. Myers & Krebs (1971b : 59) have suggested that because in vole populations animals tend to be heavier during the increase and peak phases than during the decline, and because dispersal is more common during the

increase, there may be a tendency for heavier animals to disperse. However, this supposition was not borne out in a study of resident and dispersing M.pennsylvanicus, M.ochrogaster and M.townsendii (Myers & Krebs, 1971b; Krebs et al, 1976). Their results and mine, unfortunately, are not readily comparable since their category of 'dispersers' included all voles which were caught on their removal areas. As explained above, some of these were probably voles with overlapping home ranges from the control grids or other neighbouring areas. In any case, they were not dispersers according to the definition used in this study.

The overall apparent dispersal figure of 8% of the R.pumilio lost from the control grid is very low and may appear to suggest that the majority of losses must have been deaths in situ. However, this may not be a correct deduction since it would depend on the efficiency in catching dispersers. If dispersing mice behaved differently and simply moved straight through a peripheral area, without stopping to inspect traps, then they would not be caught. Even if this were not the case, the trapping period of only four days out of every 30 may have been too short to catch many dispersers if they moved fairly quickly through the bounding grid. To solve this problem, a far more intensive trapping programme would be required.

As mentioned already, field workers are often forced to assume that emigration (dispersal) balances immigration since they have no way of distinguishing the two. This follows logi-

cally from the fact that if there are immigrants to a population then they must have dispersed from elsewhere. If the status quo in an area is to be maintained then it follows that if there is immigration there must be commensurate dispersal. The only exception would be if certain areas were being newly colonised and others vacated - in which case the two forces are not balanced, by definition. Table 33 shows that in 1975 the control grid experienced a 25% immigration of heavy adults, whereas recorded dispersal in the same period was only 8% (Table 34). If one accepts that, a priori, one would expect the two figures to approximately balance, then the large discrepancy suggests that either the method of measuring dispersal was inadequate or else that the study area was tending to be colonized at the expense of other areas.

It is possible that local areas may undergo different phases of either colonization or depletion, such that at one period an area may have large numbers of immigrants moving into it and few emigrants leaving, whereas at another time the situation may be reversed with few entering and many leaving. One might envisage an area as being in a state of dynamic flux during which its suitability as a habitat for small mammals might vary with environmental variables such as rainfall and high or low temperatures which would affect the food supply and the amount of cover available. Thus, if an area were to experience one of these favourable or unfavourable periods, it may be an unwarranted assumption that dispersal should balance immigration - there might well be times

when this is not the case and the area is either attracting or losing animals. This is an aspect of rodent ecology requiring further investigation.

It is very difficult to assess how much in error the estimate of dispersal of Rhabdomys may have been. We have recorded movements of mice of up to 300m and we know that mice can cross barriers such as streams (p. 65). Hence it is quite possible that continuous dispersal was occurring that we were unable to measure. However, to quantify this without further research would be impossible. It is interesting that Hilborn & Krebs (1976, Table 7) have equated dispersal with adult immigration, despite the fact that direct measurements of dispersal by catching tagged voles on a removal grid (their Table 5) did not agree with any of their measurements of immigration in corresponding periods. From what has been said above, I believe that it may not be justifiable to assume that dispersal and immigration are equal, unless there is additional evidence to substantiate the claim. Such evidence would be provided by very accurate monitoring of the two processes. The best way of doing this would probably be by using large numbers of radio-collared individuals but, as Hilborn & Krebs (1976) say, this is difficult with present technology.

XI.4 Summary of immigration and dispersal

Difficulties in analysing these two parameters lie in the problems of distinguishing genuine immigrants from animals

which may have been resident in the study area but which have avoided capture; and in distinguishing those which have left a home area permanently from those which may be on temporary excursions. Immigration was assessed from the number of new heavy adults (> 40g) caught in the control grid each month and also from a sample of mice caught for the first time in the congrol grid, which had previously been marked in the peripheral grid K. These analyses seemed to show that immigration was a continuous influence throughout the year but fell to a minimum in the winter months, May through August. A minimum of 23 - 34% of new mice caught each year were probably immigrants (Table 33).

Dispersal of marked mice from the control grid was studied by livetrapping in peripheral grid K, which surrounded the control grid on three sides (Fig. 2). Mice were only defined as dispersers if they had originally been marked in the control grid but their last recorded capture was in grid K and they had no livetrap history of home range overlap with both grids. The majority of mice which moved from one grid to the other in fact simply had home ranges which overlapped both grids. Table 34 shows that of 477 mice which disappeared from the control grid between February 1975 to February 1976, only 8% were identified as having dispersed on to grid K. The finding that in the same period there appeared to be at least 25% immigration suggested either that the method of measuring dispersal was inadequate or else that there was colonization of the study area. While it is likely that the measurement of emigration was inade-

quate, I also believe that the assumption that immigration always balances emigration is not justified a priori.

There were significantly more dispersers during the breeding season (phase of population increase) than during winter (non-breeding). There were twice as many male dispersers as females and the majority of them were large adults, not juveniles. The sample of true dispersers was too small to justify firm conclusions as to sex ratio and age.

XII. FOOD SUPPLY AND THE INFLUENCE OF SUPPLEMENTAL FEEDING

XII.1 Introduction

The ecological literature is strewn with debate as to which ecological factors, either alone or in combination, are responsible for the regulation of numbers of natural populations (e.g. Lack (1954b), Wynne-Edwards (1962,1965). The fact that numbers of any given species do not increase indefinitely but reach a peak density during each fluctuation implies that some factor must be preventing their actual increase beyond a certain (variable) density. Clearly, no population in nature could exist at such a density that it destroyed its food supply. Hence, food must be the ultimate limiting factor on any population. Yet, in nature, we do not normally find animals either starving or overeating their food supply and so the question arises as to whether it is food which controls populations under normal circumstances.

This study has documented pronounced fluctuations in the mouse population both from season to season and from year to year. This prompts the question as to whether limitations in food quantity or quality could (a) limit the size of the peak mouse population, and (b) cause the winter decline each year. Predation will be considered in the next chapter. Disease was not specifically investigated in this study, but was not thought to be an important mortality factor, due to the very low incidence of visible

lesions or heavy parasite infestations in over 800 autopsied specimens.

XII.2 Review of literature implicating food in population regulation

Lack (1954b) stressed the importance of food supply as a limiting factor on population increase. He thought that this was particularly true of birds and carnivorous mammals but that herbivores were probably limited by predators, since there always appeared to be ample green vegetation available and there were few recorded cases of destructive overgrazing by herbivores. This notion that herbivores were not food limited because of the apparent abundance of vegetation persisted for a long time, until more recent evidence that it is not so much the quantity as the quality of the vegetation which is important. Changes in the quality of the grazing can influence herbivore populations. For example, Sinclair (1974) has shown that both the quality and quantity of food available to a buffalo population falls below the minimum maintenance requirements of that population at certain times of the year. In the Serengeti grasslands, East Africa, there was a shortage of the only good quality component, grass leaf, in the dry season. Sinclair concluded that the buffalo population in the Serengeti was regulated by adult mortality, which was caused by undernutrition as a result of food shortage. Perhaps his most interesting point is his statement (Sinclair, 1974:292) that: "there appears to be

no foundation for hypotheses which invoke overutilization or damage as a consequence of regulation through food". In other words, a population may be regulated by its food supply (through its quality) and yet, apparently, not have overgrazed the habitat.

The view that cyclic microtine rodents are not regulated by their food supply (they are all herbivorous to some degree) has been very persistent and seems to have been based on very flimsy evidence. Chitty (1952, 1960) who studied voles (M.agrestis) in Wales, dismissed the possibility that food shortage might be responsible for the declines of the vole populations, although no study of the vegetation nor of the nutritional requirements of the voles was made and, despite his admission that the vegetation was damaged at times of high vole numbers. Summerhayes (1941) had shown, by means of exclosure cages, that the prevention of grazing by voles had some definite effects on the plant community, such as the decrease of some angiosperms and the disappearance of mosses. Lack (1954a : 30) pointed out that the food requirements of cyclic rodents had not been studied and suggested that cycles might be produced as a result of the rodent interacting with its food supply. This is also implicit in the nutritional threshold hypothesis of Schultz (1969) who suggests that heavy grazing by microtines causes changes in the availability of essential nutrients to the plants, which in turn causes reduction in plant growth, resulting in less forage being available to the rodents, which in their turn decline.

Chitty et al (1968) confined individual voles (M.agrestis) to 11 ft^2 plots on natural grassland to see how long they could maintain their body weight on this restricted diet in spring. As a result of this experiment they concluded that in the spring, fall in vole numbers could not be attributed to a lack of forage. However, they did not examine the quality of the forage available and four voles died on the plots without showing any loss in weight. Furthermore, they attributed a less than expected decline in the population in spring 1961 to an unusually mild, frost-free winter of 1960 - 61, which would have influenced both the quality and quantity of the vegetation. Krebs et al (1973) decided to abandon the search for extrinsic agents of population control such as food supply, predation and disease.

Other studies, however, have demonstrated the direct interaction of rodents and their food supply. In a study of M.californicus, Batzli (1968) found that food rather than refuge was the important vegetational factor affecting the dispersion of the mice. Wild oats (Avena) was believed to be the major food of the voles and the distribution of the voles showed positive correlations with the percent cover of Avena but not of other widespread grasses. Batzli & Pitelka (1970) have shown the effect that populations of M.californicus may have on the vegetation. They found that Microtus reduced standing crop of preferred food plants by reducing both average height and percentage cover in grazed areas. Seedfall from preferred grasses was diminished 70% on grazed areas. Batzli & Pitelka (1971) found that

seasonal changes in condition of M.californicus were correlated with dietary changes. The end of the breeding season in late spring was associated with low growth rates, low survival rates and low fat reserves. At the same time the vegetation was drying and the diet changed from one dominated by grass stems and leaves to one dominated by grass seeds. Three species of annual grass were preferred foods and the standing crop and seed production of these were severely reduced by high vole populations. They considered that reduction in food availability and quality might have caused the delay in the start of the breeding season and the continued population decline that followed the peak population.

In contrast, however, Evans (1973) did not find a correlation between the quality of the food and the annual cycle of growth, breeding and moult of M.agrestis. She used pepsin solubility as an index of food (grass) quality. The grasses had a maximum pepsin solubility for only a short period in the year, but this did not coincide with the period of most vole growth and reproduction nor of most utilization of the grass species. One possible conclusion from her work is that the quality of available food was not an important factor in the ecology of M.agrestis or, as she says, that some unmeasured aspect of nutrition was more important than pepsin solubility.

The study of the precise food habits of herbivorous rodents has been largely neglected because of the difficulty (and

tedious nature) of identifying tiny fragments of plant material in their stomachs. Godfrey (1953) studied the food of M.agrestis by the microscopic identification of fragments of plant epidermis in faecal pellets. More recently, serious attention has been given to the problem of qualifying and quantifying the diet through analysis of stomach contents and digestibility trials (e.g. Zimmerman (1965), Watts (1968), Evans (1973), Batzli & Cole (1979) and Cole & Batzli (1979).

Watts (1968) found seasonal variations in diet in wood mice and bank voles, but the importance of this may lie in its relationship to seasonal changes in rodent populations (Batzli & Pitelka, 1971). Watts (1969) says that the winter survival of wood mice is dependent on the size of the acorn crop, but that in summer the numbers are not food related, since there never seems to be a shortage of their main food (seeds). Delany (1974 : 34) says that the nature of the diet may be extremely important in initiating and terminating reproduction. Negus & Pinter (1966) showed that sprouted wheat fed to immature female M.montanus stimulated immediate onset of oestrus, as well as increase in uterine and adrenal weights. This finding, together with the more recent one of Negus & Berger (1977) that a nonbreeding winter population of M.montanus could be brought into breeding condition by feeding it limited supplements of fresh green wheat grass over a two week period, and of Berger et al (1977) that sprouted winter wheat also contained a uterine growth inhibitor substance, strongly implicates nutrition in the control (onset and cessation) of the reproductive cycle.

XII.3 The diet of R.pumilio on the Cape Flats

The diet of R.pumilio at different seasons was examined by stomach contents analysis by Shelton (1975) and King (1976). They used material from the killtrapped specimens collected during this study. No entirely satisfactory method for quantitative evaluation of food contents exists. The method employed was that of mean percentage area (Gebczynska & Myrcha, 1966) cited by Hansson (1970). The area of each food type in the stomach was measured on a 20 x 20 square ocular grid, covering an area 4mm x 4mm, under a dissecting microscope. The area of each food type was expressed as a percentage of the total area covered by all the particles. This is an index of the proportion of food of each type in the stomach (Hansson, 1970). The mean of ten ocular areas was obtained. This method has the disadvantage of applying equal ratings to flat fragments such as epidermis and round fragments such as seed.

The summarised results of Shelton (1975) and King (1976) are presented in Table 36. Although the results for 1972/73 are more variable than those for 1975/76, both studies show that for most months of the year, but particularly from December to May, seeds of the alien Acacia trees, (Acacia saligna and A.cyclops) were the most important dietary item, with a range from 27 - 81%, but usually around 50%. No stomachs were examined for October and November. Green vegetation comprising epidermis, leaf and stem made up the second most important item in most months and in some of the

TABLE 36

Summary of the diet of R.pumilio. Mean percentage area of each food type in the stomach contents. Animal matter comprises insect plus snail. Green vegetation comprises epidermis plus stem plus leaf. Seed is mainly of Acacia cyclops and A.saligna.

Date	No. of stomachs	A. cyclops funicle %	Acacia seed %	Animal %	Green vegetation %	Root %	Other %
Aug 1972	8	3,3	27,2	0	69,4	-	0,1
Dec 1972	15	15,9	52,3	6,7	24,9	-	0
Jan 1973	11	8,1	66,7	7,8	16,8	-	0,22
Feb 1973	11	8,9	62,9	0	25,0	-	0
Jun 1973	12	1,5	47,6	0,8	50,1	-	0
Sep 1973	11	0,9	81,7	0,2	17,2	-	0
Dec 1975	11	17,1	53,4	4,8	22,5	0,7	1,7
Jan 1976	15	26,9	38,4	1,8	30,6	0,1	2,5
Feb 1976	14	21,5	52,2	5,5	19,8	0,3	0,6
Mar 1976	14	24,4	44,3	5,5	23,7	0,5	1,5
Apr 1976	14	14,0	56,8	3,2	18,4	0,5	7,0
May 1976	14	9,0	55,6	4,0	28,0	0,6	2,7
Jun 1976	14	5,5	45,8	1,0	39,9	1,0	6,8
Jul 1976	14	0,7	40,8	1,6	49,7	1,0	6,2
Aug 1976	10	0,7	49,5	0,5	44,8	1,0	3,4

Data for 1972 and 1973 from Shelton (1975).

Data for 1975 and 1976 from King (1976).

winter months, May to August, it was the most important item, when it could comprise 50 - 69% of the diet. The orange-coloured funicle (seed stalk) of A.cyclops, which had a high fat content, was a favoured item in the summer months when the ripe seeds were falling. Animal matter, consisting of insects and flesh of the snail, Theba pisana, comprised a minor part of the diet. Brooks (1974) also found that R.pumilio in the Transvaal was mainly a seed eater, with seeds often making up over 80% of the diet in a 14 months period. Green vegetation was the second most important item, while in two months insects comprised 25% of the diet. On the basis of these studies, R.pumilio appears as primarily a seed-eater which at some seasons may take a significant amount of green vegetation. Curtis & Perrin (1979) and Perrin & Curtis (1980), however, suggest that R.pumilio is an opportunistic omnivore, whose diet varies seasonally. They found that it selected fruit and seeds preferentially but readily ate insects and the leaves of some shrubs. From its very wide geographical distribution, one would probably expect to find regional differences in diet.

XII.4 The natural availability of Acacia seed to R.pumilio

Since it was established that the seeds of the alien acacia trees were the most important dietary items on the study area, an attempt was made to estimate the production of seed by the trees and availability to the mice throughout the year in 1976 - 77.

Firstly, the area covered by acacia trees on the control and experimental grids was estimated using the line-intercept method of Mueller-Dombois & Ellenberg (1974) - see Chapter II. The results are presented in Table 37 which shows that Acacia cover was approximately equal in both grids at 44 - 46% of the area. Seedfall from the trees was measured by setting up 0,5m diameter plastic bags under the thickets. These were emptied each month and the collected seeds sorted and weighed. The seedfall for the whole area was extrapolated from the known area of the bags. The bags comprised less than 0,4% of the area of Acacia and hence did not reduce the seed supply for the mice. Although mice were seen to climb the trees and to chew seed pods still attached to the trees, the main seed availability to the mice occurred in the leaf litter beneath the trees. The seed content of the leaf litter was, therefore, measured by means of ten 0,5 x 0,5m quadrats on the control grid per month. All the litter lying on the surface of the soil was collected and the seeds contained in it were separated in the laboratory. The supply of litter seeds on grid E was assumed to be very similar.

The results are presented in Table 38, which shows that the trees had a restricted season of seed production. The main seed production of A.saligna was from December to mid-March and of A.cyclops from January through April. Significant quantities of seed fell from the trees only in the summer months December through March. However, due to the accumulation of seeds in the litter this food source

TABLE 37

EXTENT OF ACACIA CYCLOPS AND A.SALIGNA COVER ON THE CONTROL AND EXPERIMENTAL GRIDS, AS DETERMINED BY LINE-INTERCEPT METHOD (MUELLER-DOMBOIS & ELLENBERG 1974)

SPECIES	CONTROL GRID (0,45ha)		EXPERIMENTAL GRID E (0,44 ha)	
	% COVER	AREA COVERED(M^2)	% COVER	AREA COVERED (M^2)
A.CYCLOPS	22,7	1022	15,2	672
A.SALIGNA	21,6	972	31,2	1371
TOTAL ACACIA	44,3	1994	46,4	2043

CONTROL GRID DATA FROM KING (1976)

TABLE 38

Total biomass of Acacia seed available on control grid and degree of exploitation by R.pumilio. Seedfall collected in 40 x 0,5 m diameter bags on control grid and 25 bags on experimental grid E. Litter collected in 10 x 0,25 m^2 quadrats per month.

CONTROL GRID (0,45 ha)						GRID E (0,44 ha)
MONTH	TOTAL SEED MASS (kg) SEEDFALL	TOTAL SEED MASS (kg) LITTER	MINIMUM NO. OF MICE ALIVE	TOTAL MASS OF SEED EATEN (kg) AT 5g/DAY/ MOUSE	% OF LITTER CONSUMED	TOTAL SEED MASS (kg) SEEDFALL
*JAN 1976	131,4	NO SAMPLE	96	14,4	-	-
FEB	27,0	106,6	119	17,9	17	-
MAR	18,3	220,8	91	13,7	6	-
APR	9,8	136,6	62	9,3	7	3,8
MAY	4,4	114,8	NO TRAP	-	-	2,0
JUN	2,0	95,2	34	5,1	5	0,7
JUL	0,5	62,1	NO TRAP	-	-	0,6
AUG	0,1	68,0	11	1,7	2,5	0,1

CONTINUED ....

TABLE 38 - continued

	CONTROL GRID (0,45 ha)					GRID E (0,44 ha)
MONTH	TOTAL SEED MASS (kg) SEEDFALL	TOTAL SEED MASS (kg) LITTER	MINIMUM NO. OF MICE ALIVE	TOTAL MASS OF SEED EATEN (kg) AT 5g/DAY/ MOUSE	% OF LITTER CONSUMED	TOTAL SEED MASS (kg) SEEDFALL
SEP	0	NO SAMPLE	7	1,1	-	0
OCT	0	39,0	18	2,7	6,9	0,1
NOV	0	30,1	38	5,7	19	0,6
DEC	5,9	25,7	44	6,6	26	67,4
JAN 1977	119,5	126,0	44	6,6	5	153,2
FEB	46,4	110,9	60	9,0	8	23,7
MAR	18,7	65,4	81	12,2	19	6,3
APR	3,1	28,3	76	11,4	40	1,9
MAY	2,2	29,4	53	8,0	27	0,7
JUN	0,5	FLOOD	-			0
JUL	0	FLOOD	-			0

* CONTROL GRID VALUES FROM JAN 1976 - AUG 1976 FROM KING (1976)

appeared to be abundant throughout the year. Nevertheless, there was a noticeable decline in the quantity of seed available through the winter and spring of 1976. This could have been due to consumption by rodents and decreased availability of seed may have led to the increase in green matter in the stomachs in winter (Table 36). It can be seen from Table 36 that the months when the greatest amounts of A.cyclops funicle were eaten corresponded with the months when seeds were ripe and falling. Very little funicle was found among the seeds in the litter.

In order to test whether there was any difference in quality between ripe seeds falling from the trees and seeds accumulated in the litter, King (1976) compared the energy values of monthly samples burnt in a bomb calorimeter. The results are presented in Table 39, which shows that the energy values of newly fallen and litter seeds were very similar. It is, therefore, presumed that litter seeds were an adequate food source throughout the year.

The finding that the quantity of seeds available in the litter decreased markedly in the spring of 1976 prompted the enquiry as to whether the quantity of food (seeds) could be limiting the population. In order to establish some approximate idea as to the daily consumption of seeds by fieldmice, Shelton (1975) performed feeding trials on four captive mice (two adults of each sex), in small fish tanks. He found that when fed exclusively on Acacia seeds, these mice could more or less maintain their body

TABLE 39

Comparison of monthly energy values of newly fallen seeds collected in seedfall bags and seeds collected in litter samples.

A.C. = *Acacia cyclops* A.S. = *A.saligna*

Sample sizes in brackets.

Values for *A.cyclops* exclude the funicle (seed stalk).

1976 month	Seed sp.	NEWLY FALLEN SEEDS Mean calorific value kj/g	S.E.	LITTER SEEDS Mean calorific value kj/g	S.E.
Jan	A.C.	20,336 (5)	0,48	No data	-
	A.S.	21,283 (5)	0,28	No data	-
Feb	A.C.	18,910 (5)	0,63	19,387 (5)	0,72
	A.S.	20,234 (5)	0,87	20,188 (5)	0,91
Mar	A.C.	20,300 (5)	0,96	22,984 (5)	0,44
	A.S.	22,201 (5)	1,08	21,628 (5)	0,58
Apr	A.C.	21,110 (5)	0,45	21,259 (5)	0,86
	A.S.	21,929 (4)	0,66	21,814 (5)	0,37
May	A.C.	21,269 (5)	1,03	21,028 (5)	1,12
	A.S.	21,994 (4)	0,58	21,349 (5)	0,61
June	A.C.	21,368 (5)	0,76	21,061 (5)	0,42
	A.S.	21,741 (3)	0,59	21,043 (5)	0,79
July	A.C.	20,129 (2)	0,88	21,329 (4)	0,99
	A.S.	-	-	21,581 (5)	0,38
Aug	A.C.	-	-	21,149 (2)	0,74
	A.S.	-	-	21,207 (5)	0,91

Data from King (1976).

mass when they ate a mean of 2,6g of seed per day over a total of 23 days of experiments. It has been stated by Brody (1945) that the energy needed by small mammals to survive in the wild is about double that needed in captivity. Hence, it is assumed here that a wild fieldmouse will eat about 5g of seed per day. It is accepted that there may be a considerable margin of error in this figure, but nevertheless it should enable us to get some idea whether the population of mice might be anywhere near the limits of its food supply.

Table 38 shows the mass of seed (kg) available in the control grid litter each month; also the minimum number of mice alive and the estimated quantity of seed eaten by that number of mice. It can be seen that in November and December 1976 and April and May 1977, the months of lowest seed availability, the mice could have consumed 19 - 40% of the available seed. Consumption by the mice of the available standing crop of seed was quite variable but it seems that in some months at least they might have removed a substantial proportion of it. This does not necessarily mean, however, that an actual food shortage could have developed, since we are considering only the availability of seed, which comprised about 50% of their diet. The next step in the investigation of the food supply would be to monitor the quantity and quality of the green plants eaten by R.pumilio.

The other question which should be asked is whether all the mice on the grid had access to the seed in the litter, since

Acacia cover on the grid was only about 44%. In fact, the Acacia trees were well distributed over the grid area, so it seems probable that no mouse had to travel further than 10 - 20m in order to find seed. The majority of mice lived in the Acacia thickets and, hence, could find food at will.

Although the above findings did not reveal any obvious food shortage, the fact that the mice appeared to be able to consume a substantial portion of the standing crop in some months, suggests that if the seed crop from the trees were to be reduced, or fail entirely, in a year of unfavourable weather, then a seasonal food shortage could result, particularly in the dry summer months. There is also the consideration that the fieldmice were not the only consumers of the seeds. King (1976) suggested that the gerbil, Tatera afra, might be a competitor of R.pumilio on the basis of stomach contents analysis of a few stomachs. This revealed a seed proportion in the T.afra stomachs of 50 - 81%. Portions of the study area contained extensive Tatera burrow systems. It is thought to be a solitary species, with only one animal occupying each burrow. The actual population size was unknown but it was believed to be much smaller than the Rhabdomys population. Other competitors for the seeds were birds, chiefly the laughing dove, the Cape turtle dove and Cape francolin, Francolinus capensis. The influence of R.pumilio and these other consumers may be responsible for the marked decline in seed in the litter after the high levels of summer (Table 38).

XII.5 The experimental grid : provision of supplementary food

The experimental approach towards determining whether a population is suffering a seasonal food shortage is to supply additional food of a known quality on a known area. The population size, growth rates and reproductive characteristics can then be compared with a control population. In the present study an experimental grid (grid E) of 60 stations, 10m apart and area 0,44ha, was established 20m from the control grid. Grid E was part of the old grid K (see Fig. 2). Supplementary food was supplied in the form of commercial EPOL rat cubes in 120 x 750ml glass jars (two at each station) laid on their sides. Each jar contained about 420g of food, so that the maximum extra food available in the grid at one time was about 50kg, which was far greater than the calculated monthly masses of seed eaten in Table 38. Food was first set out on 7 April 1976 and was replenished weekly until 22 June 1977, when serious flooding in the study area rendered further field work impossible. Between 16 and 24kg of rat cubes per week were usually sufficient to replenish the bottles.

Commercial rat cubes were chosen as being the most readily available, balanced food of high nutritive value. Food preference tests were carried out in the field to ensure that the rat cubes were acceptable to the wild mice. Results are presented in Table 2, which shows that the cubes were readily eaten and had a preference rating about equal to

that of seeds. A Weende analysis of Acacia seeds collected from the study area was performed by the Department of Animal Science, University of Stellenbosch, for comparison with the composition of the rat cubes. Results are presented in Table 40, which shows that the Acacia seeds were higher in protein and fibre, but lower in carbohydrate, than the rat cubes.

XII.6 Possible influences of supplementary food on the population

Various measures were used to assess what effect the supplementary food might have had on the population, such as:

XII.6.1 Population size

Fig. 30 shows the fluctuations in total population size in grid E and the control grid, as well as the number of juveniles (< 30g) each month. It is apparent that the normal decline in winter was not prevented on grid E, but that winter numbers always remained well above those in the control grid. The spring increase in numbers began much earlier on grid E and although there was a distinct dip in numbers in December and January, the final population size at the end of the breeding season was about 50% higher than on the control grid. The first juvenile appeared on grid E in August - about two months before the first young on the control grid.

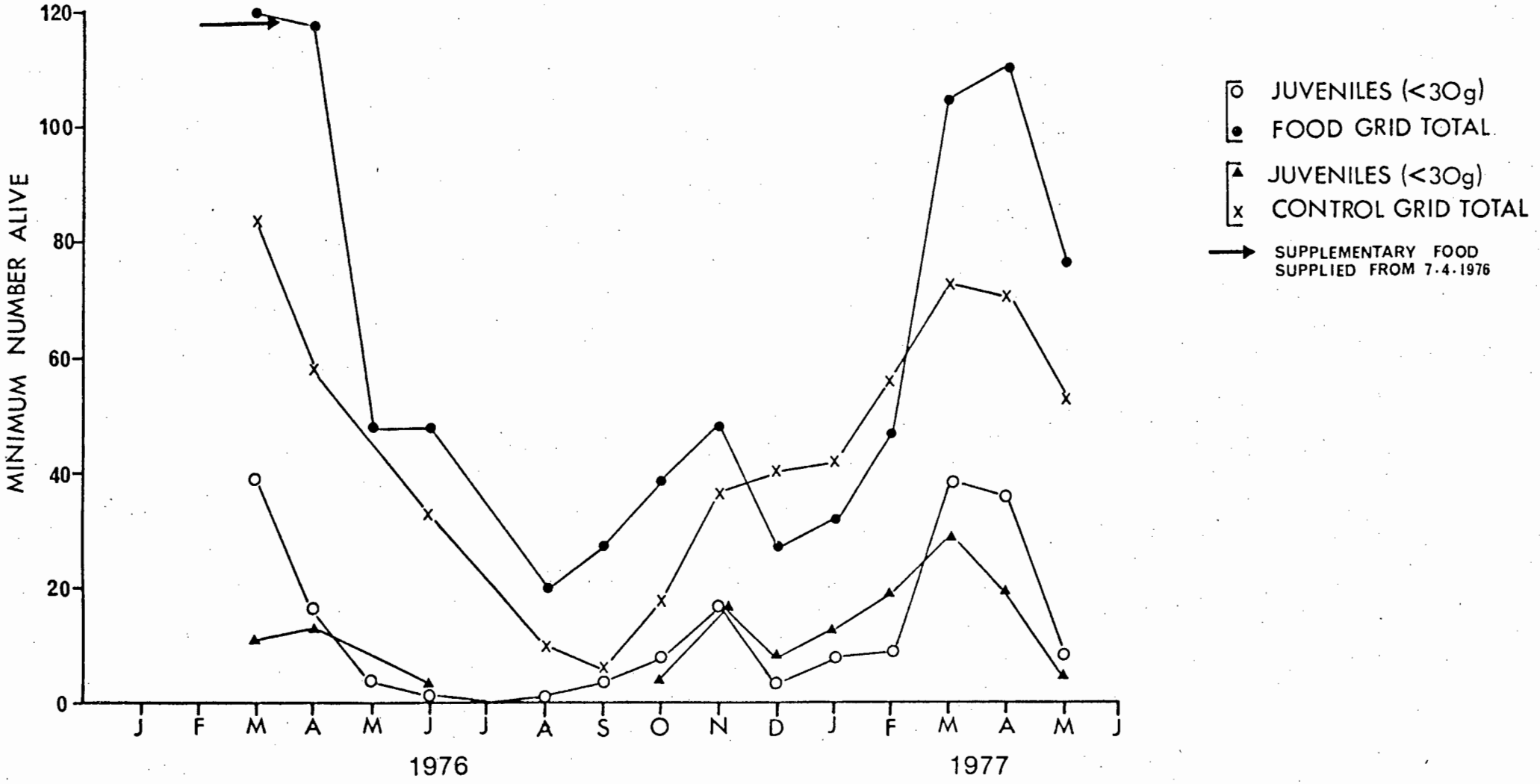
TABLE 40

Composition of natural and artificial foods (as shown by Weende analysis).

PERCENTAGE COMPOSITION					
Food type	Protein	Crude fibre	Fat	Minerals (Ash)	Carbohydrate
A.saligna seeds	24,7	19,0	10,4	4,4	41,5
A.cyclops seeds	28,4	16,8	7,6	4,0	43,2
A.cyclops funicle	12,3	27,6	43,6	1,4	15,1
EPOL Rat cubes	20,0	6,0	2,5	2,1	69,4

FIG. 30

Numbers of adult and juvenile (<30g at first capture) R. pumilio livetrapped on the control grid and grid E (with supplementary food) from March 1976 to May 1977. Additional food (rat pellets) supplied on grid E from 7 April 1976.


MINIMUM NUMBER ALIVE
120
100
80
60
40
20
0
J F M A M J J A S O N D J F M A M J
1976
1977
JUVENILES (<30g)
FOOD GRID TOTAL
JUVENILES (<30g)
CONTROL GRID TOTAL
SUPPLEMENTARY FOOD SUPPLIED FROM 7·4·1976

The winter numbers in grid E were maintained despite the loss of at least 28 mice, taken by a Cape grey mongoose which had learnt to raid the traps in the period May to August. In the same period, only about 6 mice were taken by the raider from the control grid. The mongoose was eventually shot.

Table 41 shows the number of new (unmarked) mice and the number of new juveniles caught each month, as well as the number of mice which had moved from one grid to the other. It can be seen that the number of new mice was 42% higher in grid E (368 : 259) and the number of juveniles was slightly higher (156 : 130). This may indicate a tendency for immigrating mice to move into the food grid, preferentially.

XII.6.2 Movements

If the presence of the extra food had acted as some kind of attractant, there might have been a tendency for marked mice from the control grid to migrate into the food grid. This was investigated by recording all mice which had initially been marked in one grid but which were subsequently recaptured in the other grid, at each monthly trapping session. Table 41 shows the total number of mice (including recaptures) which were caught in the 'wrong' grid each month. In parentheses is shown the number of 'new' mice in the 'wrong' grid, i.e. the number of mice initially marked in one grid which were caught for the first time in the other grid. Table 41 shows that though roughly equal

TABLE 41

Numbers of mice caught in experimental grid E with supplementary food and the control grid, during the period of the experiment from March 1976 to May 1977.
Juveniles = mice <30g at first capture
Sexes combined.

DATE	GRID E					CONTROL GRID				
	Total	New	(Juv.)	+No. from control Total	+No. from control New	Total	New	(Juv.)	+No. from grid E Total	+No. from grid E New
Mar 1976	120	58	(39)	12	12	84	29	(11)	4	4
→ Apr	118	49	(17)	11	6	58	20	(13)	4	3
May	48*	14	(4)	3	1	NT				
Jun	48*	10	(1)	4	1	33*	15	(3)	3	2
Jul	NT					NT				
Aug	20*	6	(1)	2	1	10	5	(0)	2	0
Sep	27	11	(4)	2	0	6	5	(0)	1	0
Oct	39	28	(8)	4	2	18	11	(4)	2	2
Nov	48	30	(17)	1	1	37	29	(17)	3	3
Dec	27	18	(4)	1	1	40	22	(8)	5	4
Jan 1977	32	20	(8)	2	1	42	19	(13)	6	2
Feb	47	35	(9)	4	2	56	36	(19)	5	1
Mar	104	75	(39)	5	3	73	41	(29)	6	2
Apr	110	57	(36)	9	6	71	20	(19)	7	2

continued .....

TABLE 41 continued ...

DATE	GRID E				CONTROL		GRID	
	Total	New (Juv.)	+No. from control Total	New	Total	New (Juv.)	+No. from grid E Total	New
May 1977	76	15 (8)	5		53	7 (5)	4	0
TOTAL θ	864	306 (156)	53	37	605	259 (130)	48	25

NT = No trap → Supplementary food set out

θ = Totals from April

* = Mice taken from traps by mongoose as follows:

1976	MINIMUM NO. OF MICE TAKEN FROM LIVETRAPS BY A RAIDING MONGOOSE	
	GRID E	CONTROL
May	14	-
June	8	6
Aug	6	-
TOTAL	28	6

+ = "No. from control" and "No. from grid E" is the number of mice first marked in the control grid and subsequently recaptured in grid E, or vice versa. It is the total number of marked mice recaptured from the 'wrong' grid including those with home range overlap. Hence, it is not a measure of dispersal.

numbers of marked mice from each grid were caught in the other grid (53 mice from the control grid caught in grid E and 48 mice from grid E caught in the control), the number of these that were new in grid E was 37 compared with only 25 that were new in the control - a difference of almost 50%. (The balance of the mice were recaptures). This may suggest some tendency for mice to migrate into the food grid. This is also supported by the above finding of more new mice in the food grid (if one subtracts the 14 new mice caught in May, when no trapping was done in the control grid, there were 37% more unmarked (new) mice caught on grid E than on the control). This may suggest some positive response to the experimental area by immigrants.

XII.6.3 Biomass

The biomass and mean body mass each month, as well as the total biomass and overall mean body mass for the whole experimental period, are shown in Table 42. This shows that the total biomass of R.pumilio carried on grid E (28,5kg) was 62% higher than was carried on the control grid (17,6kg). The mean body mass of 39,3g on grid E was very significantly heavier than that on the control (35,5g; $t = 7,28$ $DF = 1218$ $p < ,001$). The heavier population on the experimental grid could have been a response to the additional food.

In order to test this possibility (the mice on grid E might always have been heavier than those on the control even

TABLE 42

TOTAL BIOMASS AND MEAN BODY MASS OF R.PUMILIO ON GRID E (WITH SUPPLEMENTARY FOOD) AND THE CONTROL GRID. SEXES COMBINED

	GRID E				CONTROL GRID			
	(g) BIOMASS	(N)	(g) MEAN	(SD)	(g) BIOMASS	(N)	(g) MEAN	(SD)
MAR 1976	3989	(118)	33,8		2981	(84)	35,5	
APR	4634	(118)	39,3		2010	(57)	35,3	
MAY	1904	(48)	39,7		NO TRAP			
JUN	1931	(48)	40,2		1228	(33)	37,2	
JUL	NO TRAP				NO TRAP			
AUG	956	(20)	47,8		419	(10)	41,9	
SEP	1188	(26)	45,7		275	(6)	45,8	
OCT	1827	(38)	48,1		756	(18)	42,0	
NOV	2081	(46)	45,2		1210	(37)	32,7	
DEC	1080	(27)	40,0		1505	(40)	37,6	
JAN 1977	1272	(32)	39,8		1609	(42)	38,3	
FEB	1825	(47)	38,8		1995	(56)	35,6	
MAR	3731	(101)	36,9		2365	(72)	32,8	
APR	3276	(101)	32,4		2308	(71)	32,5	
MAY	2804	(74)	37,9		1915	(52)	36,8	
TOTAL	28509	(726)	39,3	(13,72)	17595	(494)	35,6	(13,34)

$t = 7,277$ DF = 1218 $P < 0,001$

MEAN BODY MASS CONTROL VS GRID E

before food was supplied), the mean body mass of all the mice caught on grid K stations 1 to 12 H, J and L during the preceding year, February 1975 through February 1976, was calculated (i.e. on the same area that was to become grid E in March 1976).

The mean body mass of 684 mice (including recaptures) was 39,4g (SE = 0,469). There was thus no difference in the mean body mass of mice on grid E during the year when supplementary food was supplied (mean 39,3g) and the preceding year (39,4g). However, there was a highly significant fall in the mean body mass of mice on the control grid in the same periods. Mean body mass of 1353 mice (including recaptures) on the control grid from February 1975 through February 1976 was 37,9g (SE = 0,387). This fell to 35,6g from April 1976 - May 1977 (Table 42), $t = 3,13$ $DF = 1845$ $p < ,01$. Thus there are grounds for supposing that the maintenance of the body mass on grid E at the high level of 1975 could have been due to the supply of extra food.

XII.6.4 Survivorship after first capture

Table 43 shows the mean expectation of further life in months after first capture on grid E and the control grid. This was calculated in the same way as in Table 27. If food had been limiting then the additional food might have extended the mean expectation of life by reducing the competition for available food resources. This might also have had the

TABLE 43

Survivorship (residency) after first capture on grid E (with supplementary food) and the control grid from April 1976 - March 1977.

Ex = mean expectation of life after first capture.

Number of mice in brackets.

	GRID E Ex (months)	CONTROL Ex (months)
MALES	1,33 (121)	1,53 (88)
FEMALES	1,52 (132)	1,79 (82)

Survivorship measured from the number of months individual mice were resident in each grid.

effect of reducing emigration, which would have increased the expectation of life, since emigration and mortality are equated. That this did not happen can be seen from Table 43, which shows that in fact mean expectation of life was longer on the control grid for both sexes by some 15 - 17%.

XII.6.5 Survival from birth

Table 44 shows estimated survival from birth in the breeding season on grid E and the control grid. This was calculated in the same manner as in Table 31 by counting the number of heavily pregnant females (> 54g) in month t and comparing this with the number of young juveniles (<20g) caught in month t + 1. The expectation was that if food were limiting for pregnant females then the addition of food might allow more young to be weaned per female. Table 44 shows that this was not the case since during the whole breeding season more young per female were weaned on the control grid (2,1) than on grid E (1,1). The survival of young from month to month appeared to be highly variable. The total number of juveniles of < 20g caught on the two grids was almost the same (60 on grid E, 58 on the control), but twice as many heavy (late pregnancy) females were caught on grid E (56 on grid E, 28 on the control). This suggested that more breeding may have taken place on grid E. This was tested by comparing the total numbers of sexually mature females (> 30g) captured on each grid with the number heavily pregnant (> 54g). The results (Table 44) show that on

TABLE 44

INFANT SURVIVAL FROM BIRTH TO WEANING. COMPARISON OF MEAN NUMBER OF YOUNG WEANED IN MONTH t + 1 PER HEAVILY PREGNANT FEMALE* (> 54g IN MONTH t) ON THE CONTROL GRID AND GRID E (WITH SUPPLEMENTAL FOOD). WEANED YOUNG = JUVENILES OF < 20g AT FIRST CAPTURE.

	GRID E			CONTROL			GRID E		CONTROL	
MONTH t	NO. HEAVY PREGNANT FEMALES	MONTH t + 1 NO. JUV	MEAN NO. YOUNG PER FEMALE	NO. HEAVY PREGNANT FEMALES	MONTH t + 1 NO. JUV	MEAN NO. YOUNG PER FEMALE	TOTAL NO. FEMALES >30g	% HEAVY PREGNANT FEMALES	TOTAL FEMALES > 30g	% HEAVY PREGNANT FEMALES
AUG 1976	0	3	-	0	0	0	11		5	
SEP	4	3	0,75	0	4	-	12		3	
OCT	12	5	0,42	6	15	2,50	18		8	
NOV	10	2	0,20	5	5	0,83	18		7	
DEC	3	3	1,00	2	6	3,0	14		16	
JAN 1977	4	8	2,00	6	7	1,17	12		12	
FEB	5	10	2,00	4	15	3,75	19		20	
MAR	14	25	1,79	5	5	0,83	33		21	
APR	4	4	1,00	0	1	-	32		14	
TOTAL	56	60	1,07	28	58	2,07	169	33,1	106	26,4

PROPORTION OF PREGNANT FEMALES : GRID E VS CONTROL GRID CHISQUARE = 5,12 $P < 0,05 > 0,02$

*Some females were included which were identified as being pregnant in the field, even though below 55g body mass.

grid E the heavily pregnant females comprised 33,1% of all sexually mature females and on the control grid they comprised 26,4%. This difference was significant (X^2 = 5,1 $p < 0,05$) and, therefore, the proportion of pregnant females on grid E was significantly greater than on the control.

In addition, as we have seen, both survival from birth and survival after first capture appeared to be worse on grid E with supplementary food than on the control grid.

XII.7 Discussion

In this study, the results of supplying artifical food on an experimental grid were ambiguous. The extra food did not prevent the usual winter population decline but on the other hand density did not sink as low as on the control grid. Breeding appeared to start about 1 - 2 months earlier and the mean body mass of mice was significantly heavier on the experimental area. This could have been due to the influence of additional food. There was also a significantly higher proportion of breeding females on the foodgrid. Conversely, survival was lower on the experimental grid. These anomalies were, perhaps, to be expected in view of the fact that natural food supply was not definitely identified as being limiting in the year under study.

Other workers who have supplied natural populations with

supplementary food, also seem to have had ambiguous results. Krebs & Delong (1965) found that a sparse population of M.californicus fed crimped oats showed an initial population increase lasting about 5 months, followed by a decline back to the low density from which it started. Growth rates in the experimental population were good, yet mean body weights were lower than on the control grid. Early juvenile survival appeared to be better in the experimental grid - hence lack of recruitment was not the reason for the failure of the population to increase. The reasons for the decline of the experimental population were unknown. Batzli & Pitelka (1971) pointed out that neither the adequacy of the natural diet and of supplements in relation to nutrient requirements of Microtus nor the effects of feeding stations on social structure were known.

Smyth (1966) has implicated food supply in the winter breeding of wood mice and bank voles. He found that the most important winter food for the mice was acorns and that only in years of an abundant acorn crop did the rodents breed in winter. This relationship, however, was not a simple one and it seemed that although an abundant acorn crop was a necessary condition for winter breeding, it was not a sufficient one. Some other factor also appeared to be involved and this was thought to be some quality of the population itself - possibly related to population density.

Watts (1970) measured the effect of supplementary food (wheat and oats) supplied during two winters, on the breeding of

bank voles and wood mice. He concluded that the addition of food advanced the start of the breeding season in bank voles by 2 - 3 weeks and in wood mice by 3 - 4 weeks. It did not seem to lengthen the season much. However, breeding was measured only by the number of females that were perforate, which may not have been the most reliable guide. Watts (1969) concluded that food was only one of several limiting factors for the wood mouse population and that the most important of these was the summer survival of early juveniles.

Flowerdew (1972) supplied extra food (wheat) to wood mice on the same study area used by Watts (1969, 1970) for two summers and one winter in 1968 - 69. Winter survival was not improved, which was thought to be because natural food in the form of hazel nuts was particularly abundant in the winter of 1968 - 69. However, survival of juveniles in both summers was improved, yet this did not produce a large increase in the number entering the population. The density on the experimental area was higher than that on the control only in the summer of 1968. Flowerdew (1972) concluded that there was a general upper limit to summer populations which was not imposed by food supply. However, this conclusion remains to be verified and food quality was not investigated.

Smith (1971) showed that supplemental food in the form of wild bird seed supplied over an area of 1,8ha raised the density and increased the amplitude of fluctuations in Peromyscus polionotus. However, it did not change the

pattern of the annual cycle in numbers - namely a winter increase period and a summer decline.

Hansen & Batzli (1979) supplied commercial mouse chow for one year on two 0,36ha grids for populations of Peromyscus leucopus. They livetrapped the grids for a year prior to setting out the food. They did not find any difference in density, survival, movement, reproductive intensity or weights, after feeding. Mice seemed to breed earlier in spring on the supplemental grid, and that was all. They concluded that food was not limiting density at that time. However, they observed an increase in density on all grids in the second year, which they ascribed to improved winter survival due to a greater mast crop that year.

More positive evidence for the influence of food has been found by Cole & Batzli (1978, 1979). They supplied extra food in the form of high quality commercial rabbit pellets to a population of prairie voles (M.ochrogaster) on an abandoned bluegrass pasture for a period of 18 months. Performance of prairie voles on bluegrass was known to be generally poor. They, therefore, expected to be able to significantly improve the performance of the supplementally fed population. For most of the study the density of the supplemental population was above that of the control (peak density was 50% higher). Perhaps their most significant results were that the supplemental population did not experience the winter 1975 - 76 decline of the control, but it did show violent fluctuations in density. Both populations

increased in summer 1976 and then declined rapidly and synchronously between late August and late October 1976, to very low levels. In winter on the supplemental grid there were (a) significantly more pregnant females, and (b) a higher nestling survival index. Overall survival of juveniles from first capture was significantly higher for both sexes as was litter size. Growth rates on the supplemental grid were double those on the control during winter 1975 - 76, but mean body weights of males were not higher than those on the control at that time - though they became so during spring-summer 1976.

They concluded that supplemental feeding can improve the performance of a population in poor habitat. They thought that the severe fluctuations on the supplemental grid in winter were due to heavy predation but that the decline in 1976 must have been due to some other factor. Thus, in this case the quality of the available food supply was believed to influence amplitude of population fluctuations but could not prevent what they refer to as "the periodic declines".

Additional evidence of the potential importance of the quality of the food supply has been found by Cole & Batzli (1979). They compared the demography of three populations of prairie voles living on adjacent, but distinctly different, habitats (namely prairie, bluegrass and alfalfa). Population density was by far the highest on the alfalfa habitat and lowest on the prairie. Voles had greater reproduction

and survival and higher body weights in the alfalfa than in the other habitats. Analysis of nutrients in three common food items (alfalfa, clover and bluegrass) revealed that the legumes contained more digestible energy than bluegrass and also higher levels of crude protein, calcium, phosphorus and sodium. Voles grew more rapidly, bred earlier and produced more young when fed alfalfa than when fed dandelions and bluegrass.

This evidence strongly implicates nutritional quality in influencing population density, but nevertheless they still found severe population declines on all habitats, including alfalfa, in early 1973. All populations remained low throughout 1974 and did not start to increase until the second half of 1975.

In summary, the above brief survey of the research of various workers shows conflicting results. It is not clear that food was limiting in all cases. However, voles in marginal habitats (e.g. bluegrass) have reacted unambiguously to higher food quality and in these cases food supply is strongly implicated in the control of population density. Perhaps the most important change in recent thinking is that not only the quantity of food is involved, but above all its quality. It is the right kind of food, at the right time, which may be of paramount importance.

There are various ways in which this food-control mechanism might operate. Haukioja & Hakala (1975) have suggested

that fluctuations in numbers of herbivores result from the adaptation and selection of both the host plant and the herbivores using it, during the course of one cycle in numbers. This is based on the fact that plants can produce chemicals which are toxic to herbivores and can control the concentration of these compounds. They may, therefore, react to excessive grazing pressure of herbivores by increasing production of some toxic compounds. These may, in turn, reduce the fecundity of the herbivores, producing a cycle in numbers.

Freeland (1974) suggested a hypothesis to explain cyclic fluctuations in voles which involved the amount of toxic plants in the diet. He suggested that during high vole densities, the proportion of preferred foods would be reduced and that the voles would be forced to eat increased amounts of toxic foods. This would cause a reduction in vole density and at low grazing the preferred foods outcompete the toxic ones and can return to their former abundance. As recognised by Batzli & Pitelka (1975) a rigorous test of this hypothesis is difficult since it is not known what is toxic to voles. Their analysis of data collected by Batzli & Pitelka (1970, 1971) did not support Freeland's hypothesis. They found that at high vole densities the voles did not increase their intake of specific plants, which Freeland (1974) had suggested were toxic.

More recently White (1978) has suggested a general hypothesis, applicable to all mammals, in which limits to population

growth are imposed by a relative shortage of food. This shortage lies not in the quantity of food but in its quality. Specifically, he suggests that it may be the quantity of available nitrogen which is critical and this may be limiting for the very young animals, i.e. if protein supply is inadequate for them to maintain their high body growth rates, this may lead to high mortality rates among the very young. White says that changes in the nitrogen content of the food, induced by changes in the weather, may well hold the key to an explanation of microtine cycles. Whether this is so remains to be proved. The findings that the provision of a supplemental food supply in some instances did not prevent population declines does not necessarily invalidate the hypothesis. This is because (a) predation could have played a role in some declines, and (b) the precise food requirements of the rodents had not been identified. However, in order to test the hypothesis more rigorously it seems that it would be necessary to monitor very carefully both the quantity and quality of the most important food plants (including preferred parts of the plants) throughout a complete cycle of abundance.

Cole & Batzli (1979) did not apparently find a significant reduction in the percentage of crude protein in the most important food plants (alfalfa, clover and bluegrass) of prairie voles between 1972, when vole densities were high, and 1973 when vole densities were low. However, they had figures for only four months of the year (May, July, September and November) and for no winter months. It is possible

that there was a difference in quantity or quality of the most nutritious parts of the plants between the two years. It would also have been interesting to have had measurements of quantity and quality of vegetation samples during the period January 1974 - April 1975, when the vole populations on all three study areas were very low.

XII.8 Effects of winter flooding

Heavy winter rain, combined with the low-lying nature of the Cape Flats, contributed to rather severe winter flooding in the study area from 1974 onwards (Fig. 2). This culminated in most severe flooding in 1977, when the project was abandoned. During the relatively dry years of 1972 and 1973 very little flooding was experienced and it appeared in 1977 that a definite ecological change had occurred in so far as areas which normally dried out in the summer were remaining wet throughout the year. This was apparently due to an overall rise in the level of the Kuils River.

It is presumed that flooding would have had an adverse effect on the mouse population, but the precise effect is unknown and no attempt has been made to quantify it in this study. Mice, undoubtedly, moved to drier ground as the waters rose and the trapping records showed that many mice which had been marked before periods of flooding were caught again afterwards. How many of those that disappeared were drowned is not known. However, it is not thought that flooding was

responsible for the winter decline each year, since a population decline was also experienced in 1972 and 1973 when flooding was minimal. Furthermore, during winter 1975 when flooding was severe, Rhabdomys numbers remained exceptionally high and the usual winter decline was much less than normal (see Fig. 3).

XII.9 Summary of diet, food availability and results of supplementary feeding

Food habits were investigated by stomach contents analysis. For most months of the year, but particularly from December to May, seeds of the alien acacia trees (A.saligna and A.cyclops) were the most important dietary items, with a range from 27 - 81% of stomach contents. Usually, seeds comprised around 50% of the stomach contents. Green vegetation was usually the second most important item and in some winter months it was the most important item, when it could comprise 50 - 69% of the diet.

Although the acacias had a restricted season of seed production from December to April, there appeared to be abundant seeds accumulated in the leaf litter under the trees, which were available to the mice throughout the year. Measurements of the amount of seed in the leaf litter showed a considerable drop in quantity during the winter, which was presumably due to consumption by mice and birds. It was calculated that in some months they could have eaten from 19 - 40%

of the available seed. In order to establish whether an actual food shortage could occur, in addition to monitoring the seed supply, it would be necessary to monitor the quantity and quality of the species of green plants eaten by the mice. Although measurements of Acacia seed production apparently showed an abundance of food, yet these measurements were made over only 15 months. It is felt that, as seeds made up such a large proportion of R.pumilio diet, if the seed crop were to fail in a particular year then a food shortage could develop, particularly in the dry summer months. In these circumstances, food might become a limiting factor.

Fifty kg of additional high quality food, in the form of commercial rat pellets, was supplied on an experimental grid for a period of 15 months in order to test the response of the R.pumilio population. The results were ambiguous, but there was evidence of a response by the population. The normal winter decline on the experimental area was not prevented, but numbers remained well above those on the control grid. The population size at the end of the breeding season was about 50% higher than that on the control grid. The number of new mice caught on the food grid was about 42% higher than on the control, which may suggest preferential immigration. Breeding appeared to start 1 - 2 months earlier on the food grid - one juvenile was caught in August; and there was a significantly higher proportion of pregnant females. The total biomass of mice carried on the experimental grid as well as the mean body mass was significantly higher than on the control.

Conversely, both survivorship after first capture and survival from birth seemed to be worse on the food grid. The explanation of these results must await further experimentation. The population on the experimental grid did, apparently, respond to the additional food but, on the other hand, there was lack of evidence that its numbers were controlled by the food supply. In particular, the winter decline could have been due to predation, as will be discussed in the next chapter. More careful monitoring of quantity and quality of all the major items of the food supply would be necessary before attempting to answer the question as to whether food supply controls the population size.

XIII. THE INFLUENCE OF PREDATION ON POPULATION DENSITY

XIII.1 Introduction

Apart from food shortage, the other ecological factor likely to cause in situ deaths, which was investigated, is predation. Throughout most of the five years of fieldwork on which this study was based, large mammal livetraps were set at the same time as the small mammal trapping was conducted. Three species of small carnivore (family Viverridae) occurred in the area and trapping showed that the Cape grey mongoose (body mass up to 1kg) was the only common diurnal mammal predator present on the study area. There were two nocturnal mammal carnivores present - the water mongoose (2,0 - 3,9kg) and the common genet. Since R.pumilio was the only abundant diurnal, small rodent it seemed possible that predation by mongooses could exert some influence on the rodent population. The black-shouldered kite was the only resident avian predator but this small raptor normally hunts only over open veld and was never seen actually hunting over the study area which had dense thickets of Acacia. In summer migrant steppe buzzards were present in the general area but the normal hunting technique of this species is to watch from an exposed perch, such as a telegraph pole or a fence post, and again was not seen hunting over the study area. There were some feral cats in the area which could presumably also have preyed on the fieldmice. Their influence was unknown, but it was believed to have been small since, during a year

(1976 - 77) of intensive livetrapping of carnivores, only three cats were caught, compared with 15 individual mongooses.

XIII.2 Number of Mongooses captured in the study area

The capture, mark and release of carnivores on the control grid was undertaken as an integral part of the study and baited Tomahawk livetraps were first set in May 1972. Usually about five livetraps were set each month, in different parts of the control grid, simultaneously with the rodent traps. Mongooses were marked by either ear-notching or ear-tagging with fingerling fish tags. Unfortunately, a high percentage of mongooses lost their eartags (at least 10 out of 28 tagged). In an attempt to gain insight into the population density and movements of the grey mongooses, an intensive livetrapping programme was commenced on 1st August 1976 and continued up to the end of December 1976. It was hoped to mark all mongooses present on the control grid and grid E. Nine days of trapping were also conducted in March and April 1977 and four days in November 1977. All mongooses captured during this period were marked with numbered nylon collars plus an eartag.

Between May 1972 and November 1977, 36 different grey mongooses (17 males, 19 females) were caught, of which 35 were released, on the study area. Eighteen of these (10 males, 8 females) were recaptured at least once. During the period

of intensive trapping from August 1976, 14 different mongooses were caught on the control grid and grid E.

Table 45 shows the number of different mongooses caught during each year of the study. This remained fairly constant between 1973 and 1975 at from five to seven. Twelve were caught in 1972 and 17 in 1976. The latter high figure may have partly been a reflection of greater trapping intensity in 1976 but it could also indicate more breeding by the mongooses in response to the abundant fieldmouse year of 1975. In both 1972 and 1976, the two years of highest mongoose numbers, four juveniles were captured (270 - 615g) compared with none in 1974 and one in 1973, 1975 and 1977.

Table 46 shows the number of individual mongooses livetrapped each month, which varied between none and twelve. The high figures of six mongooses in May 1972 and of 12 in August 1976 was due to the commencement of carnivore livetrapping in the control grid and in grid E respectively. The mean number of mongooses caught per month lay between 0,6 and 2,3 (Table 46). However, due to the trap-shyness of marked mongooses (see below) it seems probable that there were in fact more mongooses active on the grids than the trap records show.

During 22 hours of observation of the sand road bordering grid E (Fig. 2), spread over three days in December 1976, mongooses were only seen singly and from four to six were seen per day (although it was not possible to verify that

TABLE 45

NUMBER OF CAPE GREY MONGOOSES LIVETRAPPED, MARKED AND RELEASED PER YEAR IN THE CONTROL GRID DURING 1972 - 1975 AND INCLUDING GRID E IN 1976 - 1977.

NUMBER OF NEW MONGOOSES IN BRACKETS

NUMBER OF CAPE GREY MONGOOSES

	1972	1973	1974	1975	1976	1977
Males	7 (7)	3 (1)	4 (1)	3 (2)	6 (5)	4 (1)
Females	5 (5)	2 (0)	2 (1)	4 (2)	11 (11)	1 (0)
TOTAL	12 (12)	5 (1)	6 (2)	7 (4)	17 (16)	5 (1)
No. Juveniles	4	1	0	1	4	1

Juveniles weighed 270 - 615 g

TABLE 46

Number of individual mongooses livetrapped each month (including recaptures) in the control grid. Grid E included from August 1976.

Month	NUMBER OF CAPE GREY MONGOOSES					
	1972	1973	1974	1975	1976	1977
Jan	-	1	2	0	1	0
Feb	-	1	2	1	2	0
Mar	-	2	2	0	1	4
Apr	-	3	0	0	0	0
May	6	1	1	1	2	0
June	0	1	0	0	0	-
July	0	0	2	2	0	-
Aug	3	1	0	0	12*	-
Sept	5	2	1	0	0	-
Oct	1	0	0	2	5	-
Nov	0	1	0	1	1	1
Dec	3	1	0	0	2	0
MEAN	2,3	1,2	0,8	0,6	2,2	0,7

\- = No trapping

* = Trapping commenced in grid E

those seen on one day were all different).

XIII.3 Longevity

The lifespan of the grey mongoose in the wild is unknown, but our longest trapping records are as follows:
44 months (male, 310g juvenile at first capture);
38 months (male, 450g subadult at first capture);
31 months (female, 270g juvenile at first capture) and
26 months (male, 1000g adult at first capture).

XIII.4 Home range

It was hoped that the recapture history of each animal would reveal the extent of its home range, to enable an estimate to be made of the number of predators hunting on the study area at one time. In the event, it soon became obvious that though unmarked mongooses were relatively easy to catch, they quickly learned to avoid the traps with the consequence that recaptures were hard to obtain. Traps were frequently found disturbed and with the soft sand dug away underneath, as the mongoose attempted to get the bait without going into the trap. No satisfactory picture was obtained of mongoose movements and data were, unfortunately, too scanty for any definite home range estimates to be made. Recapture locations showed movements of from 80m to 240m in periods of 9 - 28 days and the longest movements recorded between cap-

tures were 400m for an adult male (6 months between captures) and 240m for an adult female (9 days between captures). From these data and from data presented below for home ranges of the European weasel (Mustela nivalis), it is assumed that mongoose home ranges were not less than 1,5ha in area, and could have been much larger.

It is not known to what degree home ranges overlapped, but the fact that several different individuals were caught within a few days in the same area in some months, suggested that they did. It is possible that animals avoided meeting by using common parts of the home range at different times. They were not thought to maintain territories, in the sense of exclusive areas.

For comparison, Lockie (1966) found that male weasels had territories of from 1 - 5ha in Scotland, with limited overlap between adjacent territories and a maximum range length of about 400m. King (1975) found home ranges of weasels in a wood near Oxford to vary between 7 - 15ha for males and 1 - 4ha for females, with a maximum recorded range length of 550m for a male. There was some range-sharing by mutual avoidance.

XIII.5 Food intake of captive mongoose

An adult male mongoose (840g at first capture) was live-trapped near the study area and kept in a large (10m x 5m) outdoor cage for 35 days. It was fed known quantities of mice and commercial dogfood and its weight was recorded regularly in order to determine the daily food intake necessary to maintain its weight. Its scats were collected and recorded daily. It dropped a mean of 2 - 3 scats per day.

At the end of 14 days of feeding, a daily mean of 38g/day of either freshly killed mice or commercial dogfood, its weight was 850g. For the remainder of the experiment the food ration was increased. For the next seven days it was fed an average of 68g/day, at the end of which time it weighed 870g. Seven days later it weighed 900g, being fed 74g/day and, for the final six days, it was fed 77g/day. At the end of the experiment it weight 950g. (The mean maximum weight of 14 wild livetrapped males was 940g).

XIII.6 Analysis of mongoose scats

The identification of mongoose prey was made from analysis of scats collected every two weeks from the sand road bordering the north side of grid E (Fig. 2) between July 1976 and August 1977. No attempt was made to recover all the scats from the study area as the thick vegetation would have made this impossible. From the locations where scats were act-

tually found, it appeared that mongooses in fact usually dropped their scats on open areas of bare sand.

The main constituent of most scats was rodent fur mixed with many very small bone fragments and sometimes teeth. An identification of the fur down to species was made from microscopic examination of a gelatine imprint of individual hairs on a microscope slide (Keogh 1975). In other studies such as those of Brant (1962) and Pearson (1964, 1966, 1971) the number of prey eaten by the predators was assessed from the number of pairs of rodent incisors found in the scats. In the present study this was not possible since relatively few teeth were found in the scats. Of 316 scats examined only 49 (15,5%) contained one or more incisors. Only 39 scats contained molar teeth (including those that also contained incisors). From the presence of white powdery substance present in many scats as well as hard, white objects which appeared to be the remains of semi-digested teeth, it appeared that the mongooses could, in fact, digest the teeth of their prey.

The scat analysis is presented in Table 47. It is basically a frequency analysis, which is to say that items in the scats were scored as present or absent. Although quantification of items is difficult and subjective, it was felt that some attempt at this was necessary. Accordingly, four categories of occurrence of an item in a scat were recorded. These were 'solely', 'mainly', 'some' and 'trace'. The only category considered to be exclusive was 'solely',

TABLE 47

The diet of the Cape grey mongoose on the Cape Flats from analysis of 316 scats between July 1976 and July 1977.

* Figures in parentheses indicate the number of scats in which the item was the sole or main constituent.

\+ Potamon perlatus.

* NO. OF MONGOOSE SCATS CONTAINING :

Month	No. Scats examined	RODENT HAIR R.pumilio	Otomys	Other Rodent	Total Rodent	Bone	Crab+	Insect	Feathers	Reptile	Sand
JULY 1976	3	1 (1)	2 (2)		3 (3)	2 (0)		trace		1 (0)	
AUG	27	16 (13)	5 (3)	8 (3)	21 (19)	15 (0)	13 (4)	9 (2)	3 (0)	4 (0)	11 (5)
SEPT	22	13 (11)	2 (2)	10 (1)	16 (14)	15 (0)	12 (4)	5 (0)	5 (1)	1 (0)	7 (5)
OCT	58	19 (11)	2 (0)	6 (2)	24 (13)	26 (0)	32 (14)	30 (1)	9 (3)	15 (2)	38 (23)
NOV	24	9 (6)	2 (2)	5 (4)	16 (12)	11 (0)	12 (3)	12 (1)	5 (2)	6 (2)	12 (3)
DEC	27	14 (11)	2 (2)	1 (1)	17 (14)	10 (0)	20 (10)	7 (0)	3 (2)	6 (1)	9 (5)
JAN 1977	28	14 (13)	2 (0)	3 (3)	19 (16)	12 (2)	17 (9)	6 (0)	5 (4)	6 (0)	3 (2)
FEB	21	12 (11)	0	2 (1)	14 (12)	8 (0)	8 (2)	13 (3)	5 (1)	4 (0)	5 (1)
MAR	24	10 (10)	5 (5)	7 (6)	21 (20)	16 (0)	8 (1)	7 (1)	2 (0)	3 (0)	2 (1)
APR	19	8 (7)	2 (2)	8 (5)	17 (14)	6 (0)	11 (2)	3 (0)	3 (0)	2 (0)	5 (5)
MAY	21	13 (13)	7 (7)	0	20 (20)	11 (0)	6 (1)	5 (1)	1 (0)	0	0
JUNE	21	16 (16)	4 (2)	1 (0)	19 (18)	18 (0)	5 (0)	2 (0)	1 (0)	3 (0)	3 (3)
JULY	21	13 (11)	0	9 (7)	20 (18)	19 (0)	1 (0)	1 (0)	1 (0)	5 (0)	2 (2)
TOTAL	316	158 (134)	35 (27)	60 (33)	227 (193)	169 (2)	145 (50)	100 (9)	43 (13)	56 (5)	97 (55)
%		50 (42)	11(8,5)	19 (10)	72 (61)	53 (1)	46 (16)	31,5 (3)	13,5 (4)	18 (1,6)	31 (17)

i.e. only one item per scat could be scored as 'solely', whereas two items could be scored as 'mainly', if the scat comprised about 50% of each; two or more items could be scored as 'some'.

It should be noted that the situation differed from that found by Day (1968) and Moors (1975) for the weasel in Great Britain. They found that usually only one type of prey was identified in each weasel scat. This made a frequency analysis particularly suitable and accurate. The frequent finding of more than one prey type in mongoose scats would inevitably tend to make quantification more difficult and percentages of occurrence less reliable.

It can be seen from Table 47 that the most important single item in the 316 scats analysed was rodent hair, which was present in 72% of the scats and constituted the main item in 61%. By far the most abundant species was R.pumilio which occurred in 50% of the scats and was the main item in 42%. Otomys irroratus was the next most abundant rodent, being present in 11% and the main item in 8,5% of the scats. This species is crepuscular, whereas the other species which occurred in small numbers (Tatera afra, Rattus norvegicus, Mus minutoides and Myosorex varius) were all nocturnal. The only other prey item which seemed to be important was the freshwater crab, Potamon perlatus, which occurred in 46% of the scats but was a major component in only 16%. Other items such as insect, bird and reptile (chiefly the lizard,

Mabuya capensis) although present in quite a high proportion of scats, were the main constituent in only 3%, 4% and 1,6% of scats respectively. It was noticeable that sand and unidentifiable debris was present in 31% of scats and constituted the main item in 17%. Shrews are said to be distasteful to several species of carnivores (Southern, 1964, cited by Moors, 1975). Erlinge (1975) stated that weasels in Sweden showed little interest in hunting them. Table 47 shows that shrews were eaten infrequently by mongooses but were found in 1,9% of the scats.

With regard to possible seasonal changes, it can be seen that rodents were important prey items throughout the year, but there appeared to be a drop in the degree to which they constituted the main item in early summer (October - December) which may have been correlated with low rodent population density at this season (early breeding season), although the figure for September, when rodent densities are also low, was still fairly high (rodents were main item in 64% of scats). The very high proportion of sand in the scats in October 1976 suggests that food may have been scarce that month. The drop in importance of rodents at that time was correlated to some degree with an increase in the importance of crab in the diet. Crab importance rose to a maximum in December when it was the main item in 37% of scats. From February through July the proportion of crab in the diet fell away markedly, whereas rodent importance rose to its maximum in these months. This corresponded with peak rodent densities at the end of summer.

Erlinge (1975) found that rodents were the main food of the weasel in Sweden with a frequency of occurrence of about 80% in the scats. He observed a seasonal change in feeding habits. In autumn and winter the food consisted almost entirely (94%) of rodents, while in spring and summer when rodents were scarce, their frequency in the diet dropped to about 59%.

XIII.7 Consumption of mice by mongooses

From the experiment with the captive male it appeared that it could maintain its weight on about 40g per day and could sustain fairly rapid growth on 68g - 77g per day. Although the cage was fairly large ($50m^2$), the mongoose would undoubtedly have been more active in the wild. On the basis of Brodie's (1945) estimate that small mammals require about twice the energy in the wild that they need in captivity, and of Moen's (1973 : 360) estimate that the energy cost of activity in a 30kg pronghorn antelope was 1,4 times BMR, one might guess that wild mongooses require about 60 - 80g per day, wet weight. This estimate makes no allowance for breeding females, which would require more. We can calculate the theoretical heat production of a mammal from the equation of Moen (1973 : 116) namely that Basal Metabolic Rate (BMR) = $70\ W_{kg}^{0,75}$ kcal per day, where W = body mass in kg. In the case of a mongoose weighing 1kg, this comes to 70kcal per day. We can now calculate what weight of mouse tissue would be necessary to supply this quantity of

energy. Two male R.pumilio (43,8g 30,3g live mass) were sacrificed, dried in an oven (total dry mass 20,77g) and then minced. Samples of the dry flesh were fired in a bomb calorimeter. The mean of eight samples gave a value of 5,599kcal/g. Hence, to supply its 70kcal energy requirements, the 1kg mongoose would require 12,5g of dry mouse tissue per day. Since the dry weight of the two specimens was 28,0% of the live mass, the 12,5g of dry tissue is equivalent to 44,6g live mass. This figure compares well with the observed daily food consumption necessary to maintain body mass in the captive 840g male.

According to the calculations of Moen (1973 : 362) for deer, the energy cost of activity is 1,42 times BMR and of lactation is 1,86 - 2,30 times BMR, depending on whether the doe has one or two fawns. If one applies these factors to the basic daily mongoose consumption of 44,6g/day, then the actual consumption in the wild could be from 62 - 103g of mouse per day - the higher figure being the consumption by lactating female mongooses.

The mean body mass of all R.pumilio caught each year in the control grid is shown in Table 48. This varied between about 35 - 40g. Since 50% of the scats examined contained remains of R.pumilio, it appeared that the fieldmouse comprised about half the diet of the mongooses. Since its daily requirement of 60 - 100g would be 1½ - 2,9 mice on average, it follows that mongooses probably catch an average of 1 - 2 mice per day each, with the balance of their food

TABLE 48

MEAN BODY MASS (g) OF R.PUMILIO CAUGHT IN THE CONTROL GRID EACH YEAR. BOTH SEXES AND ALL AGE GROUPS COMBINED;

	1972	1973	1974	1975	1976	1977
Mean Body Mass (g)	40,5	35,6	38,2	38,4	35,5	34,8
Sample Size (No. of mice)	209	432	302	1239	487	293

intake made up of other prey items. This reduces to about 23 - 44 mice per month, per mongoose.

XIII.8 Prey density related to minimum carnivore requirements

It is now necessary to examine the question of what prey density is adequate to support one small carnivore. During a study of weasels in a wood near Oxford, King (1975) recorded a minimum and maximum prey density of 21 - 39 rodents/ha of mean body mass 21g. She found that despite the low prey density the weasels maintained stable home ranges - probably due to the rather stable nature of prey availability. Erlinge (1974) found that the distribution of weasels in Sweden was highly correlated with prey availability and that males established territories only where there was adequate food. Parts of his study area with low rodent density were not occupied by weasels at all.

In this study the range of fieldmouse density was from 10 - 238 R.pumilio per ha, with a mean body mass of 35 - 40g. These severe fluctuations in prey density might have been expected to lead to fluctuations in the numbers of mongooses. However, the data on mongoose numbers are not really adequate to answer this question.

On the basis of data from East and Lockie (1964), Erlinge (1974) calculated that a female weasel having a home range

of 1,5ha would require a reproducing prey density of field voles (M.agrestis) of at least 10 individuals per ha in order to reproduce, in areas providing little alternative food. Citing Iversen (1972) he says that the basal metabolism of weasels is 2 - 3 times higher than that expected from the standard curve for mammals. This, presumably, explains the relatively high daily intake of food of a captive female weasel (mass 76g) whose consumption rose to about 60g of food per day while feeding young, compared with her normal 20 - 30g per day (East & Lockie, 1964).

Grey mongooses are about ten times heavier than weasels: adult male mongooses weighed from 850 - 1075g and females 670 - 940g, whereas mean body mass of male weasels was 109g and of females 65g (King, 1975). Assuming that their basal metabolic rate is not abnormally high for their size, we can accept the above consumption figure for mongooses of 60 - 100g/day.

Differences in prey density and type of habitat may profoundly affect home range size, making it hazardous to directly compare range sizes of weasels and mongooses. Nevertheless, extrapolating from the data for weasels (Erlinge, 1974) and taking into account that the mean weight of R.pumilio was at least 35g compared with about 25g for M.agrestis, then it would seem that the minimum prey density required to support one adult mongoose, eating 60 - 100g per day and having a home range of 1,5ha, would be about 10 - 20 reproducing

rodents per ha. The situation would be altered if the mongoose home ranges were significantly greater than 1,5ha. This seems quite likely but is not known for sure. The fact that an upper prey density of 238 mice per ha was observed suggests that large numbers of mongooses could be supported at times of peak rodent numbers. However, it should be borne in mind that these rodent peaks are normally of short duration and that there is a considerable lag between carnivore breeding and the time of peak prey density. Furthermore, it is axiomatic of the concept of carrying capacity that this relates to the number of organisms which can be supported at the leanest season in terms of food availability. Hence, since rodent numbers may fluctuate widely it would seem more important to establish the minimum number of carnivores which can be supported by the prey population.

In summary, on the basis of data for the weasel, it seems that an adult mongoose with a home range of 1,5ha could survive on a prey density of about 10 - 20 rodents per ha, if it had no alternative prey. Taking into account the following facts: that the combined area of the control plus grid E (including the 20m strip between them) was 1,1ha, that the lowest Rhabdomys density recorded in five years' fieldwork was 10 mice per ha and that about 50% of mongoose prey, on average, was fieldmice, then it seems likely that one mongoose could be supported indefinitely on the area of the control grid plus grid E. In summer, taking an average density of 100 mice per ha, then as many as 10 mongooses might be supported.

XIII.9 Discussion

The most important unanswered question concerns the impact that mongoose predation may have on the Rhabdomys population. Table 49 shows the total number of marked mice which disappeared from the control grid each year (being the sum of marked mice released but not recaptured each month). It can be seen that the mean number of mice which disappeared per month lay between a minimum of 10 per month in 1974 and a maximum of 34 per month in 1975. An additional 27 mice per month were calculated to have disappeared from grid E in 1976 - 77. Since this is almost identical to the 26 per month which disappeared from the control grid in 1976 and the area of the two grids was the same, the number of mice which disappeared from the combined area of 1,1ha covered by the control grid plus grid E has been calculated by doubling the number which disappeared from the control grid alone. The mean number which, therefore, disappeared from an area of 1,1ha was between 24 - 68 mice per month.

It has been calculated (above) that one mongoose probably ate between 23 - 44 mice per month. It can, therefore, be seen that one mongoose active in the area could account for all the missing mice from 1972 - 74, and two mongooses could have taken all the missing mice from 1975 - 77. The data are clearly somewhat crude and inexact and a reliable interpretation will be impossible until more is known of the home range and hunting habits of the mongooses. One would need to know the degree of overlap between adjacent home ranges

TABLE 49

Numbers of marked R.pumilio which disappeared (i.e. were not recaptured) each year from control and food grid E. These mice could have fallen prey to mongooses. Combined area of control grid plus grid E = 1,1 ha (including 20m strip between the grids).

	CONTROL GRID											
	1972			1973			1974			1975		
	R	D	%D	R	D	%D	R	D	%D	R	D	%D
JAN				50	17	34,0	25	13	52,0	88	23	26,1
FEB				77	17	22,1	11	2	18,2	112	32	28,6
MAR				71	15	21,1	26	5	19,2	149	56	37,6
APR	44	30	68,2	71	45	63,4	39	16	41,0	122	40	32,8
MAY				36	15	41,7	26	10	38,5	130	52	40,0
JUNE				35	24	68,6	29	12	41,4	101	40	39,6
JULY	26	12	46,2	18	8	44,4	22	12	54,5	98	32	32,7
AUG	17	8	47,1	14	6	42,9	8	2	25,0	73	12	16,4
SEPT	24	3	12,5	12	3	25,0	16	4	25,0	77	23	29,9
OCT	22	5	22,7	14	9	64,3	23	10	43,5	75	18	24,0
NOV	31	8	25,8	16	7	43,8	36	12	33,3	103	35	34,0
DEC	38	14	36,8	14	8	57,1	43	17	39,5	89	49	55,1
TOTAL	202	80	39,6	428	174	40,7	304	115	37,8	1217	412	33,9
Mean No. disappeared per month		15*			18*			12*			34	
No. disappeared from combined area (1,1 ha)		30			36			24			68	

R = Number of R.pumilio released. D = Number disappeared (not recaptured).

* = Figures adjusted because control grid area was increased by 25% in February 1975.

continued/...

TABLE 49 continued ...

	CONTROL GRID									GRID E		
	1976			1977			TOTAL			Mar 1976 - Mar 1977		
	R	D	%D	R	D	%D	R	D	%D	R	D	%D
JAN	83	31	37,3	42	19	45,2						
FEB	114	57	50,0	56	20	35,7						
MAR	82	47	57,3	72	24	33,3						
APR	58	43	74,1									
MAY	-	-	-									
JUNE	32	27	84,4									
JULY	-	-	-									
AUG	9	8	88,9									
SEPT	6	0	0									
OCT	18	9	50,0									
NOV	36	15	41,7									
DEC	40	19	47,5									
TOTAL	478	256	53,6	170	63	37,1	2799	1100	39,3	666	352	52,9
Mean No. disappeared per month		26			21			21			27	
No. disappeared from combined area (1,1 ha)		52			42							

and the distribution of hunting time in different parts of the range. The difficulty experienced in retrapping the mongooses suggests that radio collars would be the only reliable way to obtain home range data. Nevertheless, indications are that mongoose predation could have been responsible for most, if not all, of the mice which disappeared from the livetrapping grids.

Having said this, it still leaves unanswered the vital question posed by Krebs & Myers (1974 : 338) in relation to voles and lemmings, as to whether mortality caused by predation is sufficient to regulate rodent populations. Pearson (1964, 1966, 1971) attempted to quantify the predation of feral cats, raccoons, foxes and skunks on a M.californicus population by collecting predator scats from a 14ha study area. The number of voles eaten was assessed from the number of pairs of incisors found in the scats. Pearson found that the predators ate a high proportion of the voles during a population decline. In three successive declines of the vole in 1961, 1963 and 1965, Pearson calculated that the carnivores ate 88%, 25% and 33% respectively of the standing crop of voles. His theory is that though predators cannot prevent the increase of a breeding vole population they can be responsible for the amplitude of a cycle by depressing prey populations to very low levels. He believes that mammal carnivores continue to hunt preferred rodent prey even at very low rodent densities, thus further reducing already low populations, as long as there are

secondary prey species available to support the carnivores through the lean times. Pearson also thinks that the carnivores can influence the periodicity of the cycle by exerting continued predation pressure and thus keeping the prey population in the phase of low numbers for an extended period.

Fitzgerald (1977) studied the predation by ermine (Mustela erminea) and long-tailed weasels (M.frenata) on the winter nests of montane voles (M.montanus) under the snow in California. He found that in four successive winters, ermine are 21%, 54%, 6% and 28% of the winter population of voles. Predation was heaviest during winter 1966 - 67 when vole density was the lowest of the four years. However, predation pressure did not seem to correlate with vole density in the other years, being second highest in the year of highest vole density (1968 - 69; Fitzgerald, 1977, Fig. 7). He claims that his results support Pearson's hypothesis. However, he has not shown that it was predation that determined the minimum density of voles each year and, looking at his Fig. 7, this seems very doubtful. For example, it is not clear how predation could have been responsible for the crash in the vole population from the highest level of the study in July 1968 to the lowest density in May 1969.

Tapper (1979) suggested that a population of weasels was interacting with one of field voles (M.agrestis) on farmland in England, rather than the predators alone responding to changes in prey density. This conclusion, however, could

not be verified since he was unable to measure the direct impact of the weasel population on the voles.

In the present study, although it seemed possible for mongooses to have eaten most (or even all) of the missing fieldmice, yet this need not imply that the predators were exerting any control over the rodent population. For such control to be exerted, one would have to show that very high proportions of prey were being taken at certain times (particularly during a period of low or declining numbers according to Pearson's hypothesis) and that the proportion of prey taken varied considerably from season to season, in accord with fluctuations in mouse numbers.

The proportion of mice released which were not recaptured each month is shown in Table 49. It can be seen that the proportion of missing mice was remarkably constant for the first three years at 38 - 41%. This decreased to 34% in 1975, (the year of peak numbers), and increased to 54% in 1976 when the population showed the most spectacular decline of the study. One might have expected the proportion of missing mice to have increased in 1974, the year of lowest overall Rhabdomys density, if it were due to predation, but it remained low at 38%. Since mouse numbers fell to a minimum between August and October each year (from Table 8 it can be seen that minimum densities varied from 10 - 29 mice per ha, with the exception of 1975), it would seem that if predators had taken a high proportion of mice in those months, then they could have held the rodent population down

at low density for an extended period. However, this did not happen since the mean numbers of mice missing in those months was not higher than in other months. In every year the mouse population was starting its summer increase by October or November - and the rate of this increase did not seem to be diminished by a low minimum population, e.g. in 1976 - 77, when the lowest density population in September 1976 gave rise to the fastest growth of the whole study. This coincided with the time when there appeared to be the highest number of mongooses recorded (Table 46). There is thus no evidence that predation ever held the fieldmice at low density during this study.

If it is accepted that the mice missing each month represented mortality due to predation, then it would seem that the winter decline observed each year could have been due to predation. Thus, predation may have determined the minimum density each year. The mongooses, however, were never able to reduce the Rhabdomys density below about 10 mice per ha (Table 8) in 1976 and in the other four years it did not fall below 20 mice per ha. As already stated, nothing seemed to prevent population increase once breeding began. It is, therefore, clear that the mongooses were not exerting control over the Rhabdomys population. This type of predation seems rather akin to that of mink (Mustela vison) or muskrats (Ondatra zibethicus) described by Errington (1946). He described the muskrats which are eaten by mink as a "biological surplus".

The other question which should be asked is to what degree predation could have interfered with breeding each year. Table 44 shows an estimate of the mean number of young weaned per pregnant female each month in the 1976 - 77 breeding season. The overall mean on the control grid and grid E lay between 1,1 and 2,1 young per female. Since mean litter size was about five, it follows that there was a 58 - 78% loss of newborn young. It seems likely that much of this could have been due to predation. Yet, even such heavy losses of young as these did not prevent population growth. Clearly, more research is needed to clarify the influence of predation. One possible experimental approach would be to remove all predators from a natural area and to monitor the growth of a prey population unhindered by predation, for comparison with a control population.

N.B.

Many of the Figures and Tables from other publications referred to in Chapter XIV will be found in Appendix A.

XIV. POPULATION FLUCTUATIONS AND CYCLES IN SOME MAMMALS

XIV.1 Historical perspective

The extraordinary irregular and unpredictable irruptions in the numbers of some species of rodents in various parts of the northern hemisphere have, for centuries, been a subject for amazement and debate. Many of the historial records have been collected together by Elton (1942) in his classic work, "Voles, mice and lemmings". He recounts numerous tales of voles appearing in the fields in millions in some years, devouring all the crops and then disappearing again, as mysteriously as they had arrived. Through careful analysis of the available records he came to the conclusion that population peaks might recur at regular intervals (e.g. the "lemming years") and hence that some species (including carnivores that preyed on the rodents) were displaying regular periodic fluctuations in numbers. For example, records of the Hudson Bay Company of fur returns of arctic foxes in the Ungave district for the period 1867 - 1924 seemed to show a fairly regular four year cycle of abundance and scarcity, although some peaks were also found at intervals of 2,3 and 5 years (Elton 1942, Table 51, p.415; Krebs & Myers, 1974, Fig. 2). Vole plagues in Bavaria are claimed by Elton (1942, Table 3, pp. 54-57) to show a regular periodicity of three, four or five years between 1903 and 1937, the average being 3,9 years. "This figure is extraordinarily like the period which will be shown to occur in Norwegian lemmings and voles, British voles, Labrador voles and Canadian Arctic lemmings",

XIV.2 Discussion of the evidence for regular population cycles in some mammals

I believe that a closer inspection of the evidence for regular cycles is warranted. The data available to Elton (1942) were mostly fragmentary and inexact; for example, his assessment of the periodicity of vole plagues in Bavaria (Elton 1942, Table 3, p.54) was based on "the number of consignments of anti-vole materials of all kinds sent out in the second half of each year by the Agrikulturbotanische Anstalt of Munich". Some data could have been influenced by factors of fashion and economics quite unrelated to any biological principles (e.g. the fur return statistics for arctic foxes) and hence they should be treated with caution. Furthermore, the outbreaks of voles described by Elton appear to have been mostly in agricultural areas, involving destruction of crops, which at once raises problems as to their correct biological interpretation.

However, my main criticism concerns the actual justification for the regularity of the supposed four year cycle. If one looks, for example, at Fig. 2 of Krebs & Myers (1974), showing fur return statistics for the arctic fox from 1868 - 1924, it may be true that the peaks tend to recur at three or four year intervals, if a peak is considered to occur in the purely mathematical sense - that is when the adjacent values on each side of it are lower than itself. However, this procedure totally ignores the absolute value of each 'peak', i.e. the absolute level of numbers, which seems to

me to be biologically significant. For example, although the fur returns for 1871 and 1872 were almost identical yet, because 1872 was very slightly higher than 1871, only 1872 is considered to have been a peak year (Fig. 2, Krebs & Myers, 1974). Then, both 1875 and 1877 were higher than 1872 yet neither is considered to have been a peak since it so happened that 1876 was much higher than either of them. Again, 1879, 1882 and 1887 were considered as peaks, although all three were lower than either 1875 or 1877 (which were not peaks). The same applies to 1885, which was a very low year - in fact, it was one of the lowest years on record and yet, because the two adjacent years on either side were even lower, it was considered to have been a peak year!

This seems to me to illustrate the absurdity of interpreting the data on a purely mathematical basis, without reference to biological criteria. So, one could go on, through the rest of the data in the figure. There are several more years of high numbers which were not regarded as peaks because they fell next to a year of even higher numbers.

My approach to this problem of how best to interpret the data would be not to divide them into rigid three or four year cycles but rather into periods of generally high or low numbers. Inevitably, here one must introduce a subjective element as to what constitutes 'high' or 'low' numbers. If one looks at the general trend of numbers in Fig. 2, then it seems that a figure of 1000 fox skins traded might be a reasonable dividing line. On this basis, my interpretation

of the fur return statistics would be as follows : there were initially three years of low numbers (1868 - 70), then two years of high numbers, two years of low numbers, three years of high numbers (1875 - 77), followed by a year of low numbers, a year of high numbers, two years of low numbers, a year of high numbers and then four years of low numbers (1883 - 86) - and so on, for the remainder of the data. This seems to me a far more biologically meaningful and more flexible way of using the data.

A similar approach could be adopted towards Fig. 3 of Krebs & Myers (1974 : 276) which depicts autumn population densities in the red-grey vole between 1935 and 1965. In the first place one can note that since no trapping was conducted from 1942 - 45, (Koshkina, 1966, Fig. 1 & Table 1), the dotted cycle in the figure is conjecture. Hence, one should analyse the data only from 1946 onward. One does not know whether 1946 was a peak since there was no previous information. A peak was recorded in 1954 because it happened to be higher than the adjacent years on either side of it, but this peak was far lower than 1949, 1959, 1962 and 1964, which were not considered peaks because they either preceded or succeeded an even higher year. Although peaks recur at four or five year intervals, the actual form of each cycle is irregular. To quote David Lack (1954) on cycles in general: "the peaks themselves tend to be of different heights, while the fall and rise in numbers between each peak is not symmetrical in the way that the term cycle would suggest to a physicist". This applies to the majority of cycles analysed

by ecologists.

I still feel, therefore, that it would be more meaningful to interpret Fig. 3 of Krebs & Myers (1974), starting in 1946 and using a reference point of 15 animals per 100 trap nights, as follows: a year of high numbers, then two years of low numbers, two years of high numbers, seven years of low numbers (1951 - 57), two years of high numbers, two years of low numbers and then three years of high numbers (1962 - 64). This adequately brings out the situation in the field where one finds marked fluctuations in numbers, without imposing the artificial restrictions of necessarily adhering to any rigid cycle of abundance and scarcity.

If we next consider Table 3 of Elton (1942, p.54) concerning the periodicity of vole plagues in Bavaria, he claims that there were outbreaks in 1903, 1907, 1910 and 1915. However, examination of Table 3 seems to show that there were outbreaks in one or other of the districts of Bavaria in several other years as well. For example, in Pfalz district in 1905 and 1909; in Unterfranken in 1916; in Mittelfranken in 1911; in Oberpfalz in 1911 and 1914; in Oberbayern in 1911, 1914 and 1916; in Niederbayern in 1911 and 1914. My contention is, therefore, that the supposed four year cycle is in reality very irregular. There are undoubtedly pronounced fluctuations in population numbers, but I do not believe that they can be divided into regular cycles. Some areas may have high numbers or low numbers for several years in a row and supposed peaks within these periods of high or

low numbers may have no biological significance. Furthermore, if one looks at his Table 2 (Elton, 1942, p.22) of vole outbreaks in France from 1900 - 1935, it is clear that there is no evidence of a four year cycle - for there appear to have been major outbreaks in 1903, 1904, 1909, 1912, 1913, 1918, 1919, 1921, 1923, 1925, 1926, 1927, 1928 and 1931 (at least ten regions registered an outbreak in these years).

Another quote from David Lack's (1954) paper on cyclic mortality supports my own belief in the need for great caution before we interpret population fluctuations as being cyclic: "the papers by Palmgren (1949) and Cole (1951, 1954) provide a valuable jolt to our too facile acceptance of population cycles as a proven fact, and show that random fluctuations may produce not dissimilar effects". This point is acknowledged by Krebs (1964, p. 50) who says that if we wish to understand "cycles" we must study something more than changes in numbers. In other words, it is necessary to study the population aspects in order to understand the mechanism of the cycles. He defines a cycle as "a typically 3- to 4-year fluctuation in numbers of microtine rodents characterized by high body weights of adults in the peak summer". However, I do not believe that the data presented by Krebs are adequate to support his contention of a four year cycle in lemmings and it seems to me that his data as presented in Tables 6 - 9 are capable of other interpretations with regard to density changes than his Fig. 4 (1964, p. 19). Indeed, it is not at all clear how he derived Fig. 4 from his live-trapping and snaptrapping results as shown in his Tables 6 - 9.

I am still sceptical, therefore, of the existence of four year cycles. I would like to end this section with a third quote from Lack (1954): "the most astonishing point, to a newcomer, is that despite the enormous number of papers written on cycles, no one, so far as I am aware, has yet studied any cyclic species in the field for even the term of one full cycle". As will be further discussed in the following sections, I believe that this is still true in 1980. The only exception I can find is the study of M.pennsylvanicus and M.ochrogaster, from 1965 - 70, by Myers & Krebs (1971b). As discussed below, I do not believe that these data reveal a periodic cycle. There are no microtine species in Africa south of the Sahara and no other African species has hitherto been found to be cyclic; but relatively little research has been done. I would thus challenge the statement of Krebs & Myers (1974, p. 278): "we know of no microtine data gathered quantitatively over a three or four year period which fails to show a population cycle". Such data may well show population fluctuations but whether they show a regular cycle is still open to question.

XIV.3 Comparison of population fluctuations in R.pumilio with cyclic species and discussion of different phases of the cycle

Having already expressed my general scepticism concerning the existence of four year cycles, the next logical step seems to be to examine in some detail the different phases of a microtine cycle, as outlined by Krebs & Myers (1974).

This paper will hereafter be cited simply as 'KM'. The interesting changes in the population of R.pumilio detailed in Chapter III suggest comparison with the different phases of a microtine cycle. In any population fluctuation four phases can be arbitrarily recognised (Krebs & Myers); namely the increase phase, the peak phase, the decline phase and the phase of low numbers. This last phase may or may not be present; in other words a population may go straight from a decline to an increase phase.

In the discussion that follows, I hope to show that the different phases of the cycle are not at all clearly defined, which leads in turn to the result that the so-called periodic fluctuations of microtines do not appear to have a regular form - as is well illustrated in the comprehensive review article of KM. The population data they use to illustrate different phases of the cycle, I believe, are often capable of various interpretations. This may make it possible to interpret almost any population fluctuation data as being some part of a regular cycle.

XIV.3.1 Increase phase

According to Chitty & Chitty (1962a): "this period may be defined as the year or years in which there is a relatively large increase in the initial numbers of successive breeding populations". KM say it is a period of large increase in numbers from one spring to the next. That there is not a

uniform interpretation of this phase is shown by KM who say (p. 279): "there are two views on the structure of the increase phase. The increase phase might be a gradual, exponential build-up from low numbers over two or even three years ..... an alternative view is that the increase phase is a rapid explosion which occupies one year or less". The use of the word 'exponential' in this explanation is somewhat confusing since, depending on the size of the exponent and which part of the exponential curve a population was on at a particular time, an exponential increase could be either gradual or explosive.

As an example of the first type of increase, KM (p. 279, Fig. 5) cite the study of Hamilton (1937) who found a gradual increase in the peak numbers of Microtus pennsylvanicus each year over a period of about $2\frac{3}{4}$ years. However, during each year of the three, the population showed a summer increase followed by a winter decline - an annual cycle similar to that found for R.pumilio in this study (Fig. 3). According to this view of the increase phase, one might consider the Rhabdomys population to have been in the increase phase of a cycle from September 1973 to March 1975. Moreover, the fluctuations detailed by Hamilton (1937) are described by KM : 279 as a population cycle. However, it is not at all clear what kind of cycle it could be since it is plainly not a three or four year cycle.

As an example of the second (rapid) type of increase, KM (Fig. 6) cite an isolated increase in a population of

Microtus ochrogaster from very low levels to approximately 40 minimum number alive in a six month period, as found by Myers & Krebs (1971b). Since trapping was only over two years it is impossible to say whether this was part of a recognisable four year cycle or not. According to this view one might legitimately regard any of the summer population increases of R.pumilio from October to March each year (e.g. Fig. 3 & Table 5, 1972 - 73, 1973 - 74, 1974 - 75, 1976 - 77) as being examples of the increase phase of a cycle. Furthermore, it is not at all clear to me how the alternative views of the increase phase, either being gradual over two or three years or rapid over less than one year, can both be compatible with a three or four year cycle.

XIV.3.2 Peak phase

Chitty & Chitty (1962a) say: "It is sometimes obvious which year is peak, since both the spring and autumn numbers may be higher than in other years .... the essential feature of this phase is defined as the failure to maintain the net annual rate of increase of the preceding phase (i.e. from one spring to the next)". KM say it is defined as a period of little change in numbers from one spring to the next.

The lack of a uniform interpretation of this phase is evident since KM : 283 state that some species do not have a well-defined peak phase, e.g. Microtus californicus and M.ochrogaster. In these populations they say: "there is typically

an increase phase followed by a brief period of high numbers and then a decline phase". Although they give no examples, they state that: "the peak phase in other species is well-defined and may last for a year (or rarely two years)".

According to these different possibilities, it seems that one might regard the population of R.pumilio as having been in a peak phase from January 1975 to February 1976, since numbers were higher than normal throughout this period of a year. The definition of Krebs & Myers of: "a period of little change in numbers from one spring to the next", is too vague, since one might argue that the Rhabdomys population changed little between September 1973 and September 1974 and that, therefore, it was in a peak. Looking at Fig. 3, this would plainly be absurd. On the other hand, one might regard R.pumilio as a species similar to Microtus californicus having no well-defined peak phase, e.g. Fig. 7 of KM. However, if one examines Fig. 7 (which must have been the Tilden Control population of Krebs, 1966, though this is not stated by KM), one can note, firstly, that the study did not cover the three or four year period of a full cycle but only some 20 months of trapping. This makes it difficult to be sure what phase of the cycle the population was in. The breeding season was already in full swing when fieldwork started and breeding continued until July 1963. In females breeding did not re-commence until towards the end of December 1963 (Krebs, 1966, Figs. 2 & 3). The second point is, therefore, that what the graph shows is a phase of increase which corresponds with a period of breeding, followed

by a winter decline corresponding with a non-breeding period. When the study finished in July 1964, the population was showing another (smaller) increase phase which again corresponded with a period of breeding. This is a cycle of numbers similar to that shown by R.pumilio in this study - namely an annual increase phase corresponding with the breeding season, followed by a brief period of high numbers and then a winter decline corresponding with the non-breeding season. In R.pumilio, however, this was an annual cycle probably unrelated to any three or four year cycle. But, it is worth noting that, looking at Fig. 7 of KM one cannot say that M.californicus was not also showing a similar annual cycle - the data presented could support such a view.

The point which I hope emerges from the above is the difficulty of interpreting any given set of limited data with any degree of confidence.

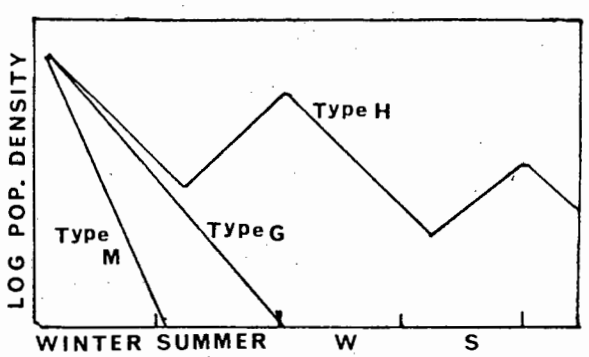
XIV.3.3 Decline phase

According to KM the decline phase of the cycle is especially variable. Chitty (1955) recognised three types of decline, namely the type M, type G and type H. Type M (after Middleton, in Findlay & Middleton, 1934) populations may fail to overwinter (Chitty, 1955). These are, therefore, 'crash' declines during the winter and early spring, following a peak. Type G (after Godfrey, 1955) populations may overwinter, be moderately abundant in the spring and then steadily decrease

throughout the breeding season. Type H populations may overwinter, be moderately abundant in the spring, maintain or slightly improve their numbers during the breeding season and then reach their greatest scarcity in the following year (Chitty, 1955). This is the most gradual decline of the three. Chitty (1955) cites two papers by Hamilton (1937, 1941) as the basis for his description of a type H, but Hamilton does not describe declines in detail and I can find nothing in either paper which could relate to the type of decline described by Chitty.

KREBS & MYERS (1974, FIG. 9)

Hypothetical diagram of the three types of population decline:



However, the classification of the decline phase of real populations into one of these categories appears to me to be very problematic, as I will endeavour to show. I believe that natural populations are too biologically variable to fit

neatly into stereotyped categories. Hilborn & Krebs (1976) monitored two declines of M.townsendii, for example, which did not fit any of the above types.

XIV.3.3.1 Type H decline

KM claim that their Fig. 7 shows type H decline in M.californicus. However, if one examines Fig. 7, it is evident that there was a severe drop in population density from over 250 voles per acre to just over 10 per acre during winter between September and the beginning of February. It seems that this decline should, therefore, be classed as a type M. The fact that the population then immediately began to increase again should not debar it from being a type M - indeed Chitty (1955) says nothing about what happens next in any of the declines. Since type H declines are defined as being the most gradual (Chitty & Chitty, 1962a, p.74) and this was clearly a 'crash' type of fall in density, I don't see how it could be classified as type H.

In a second example, KM (Fig. 11, p. 286) claim that a type H decline occurred in a population of Clethrionomys rufocanus studied by Kalela (1957). However, since Kalela trapped for only the four summer months June through September and there was no information for the other eight months of the year, I think there is insufficient evidence for a classification of the behaviour of this population. One can note that the dotted lines drawn in on Fig. 11 by KM are conjec-

ture since no trapping was done (Kalela, 1957, Fig. 6). If one compares Fig. 11 with the hypothetical diagram of a type H decline (above) it is difficult to see how it could be classed as a type H. The population recorded in 1955 was, in fact, the highest of the study and a fairly severe decline appears to have occurred in the winter 1955 - 56 (although there is no means of knowing whether the population actually declined in the winter or in the spring). The decline effectively occurred in a period much less than a year, which does not fit a type H classification at all.

In a third example KM (p. 285) cite Gaines & Krebs (1971, Fig. 5, p. 709) as showing a type H decline for Microtus ochrogaster. However, KM (Fig. 8, p. 283-4) cite another population studied by Gaines & Krebs (1971, Fig. 8) which they say illustrates a peak phase of M.pennsylvanicus. I am presuming that KM regard the population of M.ochrogaster as having been in the decline phase throughout the two year study, since if they had regarded only the second sharp decline in the winter of 1968 - 69, this would not qualify as a type H.

Now, if one compares Fig. 5 with Fig. 8 of Gaines & Krebs (1971) there are remarkable similarities between the population fluctuations of the two, and yet M.ochrogaster (Fig. 5) was regarded as having been in decline while M.pennsylvanicus (Fig. 8) was in peak phase. The two populations were studied at the same time and under the same conditions. The initial density of M.ochrogaster was somewhat higher than that of

M.pennyslvanicus, but both populations showed an immediate increase to a peak of very similar density - M.ochrogaster reaching this peak in October 1967, sooner than M.pennsylvanicus which peaked in January 1968. The real difference between the two populations lay in the fact that M.ochrogaster then declined during winter 1967 - 68 and reached a low point in March - April 1968, before beginning to increase again, whereas M.pennsylvanicus only began to decline in February and reached a low point in April - May 1968, its density at this time not sinking as low as that of M.ochrogaster. Thereafter, both populations began to increase and were once again at very similar densities (a little lower than the first peak) by October 1968. M.ochrogaster then declined sharply during winter and remained very low from March - June 1969. M.pennsylvanicus also showed a winter decline but much slower than that of M.ochrogaster and only declined to very low numbers in June 1969. At this time both populations were virtually extinct.

Thus, the overall pattern of changes described above is very similar in the two populations. They both reached similar high and low densities at similar times and the general trend of the changes was the same. The only major difference being that M.ochrogaster declined sharply during two winters whereas M.pennsylvanicus did not. However, since nothing is known of the previous history of either population - whether for example the M.ochrogaster population had recently been through a peak phase or whether the brief peak density attained in October 1967 was regarded as the peak phase, it

seems impossible to make a confident diagnosis of what stage of the cycle the populations were at, without more information. There are grounds for querying, for example, whether the M.pennsylvanicus population was really in a peak phase. The maximum density reached during the study was a MNA of about 80 mice per acre and it is quite possible that higher densities than this had been achieved in the year or years preceding the study and that this was, in fact, part of a decline phase. It seems to me that there is no sound logical basis for describing two populations as being in different stages of a cycle when both achieved similar densities at similar times and in which the sequence of changes was the same, when the only distinguishing feature was a winter decline in the one and not in the other. This is particularly so when there is no prior history of either population. The only clear trend evident in the M.ochrogaster population, for example, is a late summer increase from July to the end of October, corresponding with a period of breeding, followed by a winter and spring decline. This occurred in both years of the study depicted in Fig. 5 of Gaines & Krebs (1971). This again is consistent with what, I believe, most published examples of rodent fluctuations show - namely an annual phase of increase corresponding with the breeding season, followed by a decline in a period of non-breeding.

In the present study it would seem possible to interpret the decline of the R.pumilio population between May 1975 and September 1976 as being a type H decline, since there was

initially a winter fall in density from peak numbers followed by a partial recovery of the population during the breeding season and then a further decline to low numbers in the winter of 1976. This pattern of events seems to have all the qualifications to be a type H - and yet I have already suggested (above) that because of the unusually high density during the whole period between January 1975 and February 1976, one might regard this as being a peak phase!

This sort of situation reinforces my view that population cycles are too variable to be rigidly classified into separate compartments. An inflexible system of classification is liable to lead to error. In other words, the same cycle or pattern of population changes may be capable of more than one interpretation with equal justification.

XIV.3.3.2 Type G decline

According to the hypothetical diagram of declines (p.300) a type G decline occurs during a winter and the succeeding breeding season. KM (p. 285) cite the study of Godfrey (1955) as having found type G declines in two populations of Microtus agrestis. However, the data as presented in Table 1 of Godfrey are really too scanty to be sure about this, since she presents numbers of voles trapped only for May and August each year for 1950 - 52. It appears from her data that whereas her Rough Common population declined during the winter of 1951 - 52, and then continued to

decline in the summer of 1952, her Dell population in fact increased slightly in the winter of 1950 - 51 and only declined in the summer of 1951. The two populations thus behaved differently though both were assigned a type G decline.

KM (Fig. 6) cite the example of a decline in a population of M.ochrogaster as being a type G. However, in this case there were only four months of trapping data in the eight months prior to the start of the decline. Thus, it appears to me to be impossible to say what stage this population was at before the decline started. Hence, there is too little information to enable one to say what sort of decline it was. For example, this decline might have been the second year of a type H decline.

XIV.3.3.3 Type M decline

This is the simplest and hence the least contentious type of decline. The population experiences a severe fall in numbers during the winter following a peak. KM (p. 284) comment: "there are few examples in the literature of type M 'crash' declines that have been monitored accurately". They give three examples from the literature of what they consider to have been type M declines and concerning a fourth example they say: "a population of M.californicus which showed a type M 'crash' in 1963, was studied by Krebs (1966)". However, Krebs studied eight populations and we are not told

which one was intended. Looking at his paper (1966, Fig. 1) it seems that the only one obeying the criteria for a type M was his Tilden Control population. However, this is the same population which is presented in Fig. 7 of KM (although this is not stated by KM). As has already been noted above, this population was cited as an example of a type H decline (KM : 285)! Such are the difficulties, it would seem, of attempting to classify limited amounts of data.

XIV.3.4 Phase of low numbers

This phase is another variable aspect of the cycle since according to KM (p. 289): "in some cycles this phase is absent and populations go directly from the decline phase to the increase phase". Very little seems to be known about the phase of low numbers. As with the preceding phases already discussed, the interpretation of data relating to this phase seems to me to be problematic and subjective. KM (Fig. 12) cite the results of a study of M.pennsylvanicus by Getz (1960) as illustrating the phase of low numbers. However, I believe that there are too little data to support this assumption. In the first place, Getz (1960) trapped for only one year and there was no previous or succeeding history of his two populations. Secondly, his Marsh population had densities at least as high as several of the populations cited as examples by KM (e.g. Fig. 6, 8 & 10) which were not in the low phase. On these grounds alone, I do not see how the Marsh populations could be assigned to any particular

phase without more data. Furthermore, both populations show a clear annual cycle of summer increase due to breeding and winter decline (non-breeding) and the peak in the second summer appears to be higher than that of the first summer, though as complete data for the first summer are lacking, it is difficult to be sure about this. The overall trend, therefore, could be similar to the population M.pennsylvanicus studied by Hamilton (1937, Fig. 1), KM (Fig. 5), which was cited as an example of an increase phase. It seems to me that with the available data one could just as legitimately interpret the populations studied by Getz (1960) as being in the increase phase as in the low phase.

A population of M.californicus studied by Krebs (1966) is also cited by KM (Fig. 13) as being in the phase of low numbers. In this case, Krebs studied eight different populations and we are not told which of these is referred to in Fig. 13. However, examination of Tables 6 & 7 in Krebs (1966) makes it clear that it must have been his RFS 5 population, of which trapping started in August 1963 and ended in June 1964. This isolated period of trapping seems to me rather scanty information on which to make a safe diagnosis. For example, it is implied that numbers of voles on that area were normally higher than those found during the study - but this is unknown and it is possible that the area normally supported only small numbers of voles.

Gaines & Rose (1976) studied several populations of M.ochrogaster in Kansas. They had some difficulty in classifying

the length of the cycle they found on one of their grids (grid A) because they could not be sure whether the population was in the phase of low numbers or not, due to the absence of a priori criteria for identifying the low phase. They say (Gains & Rose, 1976 : 1157): ".... until a priori criteria are established as to what constitutes a low phase, the data can be made to fit any length of cycle we choose". This is my point precisely. The only problem is that it applies to <u>all</u> the phases of the cycle. There are no a priori criteria for identifying <u>any</u> particular phase.

XIV.4 Discussion

In the foregoing analysis of the different phases of a proposed population cycle my object has been to show that these are highly variable and that the same data may be capable of several interpretations. There are many examples in the literature, I feel, some of which I have drawn attention to above, where deductions have been drawn on inadequate data. Lidicker (1973) has drawn attention to the generally short duration of most published studies - it seems to have been accepted that a study covering one cycle of abundance was sufficient. However, I believe that one could only interpret data from a portion of a cycle with any confidence if one had data for a minimum of two successive cycles - if indeed such a cycle exists. The majority of the examples quoted by KM, in which the details of the demographic changes

during the course of the cycle are known, cover a trapping period of at most from two to three years. Therefore, despite the imaginative and painstaking studies of Microtus spp. by Krebs and his co-workers on various aspects of population fluctuations, I do not believe that any of their studies have yet demonstrated a three or four year cycle.

One of their trapping grids (control grid A) was monitored for a continuous period of five years and the observed population fluctuations of M.pennsylvanicus and M.ochrogaster on this grid have been published, in Myers & Krebs (1971b, Figs. 2 & 5). This is one of the very few studies covering such a long period where the details of the population changes are known. If a four year cycle really exists, surely it should be discernible in these data? I can find no hint of such a cycle for either species of vole. M.pennsylvanicus shows annual fluctuations which are complicated by the occurrence of winter breeding in at least three years of the study - 1965 - 66, 1968 - 69 and 1969 - 70 and, perhaps, also in 1967 - 68. Every year there was a decline in numbers in the spring, followed by a recovery in the fall or in the succeeding winter. Peak numbers were reached in about February or March each year, prior to the spring decline. Nor was there a marked difference in the size of the peak in the five years of the study; March 1967 was a little lower than the other years but otherwise the size of the annual peak was fairly consistent. Thus, what is observed in these data is basically an annual cycle with numbers increasing in late summer or autumn or even during

winter, due to breeding and then declining in the spring until recruitment raises numbers once again (Fig. 2, Myers & Krebs, 1971b).

This is the same population as described in Krebs et al (1969, Fig. 2), though only the data from 1965 - 67 were available at that stage. One anomaly is that a marked crash in numbers was recorded in May and June 1967 to a minimum of 10 males and 4 females and yet this does not appear in Fig. 2 of Myers & Krebs (1971b) nor in Fig. 6 of Gaines & Krebs (1971) which also records the same population. This anomaly was due to the poor trappability of M.pennsylvanicus in June 1967. Thus, many voles alive at that time were not trapped, leading to an artificially low value at the termination of the study (M.S. Gaines, pers. comm., J.H. Myers, pers. comm.).

The population of M.ochrogaster followed a simpler pattern in so far as there was no winter breeding except in 1965 - 66. Only in the summer of 1966 did the density of this population reach a level of 70 - 80 mice on the two acre grid. Otherwise the density remained at a very low level for the remainder of the study. The breeding seasons of 1967, 1968 and 1969 all failed to raise density beyond a maximum of about 20 mice in the grid in 1968. Once again, there was no evidence of a four year cycle and the most that can be discerned from Fig. 5 of Myers & Krebs (1971b) is that there was an annual cycle involving some increase in the population correlated with a summer breeding season (particularly in

1966 and 1968) and this was followed by an autumn or winter decline. In 1969, the population appeared to be almost extinct.

Lidicker (1973) studied a population of M.californicus on Brooks Island, San Francisco Bay, for 13 years. His population showed only a clear annual cycle related to breeding, with higher and lower densities in winter in alternate years; but as the island was only 22,3ha in size the situation was somewhat artificial. Gaines & Rose (1976) claimed that populations of M.ochrogaster on their grids B & D in Kansas had a two year cycle from 1971 - 73, but they based this assessment not on the fact that peaks were two years apart (as is normal practice when classifying cycles) but on the fact that periods of low numbers were two years apart. The continuation of this trapping from 1973 - 77 is shown in Gaines et al (1979). They acknowledge that grid B now had an annual cycle with a peak in May or June and then a decline through October each year, but they claim that density changes on grid D still had "the characteristics of a long-term fluctuation" (p. 816). In fact, grid D appeared to have two peaks each year, one in May or June and the other in winter between November and January each year. These peaks appeared to be related to breeding activity (breeding seasons were very irregular) and it seems to me that the cycle was much more like an annual one than like a long-term cycle. Since Gaines & Rose (1976) had been uncertain of the classification of the cycle on their grid A and had acknowledged that it could have the attributes of an

annual cycle, I do not believe that the available evidence supports the idea of a long-term cycle in M.ochrogaster. It is interesting none the less that they did not attempt to fit their data into the pattern of a three or four year cycle, but rather into that of a two year cycle.

Thus, in the continued absence of data that would constitute proof of a regular periodic cycle, I believe that most published studies of small mammal fluctuations show only a summer gain due to breeding and recruitment (usually in summer) followed by a non-breeding (usually in winter) decline. Undoubtedly there may be big changes in amplitude from one year to another and the picture is complicated by some microtines which may breed throughout winter and by the fact that sometimes a summer breeding season may fail almost entirely. This type of situation seems to me to be within the bounds of normal biological variability. Under these circumstances, it would appear safer to call density changes of the types catalogued by KM simply 'population fluctuations'.

In this context, it is interesting to examine the 'idealised' form of a four year cycle as depicted in Myers & Krebs (1974). According to their text and figure the increase phase lasts for approximately one year, followed by a peak phase lasting for about the same period and then a variable decline phase occupying about two to six months - a total time span of at most 2½ years. The answer to the question 'what happens next?', they say (p. 39), "is variable and impossible to predict". One possibility is that the population begins to

grow again at once, resulting in another peak at the end of the third year (Myers & Krebs, 1974 : 41). However, since the initial peak occurred at the end of the first year this means that the cycle is effectively a two year cycle. How this can be compatible with the proposed four year cycle is not explained. Another possibility, they say (p. 39), is that the population "may continue to decline and become so sparse that it is difficult to catch a single animal". However, what happens after this drastic decline is not mentioned. To be compatible with a four year cycle, it would seem that the population must remain in this low phase for at least the next 18 months before commencing its increase phase. Such a prolonged period of scarcity occurring regularly between phases of increase and decline has never been demonstrated, so far as I am aware. Indeed, what disturbs me most about hitherto published examples of cycles is their great irregularity; the supposedly regular form as illustrated by Myers & Krebs (1974, p. 41) is, I think, a myth.

The overall variability of each phase of the cycle has been discussed above and none of the examples of cycles published by KM seem to agree with the 'ideal' version, with the possible exception of a population of M.pennsylvanicus (KM, Fig. 8 and Fig. 8 of Gaines & Krebs, 1971) which went from an increase, through a peak to a decline in a period of two years. This population is also illustrated in Myers & Krebs (1971b, Fig. 3, grid I) which shows the continuation in trapping through 1969 and the first half of 1970. Here we come

across another anomaly similar to the one mentioned above for the population of M.pennsylvanicus on grid A; for Fig. 3 does not show the crash in 1969 that is shown in KM, Fig. 8. The population in June in Fig. 3 is at least 20 mice, whereas in KM, Fig. 8, it is only 3 mice (2 males and 1 female). The explanation is the same as recounted for the first anomaly, namely the poor trappability of M.pennsylvanicus (M.S. Gaines, pers. comm., J.H. Myers, pers. comm.). The subsequent trapping showed a recovery in the population in the fall of 1969 and a small drop during winter 1969 - 70. This was followed by the usual drop in numbers in the spring of 1970 when trapping ended. If one compares Fig. 3 and Fig. 2 of Myers & Krebs (1971b), then it appears that the situation on grid I was rather similar to the first three years on grid A (1965 - 67). Thus, if a four year cycle was not detectable on grid A, nor is it on grid I.

I would fully agree that the reasons for the fluctuations, the differences in amplitude, the failure to maintain a rate of increase, are themselves interesting and worthy of study, but this need not be done within the framework of a cycle of any particular length. There is, perhaps, a hint of admission of this when KM say (p. 278): "even if one denies that microtine populations cycle regularly, one must still explain their fluctuations". At the present stage of our knowledge, therefore, I believe it is less misleading to regard such fluctuations as not being periodic but irregular and possibly dependent upon some extrinsic variable such as

ELTON (1942)

Year	George's R. to C. Chidley	Ungava Bay	Ungava Inland	N. coast (reports)	N. coast (furs)
1914	..	WF & CF Sc.	..	..	..
15	WF & CF V. Sc.	WF & CF V. Sc.	..	WF & CF V. Sc.	..
16	..	WF Sc.	CF	F	..
17	..	..	..	..	..
18	..	..	..	..	..
19	..	..	..	..	..
1920	..	..	..	..	..
1	..	..	..	..	..
2	..	WF & CF Sc.	..	..	..
3	..	..	..	..	..
4	..	..	..	..	..

2

So far as possible no bias of theory has been introduced into the abbreviation of these reports; but there may be a few misinterpretations that are unavoidable. After a long course of reading these archives one has, however, a rather solid and convinced faith in the general reliability of the reports themselves, whether from white man or native. Several things can be seen at once from the table: the alternation, usually every three or four years, of scarcity and abundance (the latter sometimes coming up rather suddenly); the way different parts of the district have usually (but not invariably) kept in step—this shows best in the scarcities; the occasional disagreement in cycles of white and coloured fox; and the general confirmation that the north coast furs (put to the previous year) give to the north coast reports. It is fair to say that the table fits reasonably into the conception of a wide regional arctic fox fluctuation similar in extent and length of cycle to that of the coloured fox in northern Labrador.

Having marshalled the reports, we have now to bring along and set against them the fur returns for Ungava District (Table 51). There are certain snags about these figures which make them unsuitable for fixing the exact peak years of the cycle. But they have the great advantage of giving a continuous record. The reports are a better reflection of field conditions, but there are gaps. Together they fortify each other's weaknesses.

TABLE 51

Abundance and scarcity of arctic foxes in Ungava District, 1867–1924

For explanation of 'years' see text. Maxima (where known) are in heavy type. Fur returns include white and blue foxes. Figures in brackets are incomplete. Figures with asterisks are from a different source than the rest, but comparable (see text). (Ab.) or (+) means fox species not defined in reports. Wolstenholme omitted after 1908, Stupart's Bay after 1913.

Year	Fur returns (whole district)[16]	Reports		
		George's R. to C. Chidley	Ungava Bay	North coast
1867	?	..	+	..
8	395	..	Sc.	..
9	118	..	V. Sc.	..
1870	385	..	+	..
1	1,008	..	(Ab.)	..

ELTON (1942)

TABLE 51 (*cont.*)

Year	Fur returns (whole district)[16]	Reports		
		George's R. to C. Chidley	Ungava Bay	North coast
1872	1,096	(Ab.)	(Ab.)	..
3	512	..	..	..
4	217	..	..	..
5	1,432	..	+	..
6	4,682	..	+	..
7	[1,861*]	..	..	..
8	292*	..	..	..
9	1,300	..	..	..
1880	731*	..	..	..
1	753	..	..	..
2	1,394	..	..	..
3	498	..	V. Sc.	..
4	115	Ab.	Sc.	Ab.
5	501	..	Sc.	Ab.
6	306	..	..	..
7	1,167	..	Ab.	Ab.
8	628	Sc.	V. Sc.	Sc.
9	1,503	Sc.	+	..
1890	2,585	? Ab.	Ab.	..
1	1,119	V. Sc.	V. Sc.	..
2	979	Sc.	V. Sc.	..
3	1,216	..	(Ab.)	..
4	1,061	..	V. Sc.	V. Sc.
5	360	? Sc.	Sc.	V. Sc.
6	607	..	+	Sc.
7	2,759	V. Sc.	V. Sc. & Ab.	Ab.
8	796	V. Sc.	V. Sc.	V. Sc.
9	490	V. Sc.	V. Sc.	V. Sc.
1900	1,494	..	(+)	..
1	4,489	(Ab.)	Ab.	..
2	1,879	(Ab.)	Sc.	? Sc.
3	248	V. Sc.	V. Sc.	V. Sc.
4	3,237	+	Ab.	..
5	5,019	..	Ab.	..
6	1,189	V. Sc.	V. Sc.	V. Sc.
7	159	..	Sc.	Sc.
8	632	(? +)	Sc.	..
9	3,502	(+)	Ab.	(Ab.)
1910	547	..	Sc.	Sc./Ab.
11	78	V. Sc.	V. Sc.	? Sc.
12	131	..	..	..
13	704	..	..	..
14	429	..	Sc.	..
15	29	V. Sc.	V. Sc.	V. Sc.
16	344	..	Sc.	(+)
17	1,607	..	..	..
18	768	..	..	..
19	296	..	..	..
1920	2,397	..	..	..
1	9,797	..	..	..
2	1,806	..	Sc.	..
3	497	..	..	..
4	1,423	..	..	..

GAINES & KREBS (1971)

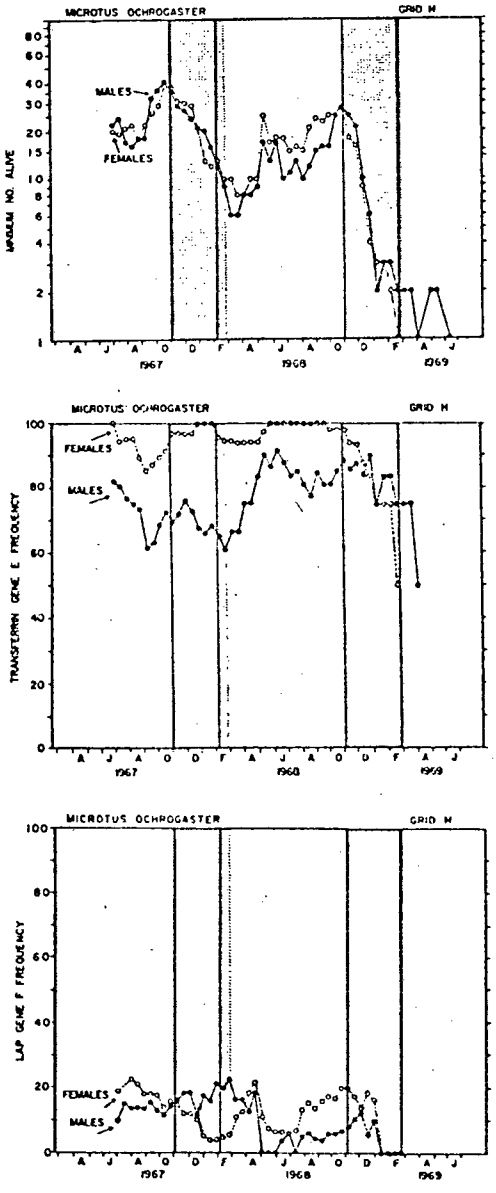


FIG. 5. Grid H, *M. ochrogaster*. See legend for Figure 3.

These changes in gene frequency and population density were calculated from the biweekly trapping periods. The two fenced enclosures were omitted from the analysis since voles on these grids had high survival rates with populations reaching abnormally high densities. After testing for homogeneity in 2 × 2 contingency tables, grids were pooled. The relationship of changes in gene frequency and population density were quantified with correlation coefficients (Table 5). Changes in LAP^F in *M. ochrogaster* males were negatively correlated with density changes, whereas in females there was no correlation between these two variables. Tf^E gene frequency changes in both sexes of this species were positively correlated with changes in population density. In *M. pennsylvanicus* populations, changes in male LAP^F frequency were negatively correlated with density changes, whereas in females the variables were positively correlated. Changes in Tf^E frequency showed a positive correlation with density changes in males but there was no correlation in females.

TABLE 5. *Correlation coefficients for changes in gene frequency* (Δp) *with population density changes* (λ) *on grids A, F, H, and I. Sample sizes are in parentheses.*

	M. ochrogaster	*M. pennsylvanicus*
Δ LAP^F males	−.24* (150)	−.26* (141)
Δ LAP^F females	−.08 (178)	.24* (135)
Δ Tf^E males	.27* (150)	−.18* (141)
Δ Tf^E females	.58** (178)	.03 (145)

* $P \leq .05$.
** $P \leq .01$.

Components of Fitness

Fitnesses of different genotypes in a population can be estimated either tautologically or physiologically. The tautological approach has been to assign fitness values to genotypes which best fit the observed changes in gene frequency. The difficulty with this method is that a number of models such as heterozygote advantage, unequal selective values in the two sexes, and frequency dependent selection, all provide good fits for the same set of gene frequency changes (Wright and Dobzhansky, 1946). The alternative approach is to

GAINES & KREBS (1971)

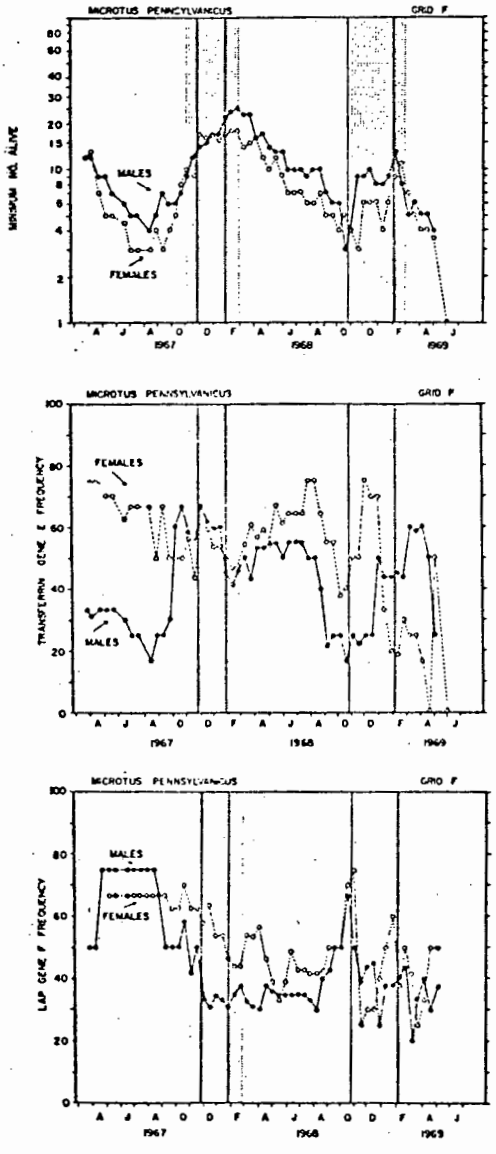


FIG. 7. Grid F, *M. pennsylvanicus*. See legend for Figure 3.

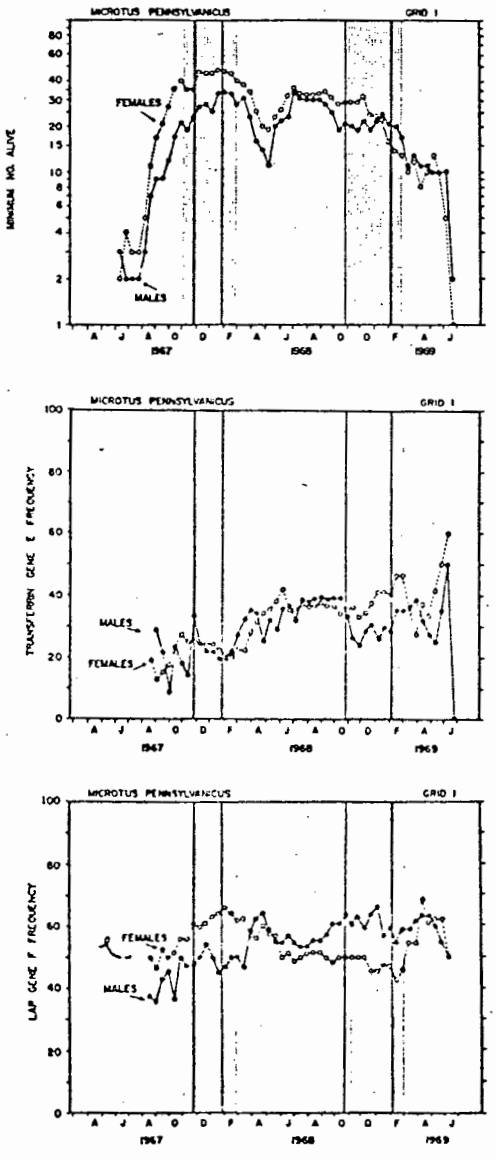


FIG. 8. Grid I, *M. pennsylvanicus*. See legend for Figure 3.

measure physiological components of fitness which include viability, fecundity, and developmental rates for different genotypes in the population (Wallace, 1948). In this section, we have attempted to combine these two methods of measuring fitness. Individual components of fitness were measured for LAP and Tf genotypes under field conditions and then related to changes in gene frequencies observed in the populations.

Viability.—Minimum survival rates were used to compare viabilities of different genotypes. Minimum survival rates for LAP and Tf genotypes were summed over different phases of the fluctuation on each grid. After testing for homogeneity the unfenced grids were pooled and survival

changes observed in a single habitat, because a given number of animals spread over many habitats will obviously be less dense than the same number in one habitat only. The explanation of these changes in habitat segregation probably lies in some form of interspecific interference, but we have no direct evidence that this is the case.

Other census methods

Visual estimates of density changes were obtained by counting the number of lemmings seen per hour of walking on the tundra. This is obviously a crude index of density but it does provide valuable supplementary information for areas where no live trapping was done.

Trace indices of fresh faeces were made in 1959 and 1960 by doing line transects through habitat types, dropping a 3-foot by 1-foot rectangle every 10 feet, and recording presence or absence of fresh green droppings. Again this is a crude index but it has the advantage of being done very quickly.

Results

Visual estimates were obtained for *Lemmus* as follows:

1959	0.43	*Lemmus*	seen	per	100	hours	walking	(based	on 465	hours)
1960	85.00	"	"	"	"	"	"	"	" 316	"
1961	0.51	"	"	"	"	"	"	"	" 393	"
1962	0.81	"	"	"	"	"	"	"	" 247	"

These estimates apply only to the summer. During the spring melt-off and the fall freeze-up lemmings may become much more noticeable.

The extent of the 1960 cyclic high may be indicated from visual reports of lemming abundance as follows: May—Chesterfield Inlet, Rankin Inlet, Coral Harbour, Eskimo Point; July—Garry Lake, Beverly Lake; August—Chantrey Inlet; and September—Repulse Bay, Ferguson Lake. It is apparent from these reports that the 1960 high occurred over at least an area 500 miles by 400 miles of the Central Arctic, thus showing that the cycle at Baker Lake was not merely a local effect.

Data obtained from trace indices and dropping boards will not be given here because they add nothing new to the observations above.

Finally, dropping boards were used as suggested by Emlen *et al.* (1957). This technique was tried in 1959 and 1960 but discontinued in 1961 because it involved a considerable amount of work and merely duplicated other census information.

Summary and conclusions

Figure 4 summarizes the density changes in *Lemmus* and *Dicrostonyx* over 1959–62.

1959 Summer: This was a summer of very low numbers of both species, with *Dicrostonyx* somewhat more abundant than *Lemmus*. It was evident by September that some increase had occurred but numbers were still very low.

1959–60 Winter: Tremendous population growth occurred over the winter in both species, the crude estimates of this increase being 25- to [illegible]-fold

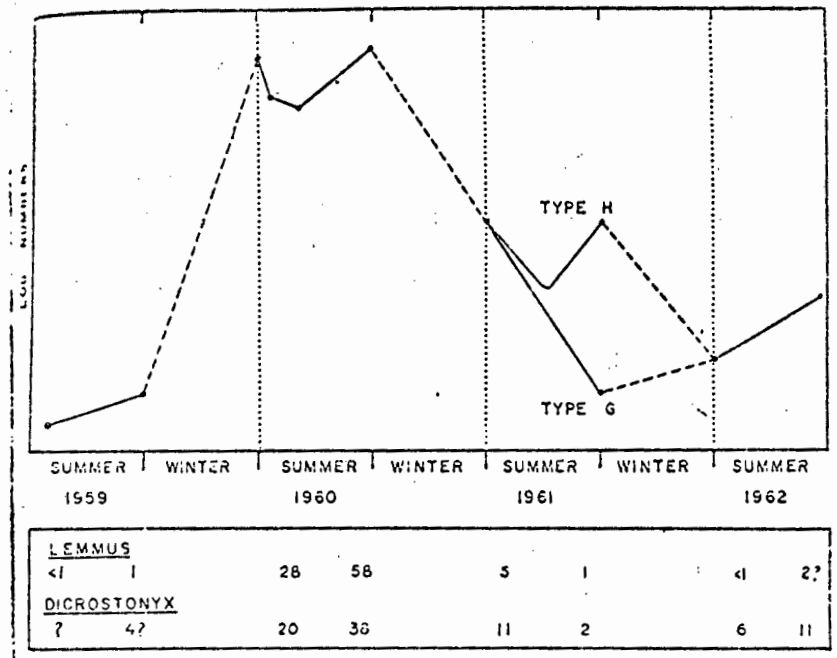


Fig. 4. Generalized density changes, 1959–62.

1960 Summer: The spring population of *Lemmus* declined considerably when the snow melted and summer breeding began. This mortality was probably between 67 per cent and 30 per cent and was concentrated in a few days. By August the *Lemmus* population had risen 2- to 3-fold from its lowest point in June and was then slightly above the spring density. The *Dicrostonyx* population also increased during this summer, but it is not known whether it showed the same drop in numbers at the melt-off. Densities were highest in this cycle during August 1960.

1960–1 Winter: A severe decrease in population density occurred over this winter, estimated at 90–95 per cent in *Lemmus* and 70–80 per cent in *Dicrostonyx* from August 1960 to June 1961. This decrease had already occurred before the spring melt-off and there was no indication of a melt-off mortality such as occurred in 1960.

1961 Summer: There were two patterns found in this summer of decline. On the Main Study Area and two outlying areas the decline continued in both species through the summer with no recovery (Type G decline; Chitty, 1955a, p. 59). On five other outlying areas partial recovery occurred through the summer (Type H decline). By the end of this summer on the Main Study Area densities in both species were about equal to those at the start of the [illegible]

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Table 6. Numbers of *Lemmus* on Quadrat 1 during 1959–62.*

Date of sampling	Winter generation	Summer generation† Y_1	Y_1'	Y_1''	Total animals
1959					
August 5–10	—	—	—	—	0
August 11–23	—	—	[illegible]	—	1
1960					
June 18–20	28[7]	—	—	—	28
July 6–8	22[7]	8	—	—	30
July 28–30	12[6]	25[4]	4[3]	—	41
August 25–7	8[3]	16	20[1]	14[1]	56
1961					
June 12–18	2[1]	—	—	—	2
June 19–25	3	—	—	—	3
June 26–July 2	5[1]	—	—	—	5
July 3–9	3[1]	—	—	—	3
July 10–16	2	2[1]	—	—	4
July 17–23	2	—	—	—	2
July 24–30	2	—	—	—	2
July 31–August 6	—	—	—	—	0
August 7–13	—	—	1	—	1
August 14–20	—	—	—	—	0
August 21–7	—	—	—	—	0
August 28–September 1	—	—	—	1	1
1962					
July 16–August 11	—	—	—	—	0

*Superscripts in the table give trap mortalities.
†Y_1 = first summer litter, Y_1' = second summer litter, Y_1'' = third summer litter.

Table 7. Numbers of *Dicrostonyx* on Quadrat 3 in 1960–2.*

Date of sampling	Winter generation	Summer generation† Y_1	Y_1'	Y_1''	Total animals
1959‡					
July 24–August 1	(3)	(3)	—	—	(6)
August 6–10	(1)	(2)	—	—	(3)
1960					
August 25–7	10[1]	13	11	4	38
1961					
June 5–11	1	—	—	—	1
June 12–18	9	—	—	—	9
June 19–25	11[1]	—	—	—	11
June 26–July 2	5	—	—	—	5
July 3–9	1	—	—	—	1
July 10–16	8	—	—	—	8
July 17–23	5	—	—	—	5
July 24–30	4	1	—	—	5
July 31–August 6	1	—	4	—	5
August 7–13	2	—	1	—	3
August 14–20	—	—	1	—	1
August 21–7	—	—	2	—	2
August 28–September 1	—	—	—	—	0
1962					
June 18–24	6	—	—	—	6
June 25–July 1	5	—	—	—	5
July 2–8	10	—	—	—	10
July 16–22	5	—	—	—	5
July 23–9	7	1	—	—	8
July 30–August 5	2	—	—	—	2
August 6–12	5	5	—	—	10
August 13–19	4	4	3	—	11

Table 8. *Lemmus* snap-trapping indices, 1959–62

Location and time period	Dry habitat‡ N[1]	Dry habitat‡ Lemmus[1]	Medium habitat N	Medium habitat Lemmus	Wet habitat N	Wet habitat Lemmus
Main Study Area						
1959						
June	711	0.0	1332	0.15	2268	0.09
July	504	0.0	1377	0.0	999	0.10
August	504	0.0	1377	0.0	999	0.20
September 1–10	153	0.0	810	0.0	477	0.21
1960						
June	504	0.79	1377	4.87	999	6.91
July	378	0.0	180	6.11	198	6.57
August	684	5.56	1377	15.54	999	21.42
1961						
June	576	0.0	1647	0.24	1449	1.10
July	1017	0.0	1917	0.30	2764	1.42
August	1260	0.0	1773	0.11	1935	0.62
1962						
June	684	0.0	2061	0.05	1971	0.61
July	378	0.0	1737	0.35	3645	1.56
August	522	0.0	1449	0.07	1629	1.99
Other areas						
1959						
August 12–17						
Prince River	18	0.0	126	0.79	576	2.43
"Ten Mile Island"	—	—	24	0.0	216	1.85
Lower Thelon River	213	0.0	—	—	387	0.78
August 26–September 5						
"New Lake"	—	—	—	—	1620	1.11
1960						
July 13–18						
Aberdeen Lake	201	0.0	226	3.54	218	16.35
July 20–3						
"New Lake"	—	—	54	33.30	306	27.12
August 15–18						
Prince River	15	6.67	96	23.95	391	17.65
"Ten Mile Island"	—	—	24	12.50	216	16.66
Lower Thelon River	213	17.37	—	—	387	27.13
1961						
July 1–13						
"New Lake"	—	—	171	0.0	540	1.48
July 26–9						
Aberdeen Lake	306	0.0	279	2.15	486	8.44
July 17–20						
"Long Island"	126	0.0	207	2.90	207	7.73
July 24–7						
"Second Island"	369	2.98	27	0.0	144	6.25
August 14–19						
Prince River	18	0.0	90	0.0	432	3.01
"Ten Mile Island"	126	2.38	54	3.70	180	7.78
"Nine Mile Island"	81	12.34	—	—	90	12.22
Lower Thelon River	153	0.0	27	3.70	360	3.33
September 1–10						
"New Lake"	—	—	297	0.67	696	3.02
1962						
July 2–8						
"New Lake"	—	—	567	0.71	954	1.15
July 11–16						
Aberdeen Lake	1086	0.18	393	2.54	747	5.35
July 17–21						
"Long Island"	108	0.0	—	—	450	0.67
"Second Island"	387	0.78	—	—	171	2.92
"Sand Island"	54	0.0	—	—	306	0.98
August 5–9						
Prince River	18	0.0	108	0.0	594	2.19
"Ten Mile Island"	198	0.0	—	—	342	0.58
"Nine Mile Island"	189	0.53	—	—	171	2.92
"Eight Mile Island"	225	4.89	—	—	135	5.93
Lower Thelon River	153	0.0	—	—	567	1.06

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Table 9

Year and time period	Dry habitats[1]		Medium habitats[1]		Wet habitats[1]	
	[2]	[3]	[2]	[3]	[2]	[3]
Main Study Area						
1959						
June	711	0.42	1512	0.58	2264	1.06
July	504	0.20	1377	0.51	993	0.71
August	504	0.20	1377	0.29	993	0.61
September 1–10	153	0.0	810	0.12	477	0.42
1960						
June	504	2.98	137.	1.31	999	0.50
July	378	10.05	180	2.22	198	0.51
August	684	7.31	1377	1.09	999	0.40
1961						
June	576	1.04	1647	1.40	1449	0.48
July	1017	2.56	1017	0.38	1764	0.62
August	1260	0.79	1773	0.85	1935	0.56
1962						
June	684	1.02	2061	1.16	1971	1.27
July	378	2.65	1737	1.96	3645	1.18
August	522	0.77	1449	1.38	1629	1.10
Other areas						
1959						
August 12–17 Lower Thelon River	213	0.0	—	—	387	0.52
1960						
July 13–18 Aberdeen Lake	201	14.43	226	6.64	218	2.29
August 15–18 Lower Thelon River	213	4.69	—	—	357	0.26
1961						
July 26–9 Aberdeen Lake	306	5.56	279	6.45	486	2.06
August 14–19 Lower Thelon River	153	0.0	27	0.0	363	0.0
1962						
July 11–16 Aberdeen Lake	1086	1.66	393	0.25	747	0.56
August 5–9 Lower Thelon River	153	0.65	—	—	567	0.18

[1]Dry habitats = lichen heath, heath, heath hummock, and moss heath.
Medium habitats = heath sedge and heath sedge hummock.
Wet habitats = sedge hummock, sedge tussock, sedge marsh, moss, and moss sedge.
[2]Number of standard trap nights.
[3]Number of *Dicrostonyx* caught per 100 standard trap nights.

Table 11. Timing of summer breeding periods in *Dicrostonyx* females, 1959–62. Dates given are insemination dates; to obtain periods of birth add 20 days.

Year	Period I	Period II	Period III	Period IV
Winter generation				
1959	June 18–28	July 10–18	August 1–10?	?
1960	May 31–June 8	June 22–8	July 15–24	No breeding
1961	June 2–14	June 28–July 10	July 21–?	No breeding
1962	June 17–27	July 9–18	July 31–August 6	August 20–?
Y_1 Summer young				
1959	—	—	?	No breeding ?
1960	—	—	No breeding	No breeding
1961	—	—	July 17–21	No breeding
1962	—	—	August 3–?	?
Y_1' Summer young				
1959	—	—	—	No breeding ?
1960	—	—	—	No breeding
1961	—	—	—	No breeding
1962	—	—	—	?

Table 12. Length of the summer breeding seasons of *Lemmus* and *Dicrostonyx*, Main Study Area, 1959–62.

Year	Length in days[1]	Time period[2]
Lemmus		
1959	81	June 12 – September 15+
1960	70	May 29 – August 9
1961	85	June 5 – August 28
1962	78	

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on the area during 3-7 September, and so the minimum number of individuals present at this time is 454.

Unfortunately I have no way of determining the accuracy of these enumerations. I feel that with the present trapping procedure I can enumerate 80-90% of the individuals in populations up to 125-150 per acre. Above this density only about 60-80% of the population could be enumerated. No areas were trapped out to verify these statements. Comparison of the observed number of mice on these areas with the capture-recapture population estimates support these beliefs, but these latter estimates contain an unknown amount of bias so that this argument cannot be relied upon. We are here running up against an ecological form of the Uncertainty Principle—we cannot know the accuracy of our enumerations without destroying the population we wish to follow.

RESULTS

Variations in population density per acre for the various study areas are shown in Fig. 1, and these data are broken down in Tables 6 and 7 for the males and females. The RFS 5 population densities are not plotted because they were so low. These variations in population size will be discussed separately for the three areas studied.

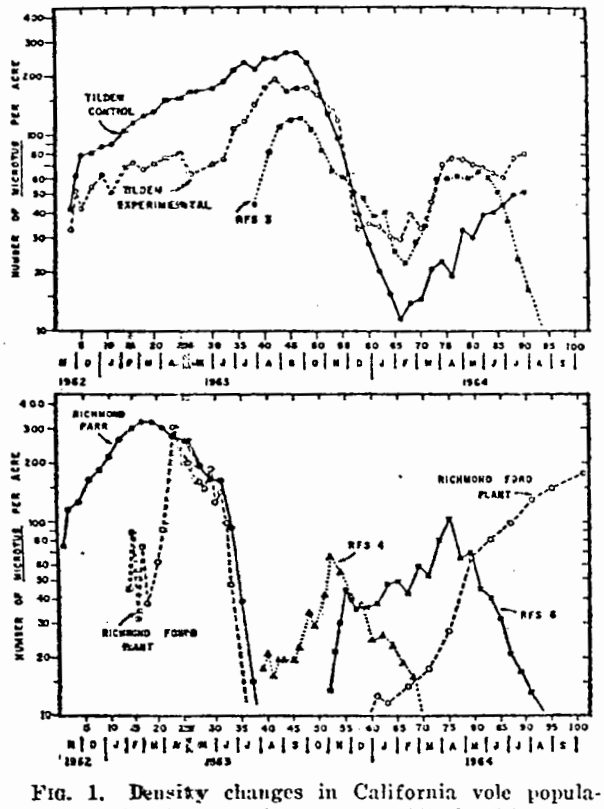

FIG. 1. Density changes in California vole populations on the live-trapping areas. All densities were obtained by direct enumeration and hence are minimum counts, except for the Ford Plant 1963 data which are capture-recapture estimates.

TILDEN PARK:

Microtus had been extremely scarce in this Tilden Park grassland during the summer of 1962; DeLong (pers. comm.) had great difficulty live trapping any mice at this time, and Pearson (pers. comm.) stopped live trapping his area after a catch of zero in March 1962. In early September when I first visited this area the vegetation was all dried out and runways were very sparse. Yet by mid-November when my live trapping began there were over 30-40 mice per acre and many juveniles were already present. The autumn rains began on 9-10 October 1962 and green vegetation appeared only about a week after this. These populations must have increased tremendously in September and October 1962, partly during the dry season when virtually no green vegetation was available for forage.

Two areas were selected for study in Tilden Park. The Tilden Control grid was followed as a natural population with no treatment. The Tilden Experimental area, which lay 300 feet to the south in a continuous grassland cut only by fire trails, was manipulated by intensive cropping of the *Microtus* population. This experiment was designed to test the prediction of Chitty (1960, p. 108) that heavy cropping of an expanding population should retain the population in the phase of increase and prevent the deterioration in survival which occurs in declining populations. All adult mice weighing 40 g or more were removed from this population from 26 November 1962 to 30 November 1963, (Table 8). I hoped to keep this experimental area reasonably free of adult mice in order that juveniles on this area could express their maximum rates of growth, survival, and reproduction. No exceptions were made to this cropping procedure; all pregnant females 40 g or over (weight including embryos) were removed. Animals less than this weight were treated normally and released.

In the Tilden Control population the count showed an initial spurt in late November, 1962, which is partly due to the initial lag in getting the majority of mice on the grid tagged. From early December 1962 to early September 1963 this population increased from 80 per acre to 260 per acre at a nearly constant rate of 3% per week. This regular increase is not found in both sexes however (Tables 6 and 7). Whereas the females seemed to increase regularly from 3 December to 12 July, the males seemed to increase from 3 December to 5 April, then stabilize or even slightly decline until 14 June, and then increase steadily to a peak at 6 September, several weeks after the females.

The Control population remained stationary through September 1963 and then began to decline in early October. This decline continued at a nearly uniform rate of 18% per week for about four months until early February 1964, reducing the population from over 250 per acre to about 11 per acre during this time. The decline appeared to start at the

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TABLE 6. Minimum number of male *Microtus* alive on the different areas, November 1962 to October 1964. All densities as number per acre.

Date	Week No.	Richmond Parr	Tilden Control	Tilden Exp.	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Ford
1962									
5-9 November	1	26.0							
12-23 November	2-3	41.0	17.4	14.7					
26 Nov.-7 Dec.	4-5	38.0	27.8	24.3					
10-21 December	6-7	62.0	38.8	27.9					
24 Dec.-4 Jan.	8-9	70.0	43.4	32.4					
1963									
7-18 January	10-11	88.0	42.8	25.9					
21 Jan.-1 Feb.	12-13	111.0							
4-15 February	14-15	125.0	47.5	28.4					25.6[a]
18 Feb.-1 March	16-17	140.0	52.1	29.9					26.6
4-15 March	18-19	129.0	57.3	34.0					19.8
18-29 March	20-21	130.0	62.5	34.5					80.0
1-12 April	22-23	125.0	65.4	37.0					121.5
15-26 April	24-25	111.0	61.8	38.0					118.3
29 April-10 May	26-27	76.0	70.1	23.8					31.0
13-24 May	28-29	66.0							53.0
27 May-7 June	30-31	64.0	60.8	26.9					37.2
10-21 June	32-33	34.0	67.2	26.3					36.7
24 June-5 July	34-35	16.0	82.2	42.6					
8-19 July	36-37	5.0	104.2	49.7					
22 July-2 Aug.	38-39	2.0	106.0	69.0	23.6	4.8			
5-16 August	40-41		123.9	89.2	50.5	6.5			
19-30 August	42-43		126.8	99.4	62.4	4.8			
2-13 September	44-45		138.4	83.1	63.5	4.8			
16-27 September	46-47		140.1	86.7	60.2	6.5			
30 Sept.-11 Oct.	48-49		128.5	81.1	50.5	12.9			
14-25 October	50-51		103.6	75.5	34.3	16.1		1.7	1.9
28 Oct.-8 Nov.	52-53		65.4	57.3	26.4	25.8		6.6	1.3
11-22 November	54-55		52.2	51.2	25.4	16.1		18.2	1.9
25 Nov.-6 Dec.	56-57		31.9	20.3	26.4	15.9		15.9	
9-20 December	58-59		17.4	10.7	23.3	14.5		13.4	1.9
23 Dec.-3 Jan.	60-61		12.8	11.7	22.3	8.7	1.2	15.9	6.5[b]
1964									
6-17 January	62-63		11.0	10.7	24.3	11.6	5.0	22.0	6.5
20-31 January	64-65		8.1	9.1	12.3	10.1	3.2	22.0	
3-14 February	66-67		5.2	8.6	8.1	8.7	0.8	19.5	7.1
17-28 February	68-69		7.5	13.7	9.1	7.2	2.4	26.8	
2-13 March	70-71		7.0	11.7	15.2	2.9	0.8	18.3	9.8
16-27 March	72-73		10.4	15.7	31.4	5.8	4.0	26.8	
30 Mar.-10 April	74-75		12.2	29.4	28.4	2.9	4.0	47.6	12.3
13-24 April	76-77		7.5	26.9	29.4	1.4	7.9	29.3	
27 April-8 May	78-79		13.9	24.4	25.4	2.9	7.9	34.2	26.6
11-22 May	80-81		13.3	23.8	26.4	4.3	6.3	25.6	
25 May-5 June	82-83		21.4	22.3	26.4	5.8	4.0	23.2	32.5
8-19 June	84-85		19.7	21.8	16.2	2.9	0.8	18.3	
22 June-3 July	86-87		18.5	21.8	13.2			9.8	36.4
6-17 July	88-89		20.3	32.0	10.1	2.9		8.5	
20-31 July	90-91		24.4	36.0	6.1			4.9	46.8
17-28 August	94-95								57.1
31 Aug.-11 Sept.	96-97							4.9	
14-25 September	98-99							2.4	
12-23 October	102-103								82.5

[a]Densities for Richmond Ford Plant for weeks 14-33 are capture-recapture estimates rather than minimum numbers.
[b]Beginning of Richmond Ford Plant introduction experiment.

same time in males and females and to proceed at the same rate in both sexes. The fall rains began on 10 October 1963 and the vegetation began growing within one or two weeks. Thus a major part of this decline occurred in the presence of green vegetation.

In mid-February 1964 new recruits began entering the Control population and it increased from mid-February to late August somewhat irregularly but at an average rate of 7% per week, a higher rate of population growth than had occurred the previous year. Males and females did not appear to increase at different rates or at different times. By late July this population had reached a density of about 50 per acre and was leveling off since recruitment was at an end.

The Tilden Experimental population began at the

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TABLE 7. Minimum number of female *Microtus* alive on the different areas, November 1962 to October 1964. All densities as number per acre.

Date	Week No.	Richmond Parr	Tilden Control	Tilden Exp.	RFS 3	RFS 4	RFS 5	RFS 6	Richmond Ford
1962									
5-9 November	1	49.0							
12-23 November	2-3	73.0	24.9	18.2					
26 Nov.-7 Dec.	4-5	89.0	40.0	21.8					
10-21 December	6-7	101.0	42.8	26.4					
24 Dec.-4 Jan.	8-9	114.0	44.0	30.9					
1963									
7-18 January	10-11	129.0	46.9	25.3					
21 Jan.-1 Feb.	12-13	154.0							
4-15 February	14-15	176.0	59.6	40.0					20.9[a]
18 Feb.-1 Mar.	16-17	183.0	65.4	42.6					43.8
4-15 March	18-19	195.0	69.5	33.0					27.1
18-29 March	20-21	172.0	68.3	37.0					63.7
1-12 April	22-23	145.0	85.7	40.0					138.0
15-26 April	24-25	150.0	88.0	42.1					101.7
29 Apr.-10 May	26-27	116.0	96.1	39.5					127.1
13-24 May	28-29	99.0							98.3
27 May-7 June	30-31	98.0	110.6	44.6					89.3
10-21 June	32-33	59.0	120.4	49.2					31.1
24 June-5 July	34-35	23.0	132.0	65.4					
8-19 July	36-37	10.0	128.0	68.4					
22 July-2 Aug.	38-39	6.0	111.7	73.0	20.4	12.9			
5-16 August	40-41		119.9	84.2	31.2	14.5			
19-30 August	42-43		119.9	92.3	47.3	14.5			
2-13 September	44-45		121.5	84.7	55.9	14.5			
16-27 Sept.	46-47		122.7	85.7	60.1	16.1			
30 Sept.-11 Oct.	48-49		104.2	92.3	57.0	21.0			
14-25 October	50-51		82.8	83.7	49.0	25.8		3.3	0.7
28 Oct.-8 Nov.	52-53		62.5	75.5	39.5	40.3		14.9	0.7
11-22 November	54-55		43.5	67.9	35.5	38.7		26.5	1.3
25 Nov.-6 Dec.	56-57		31.3	39.6	28.4	24.6		19.5	
9-20 Dec.	58-59		22.0	22.3	24.3	23.1		23.2	1.3
23 Dec.-3 Jan.	60-61		15.1	23.8	16.2	15.9	2.5	22.0	5.9[b]
1964									
6-17 January	62-63		9.3	23.4	16.2	14.5	2.5	25.6	5.2
20-31 January	64-65		7.5	21.3	13.2	13.0	2.4	26.8	
3-14 February	66-67		6.4	20.8	14.2	10.1	0.8	23.2	7.1
17-28 February	68-69		6.4	25.8	19.3	8.7	1.6	31.7	
2-13 March	70-71		7.5	21.8	19.3	5.8	2.4	34.2	7.8
16-27 March	72-73		10.4	30.0	28.4	2.9	4.8	52.5	
30 Mar.-10 Apr.	74-75		10.4	41.6	31.4	5.8	7.9	53.7	15.0
13-24 April	76-77		11.6	49.2	32.4	4.3	11.9	35.4	
27 Apr.-8 May	78-79		19.1	50.2	34.5	8.7	7.1	35.4	38.3
11-22 May	80-81		16.8	46.2	38.5	5.8	6.3	19.5	
25 May-5 June	82-83		18.0	45.6	34.5	2.9	0.0	17.1	48.8
8-19 June	84-85		20.9	42.6	35.5	1.4	0.8	13.4	
22 June-3 July	86-87		26.1	39.1	23.3			11.0	61.7
6-17 July	88-89		29.6	44.1	13.2	1.4		8.5	
20-31 July	90-91		27.2	43.7	10.1			8.5	82.5
17-28 August	94-95								90.4
31 Aug.-11 Sept.	96-97				4.1			7.3	
14-25 September	98-99							2.4	
28 Sept.-9 Oct.	100-101				3.0				
12-23 October	102-103								93.6

[a] Densities for Richmond Ford Plant for weeks 14-33 are capture-recapture estimates rather than minimum numbers.
[b] Beginning of Richmond Ford Plant introduction experiment.

same density as the Control but was cropped intensively after the first trapping. I was unable to hold this population down by intensive cropping. A very high immigration rate, particularly of adult mice, more than offset the cropping. For example, 107 adults were removed from this two acre field between 1-5 April 1963, and two weeks later 115 adults were caught, only 20 of which were tagged residents. A total of 1758 *Microtus* were removed from this field between November 1962 and November 1963. In spite of all this removal the Experimental population continued to increase irregularly at a rate only slightly less than the Control. Unfortunately the field could not be fenced to prevent this immigration.

In early June 1963 individual growth rates began

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ing season of the vegetation and was complete before the dry season set in.

RICHMOND FIELD STATION:

Live trapping at the Richmond Field Station (RFS) was begun in late July 1963 when the Parr Field and Ford Plant populations disappeared. I know nothing about the past history of these populations.

The RFS 3 population was already at a high density when we began work there in July 1963. The apparent large increase in density during August on this area is mostly an artifact caused by the first weeks of live trapping a dense population. In September the population reached a plateau of at least 120 per acre, then from early October to mid-February gradually declined at an average rate of 8% per week.

Recruitment began increasing the RFS 3 population in mid-February 1964 and the pattern of change was very similar to that of the Tilden Experimental population, increasing very abruptly during late February and March and then remaining at a plateau during April, May and early June. In June this population began to decrease very rapidly at a nearly uniform rate of 19% per week, in marked contrast to the Tilden Experimental population. By September 1964 only a few individuals remained on the area.

The RFS 4 population was at a low density, 15-20 per acre, when began working this area in August 1963. In mid-September this population suddenly began increasing, and tripled in density in seven weeks during the last part of the dry season. The bulk of this increase consisted of 35 adult immigrants. Where these immigrants came from is not known; only two were marked individuals from RFS 3 even though this area seemed to be the only local source of such large numbers of mice. This population reached a peak of 60-70 per acre in late October, and just as abruptly began declining when the vegetation began to grow. This decline continued for six months from November to April at a more or less regular rate of 9% per week. The population recovered slightly in late April and early May by the influx of eight marked immigrants from RFS 6, but then continued its decline to a very low density by July.

The RFS 5 population was sparse in August 1963 when this area was first trapped. Although the area was trapped regularly from August to December scarcely any *Microtus* were caught (maximum of two in any one trapping). The population increased to about 5 per acre in January and February, then increased during March and April to a peak of 15-20 per acre in late April. It then declined during May and June at a rapid rate so that by the end of June only one *Microtus* could be caught on the area.

The population changes in the RFS 6 population have been discussed in detail elsewhere (Krebs and DeLong, 1965). This population was supplied with supplemental food in the form of oats from 21 October 1963 onward, and in addition the vegetation on the north half of the grid was fertilized on 14 January 1964 with SN/10P fertilizer at 400 pounds per acre. The initial increase in November is largely due to immigration from the RFS 4 grid. From December to February only slight population growth occurred, but the population rose abruptly in March to a peak in early April around 100 per acre. It then declined rapidly through the rest of the spring and summer, dropping about 13% per week, to a very low density in September 1964. The pattern of population change on this area strongly resembles that found on the RFS 4 area five months earlier.

Every one of the four areas live trapped on the Richmond Field Station showed a different sequence of population changes. The only attribute they shared was in all being at a very low density at the end of the study period.

REPRODUCTION

Reproduction can only be measured indirectly in a live trapping program and this restricts one's interpretation of the results. The characteristics of the external reproductive structures are not always assessed unambiguously and there is some overlap in all the classifications. Nevertheless substantial changes in reproductive rates should show up clearly in the condition of these external indicators, and I shall concentrate here only on major reproductive changes.

LENGTH OF BREEDING SEASON

Breeding was already in full progress when work began on the Parr Field and Tilden Park grids in November 1962. Consequently we cannot pinpoint the start of breeding on these areas except to remark that breeding must have begun several weeks before the autumn rains, which began on 9 October, since young mice 4-6 weeks old were already present on these areas in November.

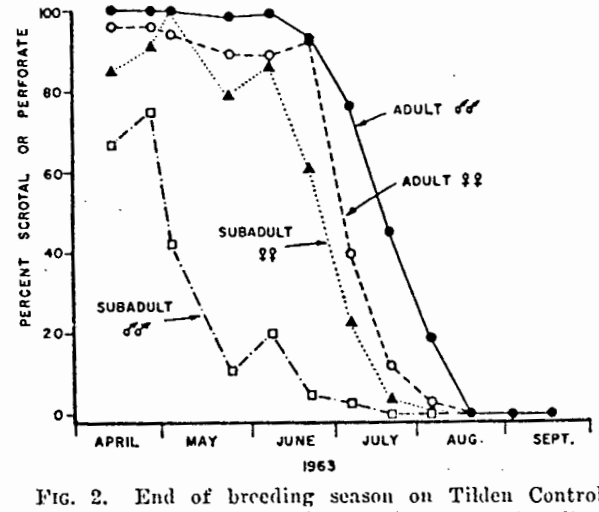

FIG. 2. End of breeding season on Tilden Control area in 1963. Subadults (26-39 g) stopped breeding earlier than adults (≧40 g), particularly in males.

KREBS (1966)

The end of the breeding season varies with the age-group considered (Fig. 2), at least in the males. The subadult males (26-39 g group) went out of breeding condition about 6-12 weeks ahead of the adult males. This difference between subadults and adults was slight in the females.

The end of the 1962-3 breeding season was simultaneous in the males from the Parr Field, Tilden Control, and Tilden Experimental areas. The subadult males stopped breeding in May and June and the adults in July. In the females there appear to be slight differences between the Richmond Parr Field which stopped in early July, the Tilden Control which stopped in mid-July, and the Tilden Experimental which stopped in early August. These slight differences appear in both subadult and adult females.

There was considerable variation in the onset of the 1963-4 breeding season both among sex and age groups and among different areas. Males on the Tilden Control area responded to the mid-October rains by beinning to breed in early November (Fig. 3), but on the adjacent Tilden Experimental area males did not begin breeding until late December. Little difference occurred between the females on these Tilden areas: both began breeding in numbers only in late December. The Richmond Field Station grids behaved differently. On RFS 3 and RFS 6 intensive breeding began in both males and females in early November, three to four weeks after the first rains. There was a small amount of breeding throughout August and September on RFS 3. RFS 4 was unique in having continuous breeding throughout the dry season from August to October, although only a few individuals were involved.

The onset of the effective breeding season can also be measured by the date the first juveniles appear in the live traps. On RFS 3, RFS 4, and RFS 6 this occurred from 11-22 November 1963, whereas on the two Tilden grids it occurred on 17-21 February 1964. If we allow six weeks from conception to reaching trappable size, then some females on the Richmond Field Station must have conceived just at or shortly after the first October rains, while Tilden Park females did not conceive until early January, some 13 weeks after the first autumn rains. The August and September breeding activity on RFS 4 apparently did not produce any recruits to this population.

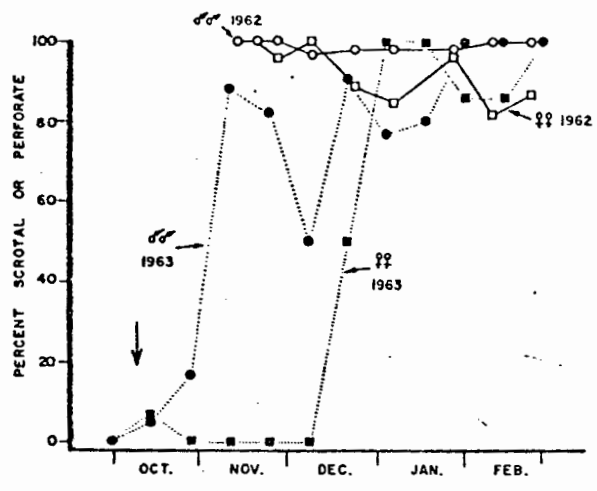

FIG. 3. Beginning of breeding season on Tilden Control in fall 1962 and 1963. Note the delayed onset of breeding particularly in females during the 1963 decline. Breeding must have begun at least six weeks before the first 1962 observations were made. Vertical arrow marks the onset of autumn rains in both years.

The end of the 1963-4 breeding season was also variable. On the two Tilden Park grids there was still a considerable amount of breeding going on at the end of the study in late July, but breeding was definitely falling off. Subadults males on these areas seemed to stop breeding in late June. Breeding definitely stopped earlier on the Richmond Field Station areas: on RFS 3 and RFS 6 breeding had stopped almost entirely by late June, at least 4-6 weeks ahead of Tilden Park. Subadult males on these Richmond areas stopped breeding in May or early June. In contrast the Richmond Ford Plant population, which was rapidly expanding, did not finish the main breeding season until late July, similar to Tilden Park.

There are thus large differences in the onset and cessation of the breeding season in the California vole. The Tilden populations which had begun breeding in the dry season in 1962 did not start breeding until late December 1963, some ten weeks after the first autumn rains. The breeding season seemed to stop slightly earlier in populations which were declining (Parr Field, 1963; RFS 3 and RFS 6, 1964) than in increasing populations (Tilden, 1963; Ford Plant, 1964).

INTENSITY OF BREEDING

The intensity of breeding on an area can be measured indirectly by various external sexual characteristics. I shall assume here that large changes in these reproductive measures are an indication of significant changes in either litter size, pregnancy rate, prenatal mortality, or age at sexual maturity. Any conclusions from these indirect measures must be made subject to a later direct test by autopsy methods.

In the California vole breeding begins each fall or winter, quickly reaches a plateau, and remains there until the following spring or summer when it falls off very rapidly. To estimate the average level or intensity of this plateau I have summed all the separate weekly observations over the entire breeding season. The same time limits were used for all grids to avoid possible seasonal effects; this means that some data must be discarded because voles on one area were still breeding while they had stopped on others (e.g. Tilden areas, July 1964). Only on one area (Parr Field, see below) could any definite trend be detected during this period. Extreme variability occurred on some areas with small samples.

ELTON (1942)

tend to apply for help. And we may assume a thoroughness of organization that has always been an attribute of the staffs of German governments. Then the maps do not stand alone: they are supported by the detailed reports already mentioned. Finally, the whole series of observations was in charge of the same man.

The 1914 report was followed by several more that brought the published story up to the end of 1916. Besides the maps and descriptions, Hiltner provides certain statistics. The most useful are the numbers of consignments of counter-vole materials of all kinds (poisons, cultures, and so on) sent out to the infested areas. Comparison with the maps shows that the dots on them represent these figures, and therefore that each unit was a particular place, not just a particular parcel (for several might have gone to one place). Assuming that there was something like a uniform demand in proportion to the vole damage each year, the figures illustrate (though they do not exactly define) the changes in damage and therefore in concentration of voles. With this thought in mind we shall not attribute too much importance to small differences in the figures shown in Table 3.

TABLE 3

Periodicity of vole plagues in Bavaria from 1902 to 1916 (autumn situation)

The figures in the main part of the table represent the number of consignments of anti-vole materials of all kinds sent out in the second half of each year by the Agrikulturbotanische Anstalt of Munich. For 1902–4 Hiltner's notes have been converted roughly into symbols: + means serious outbreaks, (+) means locally serious, — means none or comparatively few.

		N. Bavaria				*S. Bavaria*				
Year	*Pfalz*	*Unter-franken*	*Mittel-franken*	*Ober-franken*	*Ober-pfalz*	*Schwaben*	*Ober-bayern*	*Nieder-bayern*	*Total (omitting Pfalz)*	*Total*
1902	+	+	—	—	—	+	+	—	..	..
1903	—	—	+	—	+	+	+	+	+	..
1904	—	(+)	—	—	—	(+)	(+)	—	..	..
1905	76	7	2	5	3	15	59	12	103	179
1906	0	5	5	0	11	19	61	16	117	117
1907	11	207	138	12	81	106	159	138	841	852
1908	24	6	4	3	13	11	73	47	157	181
1909	141	4	2	0	3	6	25	2	42	183
1910	38	115	112	41	59	197	268	111	903	941
1911	15	14	96	31	93	83	170	215	702	717
1912	34	9	5	7	4	21	111	6	163	197
1913	23	42	17	. 5	8	18	101	· 7	198	221
1914	17	5	19	16	77	29	151	113	410	427
1915	47	43	45	18	16	96	175	54	447	494
1916	8	78	16	3	5	30	189	13	334	342

It is necessary to look only for the major trends. In this table only the figures for the second half of the year are given: the others are in Hiltner's reports, but the autumn situation (at the end of the breeding cycle) gives

TABLE 2. VOLE OUTBREAKS IN FRANCE, 1900–35

		1900	1901	1902	1903	1904	1905	1906	1907	1908	1909	1910	1911	1912	1913	1914	1915	1916	1917	1918	1919	1920	1921	1922	1923	1924	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	193
TOTAL		..	..	..	12	21	4	4	5	0	13	5	7	26	38	9	..	6	1	16	18	8	21	6	15	2	19	24	31	25	8	9	10	1	1	4	..
Ain	4	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	×	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..
Aisne	15	..	..	..	×	×	..	..	×	×	×	×	×	×	×	..	..	..	..	×	×	..	×	..	..	..	..	..	×	×	..	..	..	×	..	..	..
Allier	2	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Ardennes	12	..	..	..	..	×	..	..	..	..	..	..	..	×	×	..	..	..	..	..	×	×	×	..	..	..	×	×	×	×	..	×	×	..	..	..	..
Aube	11	..	..	..	..	×	..	..	..	..	..	..	..	×	..	..	..	..	..	×	×	..	×	×	×	..	×	..	×	×	..	..	..	..	×	..	..
Averon	1	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	×	..
Bas Rhin	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	×	×	..	..	..	..	..
Calvados	13	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	×	..	×	×	..	×	..	×	..	×	×	×	×	×	..	..	..	..	..	..
Cantal	2	..	..	..	..	..	..	..	..	..	×	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Charente	8	..	..	..	×	×	×	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	×	..	..	×	×	×	..	..	..	..	..	..	..
Charente-Inférieure	12	..	..	..	×	×	×	..	..	..	×	..	..	×	×	×	..	..	..	..	..	..	×	..	×	..	..	×	×	×	..	..	..	..	..	..	..
Cher	6	..	..	..	..	..	..	..	..	..	..	..	..	×	×	/	,	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Corrèze	1	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Côte-d'Or	10	..	..	..	..	×	..	..	×	..	..	..	..	×	..	..	..	..	..	×	..	..	×	×	..	..	..	×	×	×	×	..	..	..	..	..	..
Deux-Sèvres	9	..	..	..	×	×	..	..	..	..	..	..	..	×	×	×	..	..	..	..	..	..	..	..	..	..	..	×	×	×	×	..	..	..	..	..	..
Doubs	3	..	..	..	..	..	..	..	..	..	×	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Drôme	1	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..
Eure	12	..	..	..	..	..	..	..	..	..	×	..	..	×	×	..	..	..	..	..	..	..	×	×	×	×	×	×	×	×	..	×	..	..	..	..	..
Eure-et-Loire	13	..	..	..	×	×	..	..	×	..	×	×	×	..	×	..	..	..	×	..	×	..	..	..	..	..	..	..	×	×	..	..	..	..	..	×	..
Gironde	3	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..
Haute-Loire	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..
Haute-Marne	10	..	..	..	×	×	..	..	×	..	..	..	..	×	×	..	..	..	..	×	..	..	×	×	..	×	..	×	..	..	..	..	..	..	..	..	..
Haut Rhin	5	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Haute-Saône	6	..	..	..	..	×	..	..	..	..	..	..	..	×	×	..	..	×	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Haute-Savoie	2	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	×	..	..	..	..	..	..	×	×	×	..	..	×	..	..	..	..
Indre	8	..	..	..	..	..	..	..	..	..	×	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	×	×	..	..	..	..	..
Indre-et-Loire	3	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	×	×	..	×	×	..	..	..
Isère	10	..	..	..	..	..	..	..	..	..	×	..	..	..	×	..	..	..	..	×	×	×	×	..	..	..	..	..	..	×	..	..	..	..	..	..	..
Jura	11	..	..	..	×	×	..	..	..	×	×	..	..	×	×	..	..	..	..	..	×	×	×	..	..	..	..	×	×	×	..	..	..	..	..	..	..
Loir-et-Cher	9	..	..	..	..	..	..	..	×	×	..	×	..	..	..	..	..	..	..	..	×	..	×	..	×	..	..	×	×	×	×	×	..	×	..	..	..
Loiret	13	..	..	..	×	×	..	×	..	..	..	×	×	..	..	..	..	..	..	..	×	..	×	..	..	..	..	×	×	×	..	..	..	..	..	..	..
Lozère	2	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	×	..
Maine-et-Loire	7	..	..	..	..	×	×	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	×	×	×	×	..	×	×	..	..
Marne	16	..	..	..	×	×	..	..	..	..	..	..	..	×	×	×	..	..	..	×	×	×	×	..	×	..	×	×	×	×	..	..	..	..	..	×	..
Meurthe et Moselle	7	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	×	..	×	×	..	..	..	×	..	..	..	..	..	..	..	..	..	..
Meuse	11	..	..	..	..	×	..	..	..	..	..	..	..	×	×	..	..	..	..	×	..	×	×	..	×	..	×	..	×	×	×	..	..	..	..	..	..
Moselle	4	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	×	×	..	..	..	..	..	..	..
Nièvre	1	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..
Nord	6	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	×	..	×	×	..	..	..	..	×	×	..	×	×	..	..	..	..
Oise	11	..	..	..	..	..	..	..	..	..	..	..	×	..	×	..	..	×	..	×	×	..	×	×	..	..	..	..	×	×	..	×	×	..	..	..	..
Orne	1	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	×	×	..	..	..	..	..
Pas-de-Calais	5	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..
Puy-de-Dôme	10	..	..	..	..	×	..	..	..	..	×	..	..	..	×	×	..	×	..	×	×	..	..	..	..	..	..	×	×	×	..	..	..	..	..	..	..
Saône-et-Loire	2	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..
Savoie	4	..	..	..	..	..	×	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	×	×	..	..	..	..
Seine-et-Marne	8	..	..	..	..	×	..	..	..	..	..	×	×	..	×	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..
Seine-et-Oise	10	..	..	..	..	×	..	×	..	×	×	..	×	..	×	..	..	..	..	..	..	..	×	×	×	×	×	×	×	..	..	×	..	..	..	..	..
Seine-Inférieure	9	..	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	×	×	×	×	..	..	..	×	×	×	..	..	×	..	..	..	..
Somme	13	..	..	..	×	..	..	×	..	..	..	..	×	..	×	..	..	..	×	×	×	..	×	..	×	..	..	×	×	×	..	..	..	..	..	..	..
Vendée	8	..	..	..	×	×	..	..	..	..	..	..	..	×	×	×	..	..	..	..	..	..	..	..	..	..	..	×	×	×	..	..	..	..	..	..	..
Vienne	6	..	..	..	×	×	..	..	..	×	..	..	..	..	×	..	..	..	..	..	..	..	×	..	..	..	..	×	..	×	..	..	..	..	..	..	..
Vosges	7	..	..	..	..	..	..	..	..	×	×	..	..	×	×	..	..	×	..	×	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..
Yonne	6	..	..	..	..	..	..	..	..	..	..	..	..	×	×	..	..	..	..	..	..	..	..	..	..	..	..	×	..	..	..	..	..	..	..	..	..
References					10, 26, 43, 52, 57	8a, 42, 10, 22, 45, 56	8a, 12	12	12	12	7, 7a, 12, 64	12, 13, 22	12	12, 15, 19, 49, 53, 59, 60	15, 28, 29, 53, 61	8a, 30		31, 53	See text, p. 22	32	20, 27, 33	21, 34, 53	34, 35, 51, 53	35, 51, 53	1, 36, 51, 53, 55	36, 53, 55	37, 45, 53, 55	8a, 38, 51a. See text p. 22	8a, 38, 30	8a, 30	8a, 40	8a, 41	42	48	8a	8a	

(1942) NO 1.77

summarized the bulk of the historical data on voles and lemmings. Table I gives the peak years for the Norwegian lemming in south Norway for almost 80 years. Peak years tend to recur at three- or four-year intervals. Figure 2 shows fur returns for the arctic fox

TABLE I

Peak years for the Norwegian Lemming in South Norway, 1862–1938.
(After Elton, 1942)

1862–3	1883–4	1906	1930
1866	1887–8	1909–10	1933–4
1868–9	1890–1	1918	1938
1871–2	1894–5	1920	
1875–6	1897	1922–3	
1879–80	1902–3	1926–7	

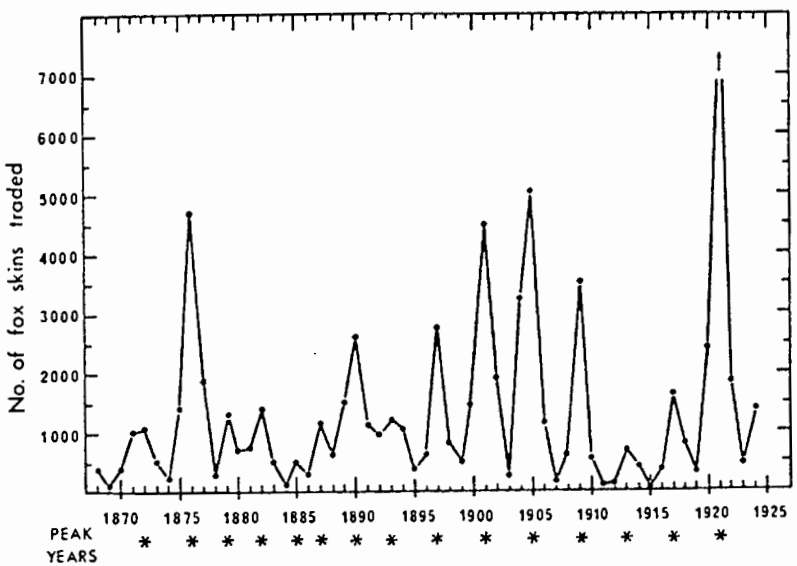

FIG. 2. Fur return statistics for the arctic fox in Ungava District, 1868–1924. (Data from Elton, 1942, pp. 415–416.)

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(*Alopex lagopus*) in Ungava from 1867 to 1924. Fur returns are unreliable indicators of absolute population changes but do tend to reflect the observations of trappers and naturalists (Elton, 1942). These data show a three- or four-year cycle in arctic fox populations, which follow the abundance of lemmings.

Koshkina (1966) reports data from a standard kill-trap census of voles in the boreal forest of the Kola Peninsula (Fig. 3). Thirty years of

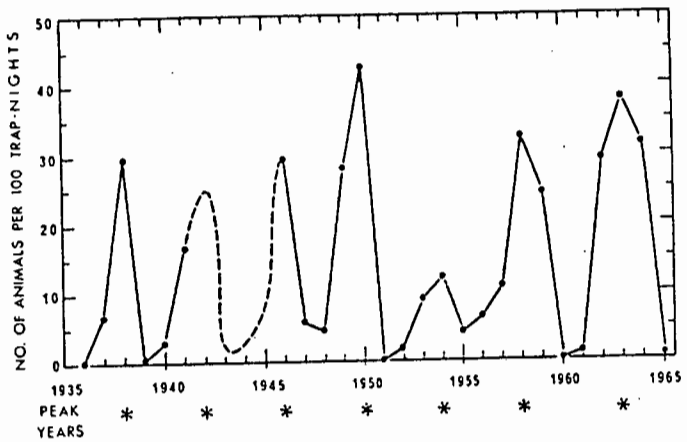

FIG. 3. Autumn population densities in the red-grey vole, *Clethrionomys rufocanus*, from the central Kola Peninsula. (After Koshkina, 1966.)

observations cover seven population cycles with a period of four or five years between peak numbers. These records comprise one of the longest runs of quantitative information on vole numbers. Chitty and Chitty (1962) report population trends in *Microtus agrestis* from Lake Vyrnwy, Wales, from 1932–1960 (Table II). Qualitative assessment of the phase of the population cycle was obtained from a mixture of snap-trapping and live-trapping studies over this 28-year period (except for World War II). Peak populations recur at intervals of four years usually, although three- and five-year cycles were found. Similar observations have been made on the brown lemming at Barrow, Alaska (Fig. 4).

Many other studies of shorter duration could be cited here. There are 18 genera and 105 species of voles and lemmings (Arata, 1967), and perhaps only one-fifth of these species has been studied in depth. We will assume here that the species studied have been representative of the group, and will draw our conclusions from an incomplete sample.

Populations of voles and lemmings thus fluctuate with a period [illegible] four years usually, although two-, five- and

must describe them in detail. At what season does the increase begin? How long is the peak phase? When does the decline begin and how rapid is it? We now attempt to answer some of these questions.

1. Increase phase

The increase phase is defined as a period of large increase in numbers from one spring to the next (Chitty and Chitty, 1962). There are two views on the structure of the increase phase. The increase phase might be a gradual, exponential build-up from low numbers over two or even three years. Koshkina (1966) suggests that the number of *Clethrionomys*

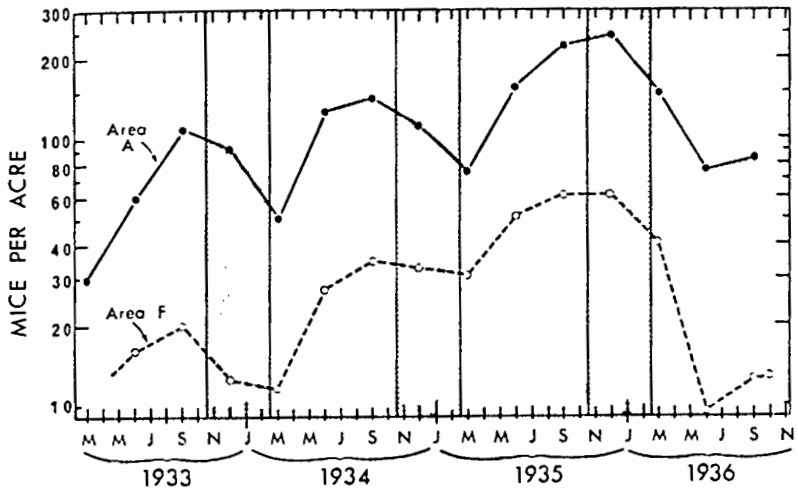

FIG. 5. A population cycle of *Microtus pennsylvanicus* on two areas near Ithaca, New York. Winter months are shaded. (After Hamilton, 1937.)

on the Kola Peninsula gradually increases over three summers to a peak. Pitelka (1958) states that brown lemming cycles in northern Alaska have two successive winters of rapid population growth so that numbers build up gradually over two years. Fuller (1969) found that *Clethrionomys gapperi* and *C. rutilus* in northern Canada increased from an extreme low in 1964 to a peak in 1966. Hamilton (1937) described a population cycle of *Microtus pennsylvanicus* in New York in which the increase occurred gradually over two years (Fig. 5). Populations increased in the summer and dropped back during the winter months, so that the net annual increase was relatively small from 1933 to 1935. Bodenheimer (1949) states that populations of *M. guentheri* in Israel increase gradually over two years to reach a peak.

An alternative view is that the increase phase is a rapid explosion

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which occupies one year or less. Table II shows that a number of populations studied by Chitty and Chitty (1962) went through the increase phase in one year. Our studies of *M. ochrogaster* and *M. pennsylvanicus* in Indiana have provided several examples of rapid increases; Fig. 6 gives one example. We never found in the Indiana *Microtus* a gradual increase of the type Hamilton (1937) observed (cf. Fig. 5). Newson (1963) describes a period of increase in *Clethrionomys glareolus* near Oxford that occupied one year.

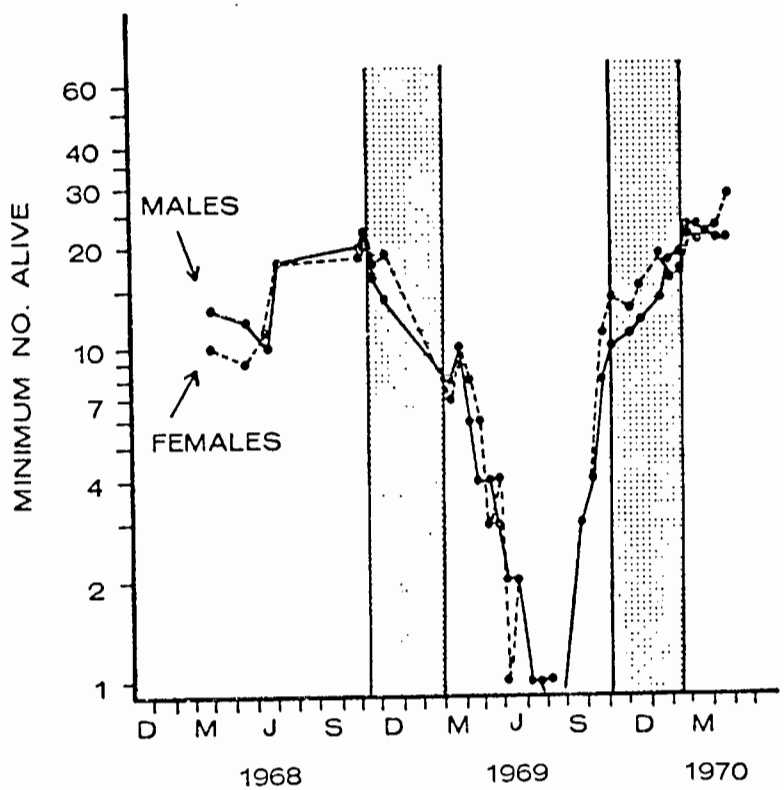

FIG. 6. A decline and subsequent increase in *Microtus ochrogaster* on the Carlson Farm area in southern Indiana. Winter months are shaded. Vertical lines delimit breeding period. (From Myers and Krebs, 1971.)

In Table III we present data on the instantaneous rate of population growth (r) for the increase phase of the population cycle. Data are presented only for populations trapped intensively at monthly intervals (or less); we include some winter estimates derived from an accurate fall sample and a spring sample. Some of the rates of increase in Table III are unusually high. The three high values for *Clethrionomys glareolus*

2. *Peak phase*

The peak phase is defined as a period of little change in numbers from one spring to the next (Chitty and Chitty, 1962). The peak phase is usually obvious, since population densities are typically much higher than they are in other phases of the cycle. Some species, however, do not have a well-defined peak phase. *Microtus californicus* is one example (Fig. 7); *M. ochrogaster* is another (Krebs *et al.*, 1969). In these populations there is typically an increase phase, followed by a brief period of high numbers, and then a decline phase.

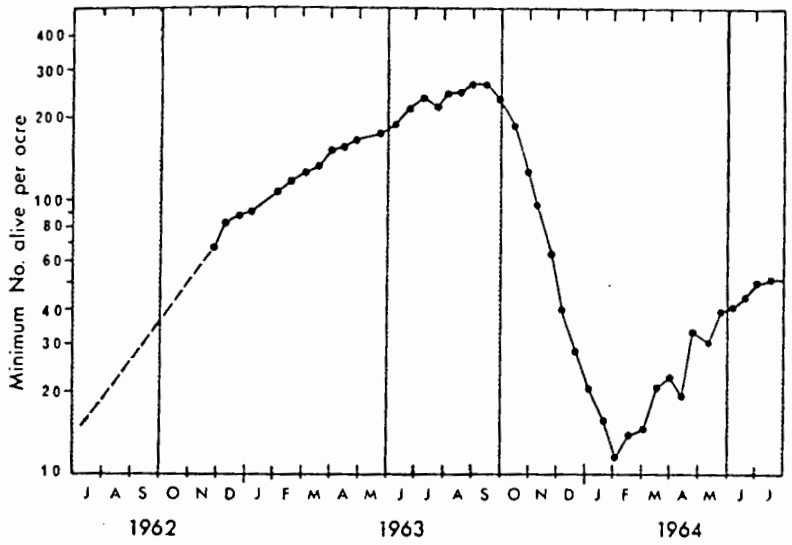

FIG. 7. A population cycle in *Microtus californicus* at Berkeley, California. (After Krebs, 1966, and Pearson, 1971.)

The peak phase in other species is well-defined and may last for a year (or rarely two years). Chitty and Chitty (1962) show that the peak year in *M. agrestis* begins with a spring decline in numbers that may come at slightly different times in the two sexes. This spring decline is followed by a more or less rapid rise in numbers so that in the fall of the peak year numbers are roughly the same as they were in the spring. Thompson (1955a) described a spring decline in the brown lemming during the peak year, and Krebs (1964a) also observed this drop in lemming populations in northern Canada. Figure 8 shows a spring decline in a peak phase of *M. pennsylvanicus* in 1968. In this particular case both males and females declined from February to early May and the population then recovered to high numbers in late summer. Half

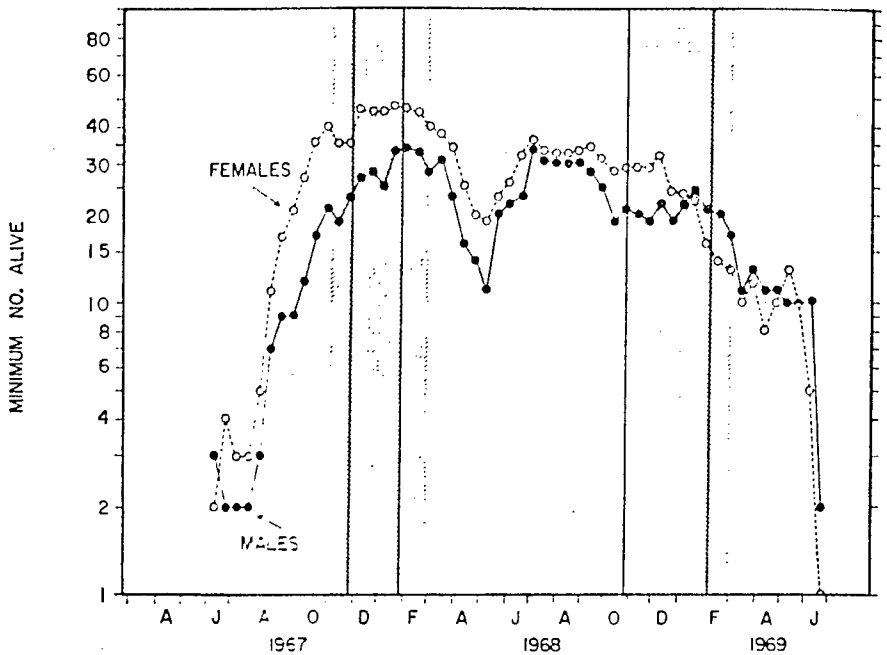

FIG. 8. A population cycle of *Microtus pennsylvanicus* in southern Indiana. (After Gaines and Krebs, 1971.)

of the population may disappear during this spring decline of the peak year.

3. Decline phase

The decline phase of the cycle seems especially variable. Chitty (1955) recognized three types of decline (Fig. 9). The most gradual type of decline is the Type H. Numbers fall gradually over one to two years with some recovery during the breeding season. Type G declines are gradual declines in which there is no recovery during the breeding season; numbers fall over one year or less. Type M declines are "crash" declines in which numbers fall to a low during the winter and early spring after a peak year. Of ten declines studied in *Microtus agrestis*, Chitty and Chitty (1962) classed three as Type M "crashes", four as Type G or intermediate to M and G, and three as Type H declines.

There are few examples in the literature of Type M "crash" declines that have been monitored accurately. Some of the brown lemming declines at Barrow, Alaska, have probably been of this type (see Fig. 4). Zejda (1967) studied a peak and decline of a *Clethrionomys glareolus* population. The population peaked in September 1964, gradually

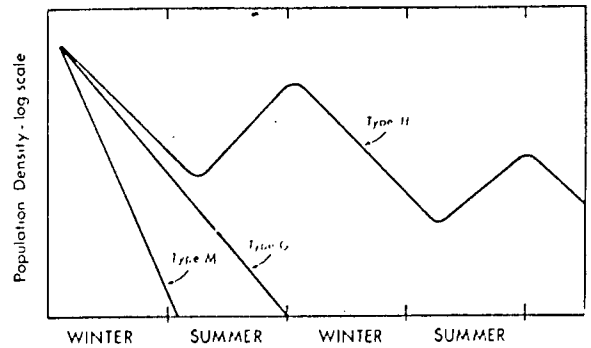

FIG. 9. Hypothetical diagram of the three types of population declines recognised by Chitty (1955).

declined through December, then dropped very rapidly and completely disappeared by mid March 1965. Krebs *et al.* (1969) monitored a population of *Microtus ochrogaster* (Fig. 10) which began declining in October 1966, fell rapidly through December, and then more gradually until completely disappearing by April 1967. A population of *M. californicus* which showed a Type M "crash" in 1963 was studied by Krebs (1966).

The Type G decline in which numbers fall continuously through a breeding season was first described by Godfrey (1955) for two populations of *M. agrestis*. A Type G decline was found in the lemmings *Lemmus trimucronatus* and *Dicrostonyx groenlandicus* in northern Canada by Krebs (1964a). Figure 6 shows a Type G decline in *Microtus ochrogaster* from Indiana. Many of the declines described by Krebs *et al.* (1969) and Gaines and Krebs (1971) for *M. pennsylvanicus* were probably Type G declines since they occurred during the breeding season, but they were followed very quickly by a return to the phase of increase.

Type H declines were first described by Hamilton (1937) for *M. pennsylvanicus*. Figure 7 shows a Type H decline in *M. californicus*. Kalela (1957) studied a population cycle of *Clethrionomys rufocanus* in Finnish Lapland; some recovery of the population was indicated after the initial decline, and hence a Type H decline occurred (Fig. 11). Koshkina (1965) presents data from two declines of *C. rutilus* in the boreal forest of the U.S.S.R.; both declines fit the Type H classification. Gaines and Krebs (1971, p. 709) show a Type H decline for *Microtus ochrogaster* in Indiana.

The recovery of the population during a Type H decline may be substantial, and this has caused much confusion about cyclic fluctuations in the literature. Chitty and Chitty (1962) observed that autumn population densities in *Microtus agrestis* could be nearly equal for

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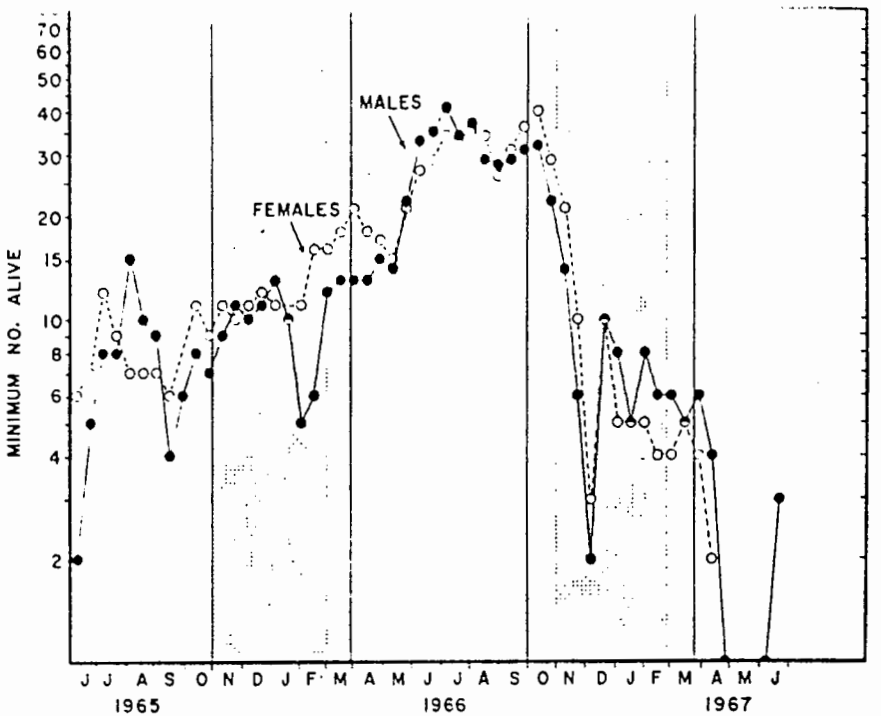

FIG. 10. A population cycle of *Microtus ochrogaster* in southern Indiana. A Type M decline occurred in the fall of 1966. (After Krebs *et al.*, 1969.)

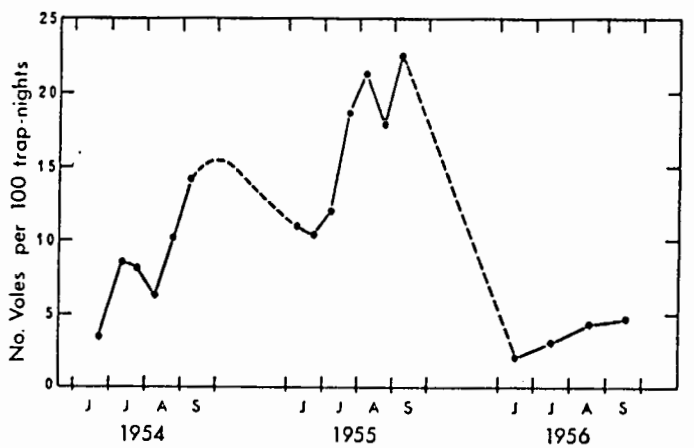

FIG. 11. A population cycle of *Clethrionomys rufocanus* in northern Finland. A Type H decline occurred in 1956. (After Kalela, 1957.)

4. Phase of low numbers

Populations may fall to low numbers and remain there for one to three years, but in some cycles this phase is absent and populations go directly from the decline phase to the increase phase (e.g. Fig. 6). Very little is known about the phase of low numbers in voles or lemmings. Koshkina (1966) suggested that populations of *Clethrionomys rufocanus* on the Kola Peninsula did not have a phase of low numbers but after declining began to increase gradually over two or three years. Norwegian lemming populations on the Kola Peninsula, however, did go through phases of scarcity for several years.

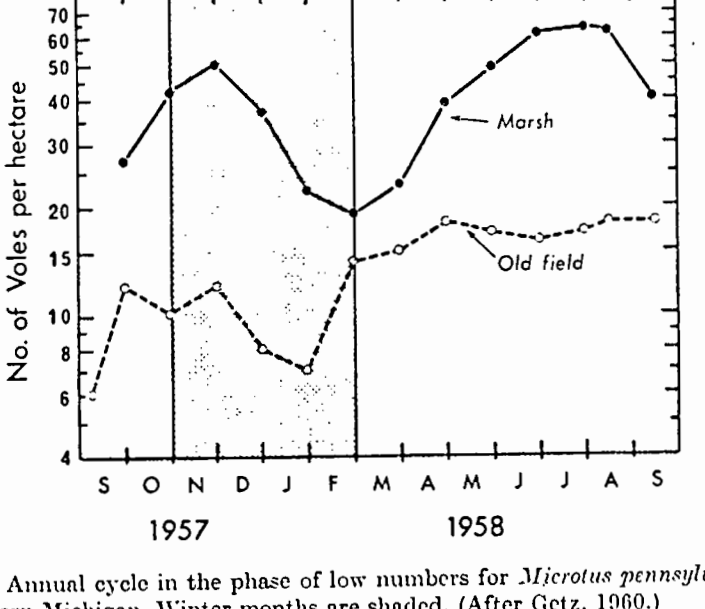

FIG. 12. Annual cycle in the phase of low numbers for *Microtus pennsylvanicus* in southern Michigan. Winter months are shaded. (After Getz, 1960.)

Getz (1960) studied a Michigan population of *Microtus pennsylvanicus* that was apparently in the phase of low numbers (Fig. 12). In both marsh and old field habitats voles showed an annual cycle with little net change in numbers. During the spring and summer increase the population grew at 7% per week, but this was not sustained. Krebs (1966) described a similar sequence in *M. californicus* in the low phase (Fig. 13); numbers rose rapidly for a short time but then fell back during the breeding season to the low density at which they started. We do not have a sufficient number of descriptions of low populations

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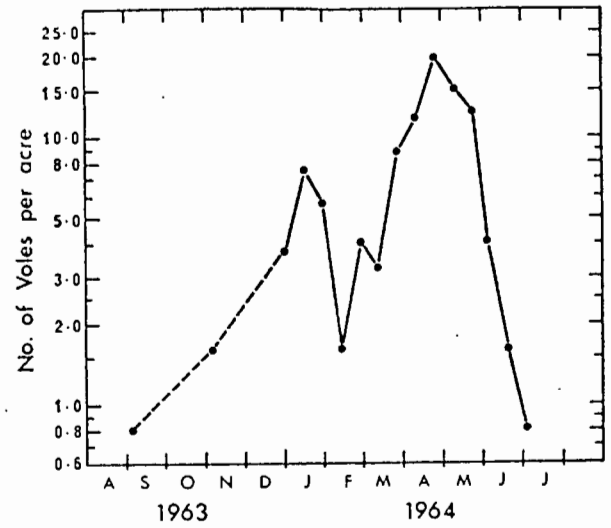


FIG. 13. Annual cycle in the phase of low numbers for *Microtus californicus* at Berkeley, California. (After Krebs, 1966.)

of any vole species to say if the patterns shown in Figs. 12 and 13 are general. Pearson (1963), for example, shows a three-year period of great scarcity in *M. californicus* but his data are not sufficient to determine whether the sequence of density change displayed in Fig. 13 applied to the three years.

Until there are more data on the phase of low numbers we will not be able to distinguish two quite different interpretations of this phase:

1. that the population declines to a level below our accuracy of measurement and then begins to grow geometrically back to the next peak; the early stages of this geometric growth we call the "phase of low numbers" but such a name reflects more our inability to measure changes in low density populations than the biological reality;
2. that the population declines and remains low for a long period: brief spurts of population growth may occur but numbers quickly fall back to a low level; this "start-stop" type of population curve persists until the phase of increase occurs, and the net population

MYERS & KREBS (1971b)

Holes 3 cm in diameter in alternating ends of metal separators permitted the vole to go from one level to the next in a zig-zag manner. A clear plastic door covered the front of the maze. A vole which entered the maze could walk to the opposite end where a hole led to the next level. By traversing back and forth he could go up as many of the 24 levels as he chose. Voles were left in the maze for 2 nights with a laboratory light schedule approximating that in nature at the time. The extent of a vole's exploratory activity was recorded by the disturbance of small pieces of paper placed across the holes between levels such that they would be pushed aside if the vole went through the hole. The number of levels explored was recorded for each vole tested. The mazes were cleaned with soap and water after each use and the cages after several uses.

RESULTS

Relation of dispersal to population density

The first question to be investigated in a study of dispersal is whether dispersal is directly related to population density. If behavioral interactions leading to dispersal are important, then it is likely that the amount of movement from a population will be a function of the quality as well as the quantity of individuals making up the population. However, if dispersal is simply a means of draining off excess animals, close correlation between the amount of dispersal and population density is expected.

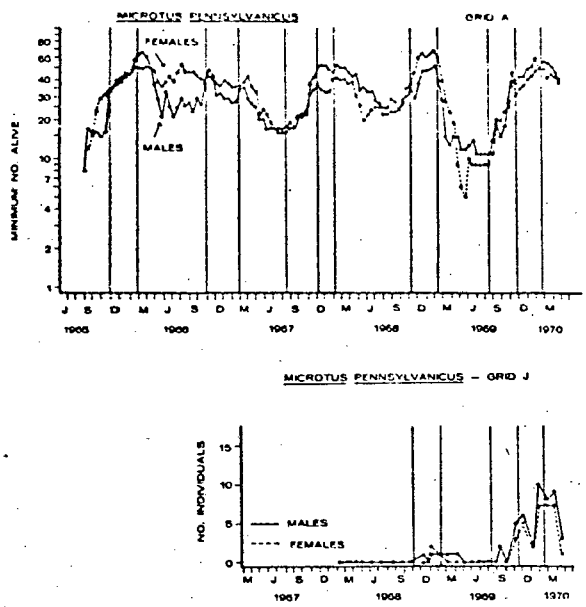


FIG. 2. Population changes of *Microtus pennsylvanicus* on control grid A and experimental grid J. Densities for grid J are the totals for two trapping periods except when no animals were caught in one of the trapping periods. Vertical lines mark divisions between "summer" and "winter" breeding periods. Winter months (November to February) are shaded.

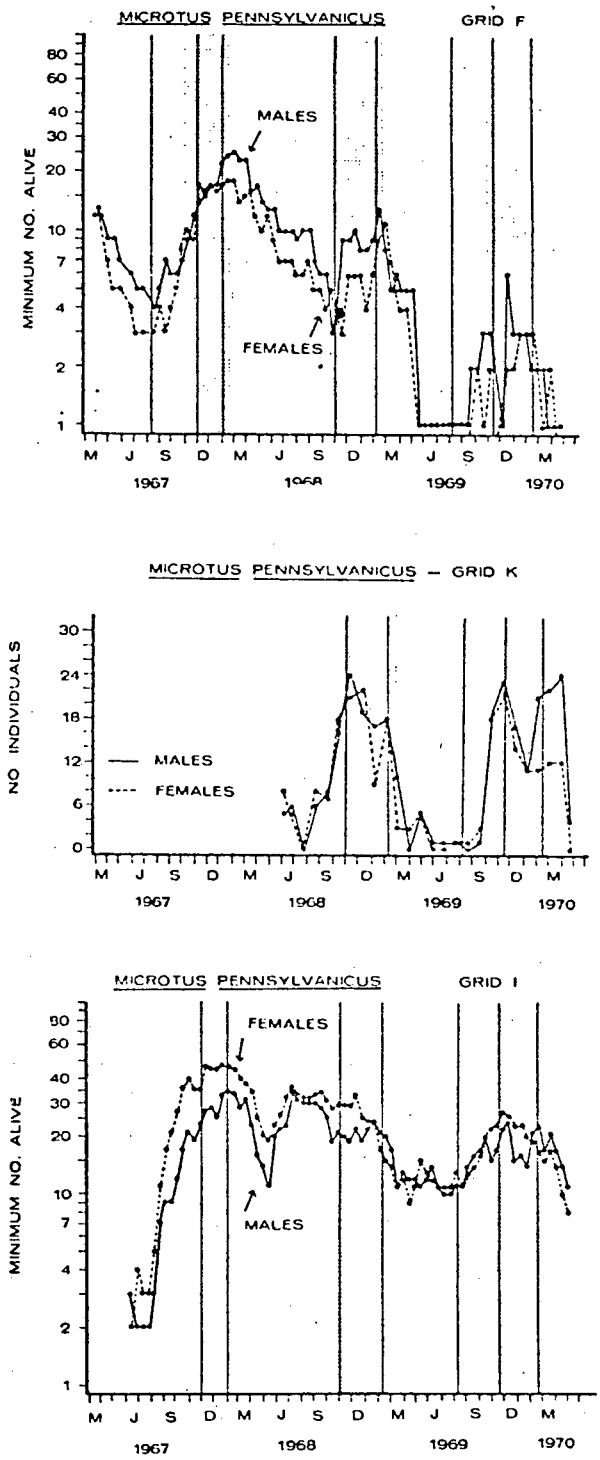
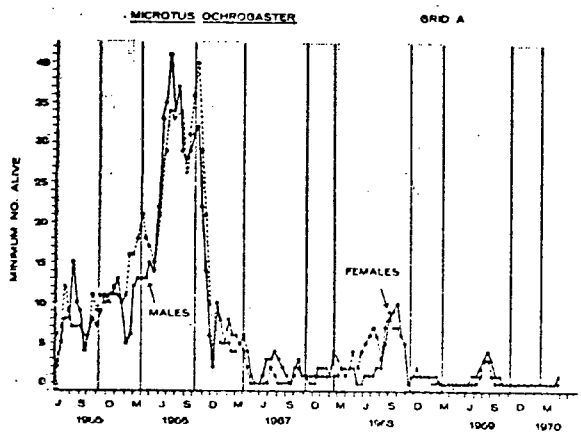


FIG. 3. Population changes of *Microtus pennsylvanicus* on control grids F and I and experimental grid K. Densities for grid K are the totals for two trapping periods except when no animals were caught in one of the trapping periods.

Microtus pennsylvanicus.—The dispersal patterns of *Microtus pennsylvanicus* on experimental grid J and control grid A were compared (Fig. 2). In the summer and early fall of 1968, while control pop-

MYERS & KREBS (1971b)



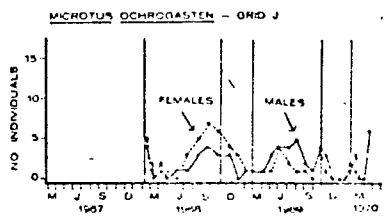


FIG. 5. Population changes of *Microtus ochrogaster* on control grid A and experimental grid J. Densities for grid J are the totals for two trapping periods except when no animals were caught in one of the trapping periods.

dispersing animals, whereas the population on grid F was an actively reproducing resident population, at least during the first part of the study.

The origin of the *Microtus ochrogaster* moving into the study area in the spring of 1970 remains a mystery. The population of *M. ochrogaster* at the Carlson Farm 4.8 km (3 miles) south of the main study area was at high density at this time. It is assumed that other populations of *M. ochrogaster* in the vicinity were increasing or at high densities and that these were the source of the dispersing animals.

In summary, the analysis of the relationship of dispersal and population density in *Microtus ochrogaster* is confounded by the low densities of nearby "resident" populations. The lack of significant correlation of the number of voles moving into the vacant grid K and the density on grid F, which had the highest population of *M. ochrogaster* of the three control grids on the Kent Farm study area, is an indication that, as in *M. pennsylvanicus*, dispersal is probably not directly related to density of the resident population.

Dispersal and survival

Throughout the study the survival of animals resident on control grids was followed. Since a number of animals that were tagged in control populations dispersed and were removed later from experimental areas, the proportion of loss that was due to dispersal could be calculated. For each seasonal period the

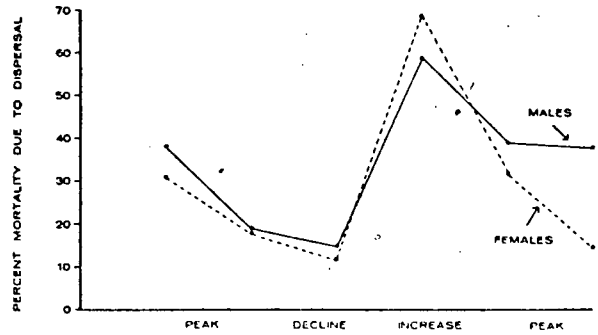


FIG. 6. Percentage of loss known to have been due to dispersal for control populations of *Microtus pennsylvanicus* on grids F and I. Populations declined in the summer of 1969 and increased in the fall of that year.

number of animals lost from control populations was tallied, as was the number which was caught later on an experimental area. For each period the proportion of mortality that was due to known dispersal could be calculated. The data for *Microtus pennsylvanicus* on grids F and I showed the same trends and so were combined (Fig. 6). Known dispersal accounts for the greatest proportion of the losses in control populations during the increase phase of the population cycle. During the population decline, when survival was low in control populations, only a small proportion of the disappearing animals were captured on grid K. Only during the increase period was there a number of animals leaving grid A that were later caught on experimental grid J. The proportion of animals known to have dispersed from grid A is lower than that on grids F and I but, even so, approximately a third of the mortality measured on grid A during this period can be accounted for by dispersal (males = 0.33 and females = 0.27). The control grid A and experimental grid J are approximately 200 m apart and fenced grids partially separate them, so movement between the areas is not direct. All together 41% of male and 30% of female losses in all control populations could be accounted for by known dispersal.

Very few data of this sort are available for *Microtus ochrogaster*. However, the greatest population density was reached in the first period of the study, and during this time 33% of the male mortality in the control population on grid F could be accounted for by dispersal to grid K whereas only 8% of that of females could be accounted for in this way. Over the complete study 24% of the mortality of male *M. ochrogaster* on grid F could be accounted for by dispersal, but only 6% of that of females was known to be due to dispersal.

Whether vacant areas "attract" dispersers is not known. However, the change in proportion of mortality which was known to have been due to dispersal in *Microtus pennsylvanicus* over the cycle should not

CONCLUSION

'Dynamics' is related to force and movement and hence to change. Population dynamics is, therefore, about changes in populations and the study of the reasons for those changes. The study of the stability and instability of populations has for many years been one of the central themes of ecologists. Do animals maintain a stable equilibrium density and if so, how? Southern (1979) has pointed out that ecologists may be divided into two camps, depending on whether they are more impressed with the stability or instability of animal populations. He cites David Lack (1954b, 1966) as a champion of the theory that the numbers of animals are regulated by density-dependent mortality factors - those whose impact tends to cancel any departure from an equilibrium level upwards or downwards. This contrasts with the view of Elton (1927) who thought that animal populations did not remain stable for long and that many species suffered violent fluctuations.

This study has demonstrated marked changes in the density of the fieldmouse, R.pumilio, both from season to season and from year to year. Furthermore, despite five years continuous fieldwork we are not able to say that we have observed the highest or lowest densities that the species could experience. From the point of view of the population biologist, these fluctuations invite the question: "what determines the population peak, i.e. what prevents unlimited increase; and what determines the lowest density, i.e. what

prevents decline to extinction?"

We cannot answer either of these questions satisfactorily, but to take the second (slightly easier) question first, the data presented in this study seem to show that mongoose predation could have had a significant impact on the field-mouse population and could have been responsible for the winter decline in numbers. What determines the minimum density of R.pumilio is possibly related to the number of predators hunting in a given area. The more predators, the lower will the mouse density be reduced. One can suppose that as the mouse density falls so the effort required by a mongoose to catch one mouse increases, until the mouse population is so sparse that the energy expended by the mongoose is greater than the return from its food. At this stage, the mice are immune from further predation. The data on mongoose density obtained in this study were too inadequate to test this hypothesis. A more intensive effort to measure the density of carnivores in a given area, over a longer period of time, combined with careful monitoring of their diet and simultaneous livetrapping of the prey population would be necessary for this purpose.

The first question, as to what prevents indefinite population increase, is more difficult to answer. The fact that the observed peak population in different years of this study showed such lack of stability does not immediately suggest some kind of intrinsic regulation by social behaviour - since that would suggest a more stable level of population density.

It was shown that the reproductive potential of R.pumilio was very far from being realised since females seemed to produce far fewer young per breeding season than their theoretical capability. This suggests an extrinsic agent of control.

In contrast to the situation in R.pumilio is the case of the wood mouse in Wytham Woods, Oxford (Watts, 1969, cited by Southern, 1979). Southern points out that numbers of wood mice tended to level off at about the same density in winter (December) each year, though the events during the rest of the year could follow different courses. However, though various explanations were set forth to explain the events of the rest of the year, there was a conspicuous absence of any explanation as to what determined the constant density each winter. What factor prevents further population increase? This is surely the question requiring an answer?

Nobody has satisfactorily answered this question for any natural population, so far as I am aware. Since food is the ultimate limiting factor, among a complex of ecological factors, it seems logical to start with an investigation of food supply. Although natural food supply was investigated in this study, it seems that it would have been necessary to do so over a longer period, in conjunction with observed changes in the R.pumilio population, and also to investigate a wider spectrum of the food items of R.pumilio than just Acacia seed, before a connection might be demonstrated between mouse density and food availability. In

view of the increasing number of recent studies which have demonstrated the connection between forage quality and animal numbers, e.g. Sinclair (1974, 1975); Cole & Batzli (1978, 1979) this line of research currently seems especially appealing.

In particular, I would suggest that the hypothesis of White (1978) merits testing. He says that animals live in a variably inadequate environment wherein many are born but few survive. The single most important factor limiting their abundance is a relative shortage of nitrogenous food for the very young. Most young animals cannot obtain enough of this food to maintain their very rapid growth. In this regard, White suggests that weather may be important more often than is immediately obvious, because variation in the weather (especially of the amount of rainfall) seems to be the major factor influencing the amount and nutritional quality of the food available for herbivores. We should, therefore, at least be prepared to rigorously test the hypothesis that it is some kind of relative food shortage which affects the survival of young rodents and hence produces the remarkable changes in abundance observed in nature.

In this connection it is interesting that in this study the season of poorest R.pumilio reproduction and lowest peak density (1973/74) followed the driest year of the study (1973) when rainfall was little more than half the normal mean value (Table 1). The following year (1974) rainfall more than doubled and the subsequent breeding season of

1974/75 was the most successful and resulted in the highest population peak of the study. This suggests interesting and challenging avenues for future research.

SUMMARY

In view of the fact that the long-term study of small mammal populations in southern Africa has been largely neglected, this project was an attempt to document more accurately than has hitherto been the case in Africa, the population changes in a small rodent, the striped fieldmouse, Rhabdomys pumilio, over a relatively long period of time. It was felt that the usual field study of one or two years duration was insufficient to obtain reliable data on demographic parameters. This was because it was important to document the variability of population data and to have as large sample sizes as possible. The fieldmouse is an omnivore but mainly granivorous and the habitat chosen was favourable for the mice, being dominated by thickets of alien Acacia cyclops and A.saligna, which provided abundant food (seeds) all year round, as well as cover and shade.

The study was conducted on the Cape Flats, an area of low-lying sand dunes, on the banks of the Kuils River. Live-trapping grids were established, consisting of parallel rows of trap stations, 10m apart. The overall size of the study area was 2,55ha with a total of 156 stations. This comprised a central control grid of 60 stations (0,45ha), which was first trapped in April 1972 and where regular monthly trapping for 4 consecutive days and nights was conducted from July 1972 through May 1977. This was surrounded on three sides by peripheral grid K of 96 stations arranged in three parallel rows (see Fig. 2). Trapping was conducted in

grid K from February 1975 through February 1976 in an attempt to detect dispersal of mice from the control grid. From March 1976 through May 1977 trapping was conducted in a third grid, experimental grid E, which was established in the north side of the old grid K. It comprised 60 stations (0,44ha), in which supplementary food was supplied in the form of commercial rat pellets. The effects of the extra food on the population of mice were compared with the control grid. The mice were readily captured in box-type aluminium Sherman livetraps and all mice caught were marked by toe-clipping and released. A total of 2281 R.pumilio were marked and released during the five year study. In addition, over 860 specimens of R.pumilio were killtrapped for autopsy in the laboratory. These yielded information on reproduction, food habits and morphological characteristics - particularly skulls for age determination by tooth wear.

The results of five years livetrapping at monthly intervals showed that the population was in a constant state of flux, either increasing or declining (Fig. 3). The graph of numbers revealed both a regular annual cycle and an irregular interannual fluctuation. The annual cycle was related to breeding and amounted to the fact that the population increased during the 6 - 8 month summer breeding season and declined steadily during the non-breeding winter months. The peak in numbers was reached at the end of summer, usually in March each year and the population was at its lowest density in spring, just before the start of the new breeding season. The interannual variation recorded the

fact that neither the peak nor the trough in population density was the same for two years running - there were considerable fluctuations in maximum and minimum population density from year to year. The extreme case monitored in this study was the contrast between 1974 and 1975, when throughout the latter year population density was three to four times what it was in 1974. The highest density recorded was about 238 R.pumilio per ha in 1975 and the lowest about 10 per ha in 1976. The area used for these density calculations was the control grid area plus a border strip (total 0,7ha). The peak biomass of R.pumilio ranged from 2,5 kg/ha in 1974 to 9,4 kg/ha in 1975.

The study of home range was not an integral part of this study but analysis of recapture locations showed that the mean distance between successive recaptures was 8,6m. This indicated a small home range. Johnson (1980) found a mean home range size of about 500m^2. The longest distance recorded between points in the same home range was about 70m and the longest movement recorded for mice which had moved off the study area was 300m.

Using the skulls of known-age mice up to 16 months old, Henschel (1977) was able to identify 8 age classes on the basis of tooth eruption and wear. In the field the only criterion available for age determination was the body mass of the mice. Mice of up to 30g could be aged reasonably accurately, but beyond that the variation in body masses introduced serious inaccuracies.

R.pumilio weighs 2,5 - 3,0g at birth. Growth in the field was plotted from birth. This revealed that the initial growth of females in summer, up to 30g body mass was significantly faster than that of males. Females reached 30g in an average time of 49,5 days, whereas males took 61 days. Thereafter, growth evened out so that both sexes reached a mass of 40g in 122 - 124 days.

Males more than four months old weighed an average of at least 47g (class 5) and the heaviest male ever livetrapped weighed 78g. Female weights are complicated by pregnancy but in July month, when no females were pregnant, males were significantly heavier than females (males 39,5g; females 33,6g). During winter, conditions for growth are much less favourable than in summer. Nevertheless, adults maintain their weight and the young grow slowly.

There was a long breeding season which commenced in September (spring) and ended in April (fall), but the most important breeding months were October to March, when about 75% of mature females were pregnant or lactating. Breeding took place in the dry summer months, with little rainfall (Fig. 13). There was no breeding in the four winter months with high rainfall. Females became sexually mature at a weight of 26 - 31g when they were aged 6 - 7 weeks and males at 35 - 40g when they were 11½ weeks old or more. Judged from the mass of the testes and seminal vesicles, males appeared to be most reproductively active from September through February. At least 78 - 90% of young females born early in

the breeding season bred in the same season unless they were under six weeks old at the end of March, in which case they overwintered in the non-parous state. The proportion of young males which attained sexual maturity in the season of their birth was lower than that of females (43 - 75%). Mean litter size of 145 litters was 4,9 embryos per litter, range 2 to 9. Multiparous females (5,1 embryos per litter) had significantly larger litters than young primiparous females (4,4 embryos per litter). There was a significant correlation of litter size with body mass (Fig. 22). Heavier females tended to have larger litters. There was little difference in the mean litter size from year to year but the largest litters were in 1974/75 - the year of peak density. Pregnancy rate was also significantly higher that year than in the other years of the study. There were no significant differences in the length of the breeding season from year to year. The mean gestation period was 25,5 days and since there was a post partum oestrus it was theoretically possible for a female to produce about 7 litters in a complete breeding season, provided she survived the whole season. The actual production was found to be from 1,3 to 2,3 litters per season per female, with an overall mean of 2,0 litters per season. The lifetime production of very old females was found to be about 4 litters. These figures were based on counts of uterine scars. There appeared to be heavy mortality of the nestlings, since the overall number of young weaned per pregnancy was 2,13 representing about 58% mortality. The number of young weaned per pregnancy in different years of the study varied from 1,5 to 4,0.

The sex ratio of the mice was estimated in two ways: (1) residents - from the proportions of males and females alive in the population at any instant and (2) recruits - from accumulating the numbers of new recruits (unmarked mice) each trapping session over a long period. Among residents there was a deficiency of males (45 - 48% males), whereas among new recruits there was a significant excess of adult males, but approximate equality among the juveniles. Females were captured for significantly longer than males. When translated into survivorship curves, these data revealed a longer expectation of life after first capture for females than for males. It is believed that the greater survival of females was the most important factor explaining the excess of females among the residents. The excess of adult males among the recruits, on the other hand, was believed to be caused by differential trappability of adult males. This was apparently due to pregnant and lactating females tending to avoid the traps. The sex ratio at birth was 47,1% males (N = 27 litters), which was not statistically significant.

Mortality was estimated in two ways: (1) survival after first capture, and (2) survival from birth. Survival is the complement of mortality. Survival after first capture was measured from the number of months that mice were captured in livetraps. The majority of mice (42 - 47%) were caught for only one month. 'Survivorship' curves (i.e. residency curves) were prepared. Females were caught for significantly longer than males ($p < 0,001$). The mean expectation of life from first capture was only 1,9 months

for males (maximum 13 months) and 2,5 months for females (maximum 15 months) taken over the whole study. There were relatively big changes in this parameter in different years. There is a serious source of error in this parameter, in that mice which are no longer caught are assumed to be dead - whereas they may merely have dispersed elsewhere.

Survival from birth was assessed from the number of young weighing under 20g livetrapped each month, compared with the number of heavily pregnant females one month previously. The longest lifespan recorded in the field was for 2 females which were about 19 months old. The mean expectation of life at birth was only 1,65 months for females and 1,52 months for males. These low values were chiefly due to the high nestling mortality of about 58%. There was considerable variation in nestling mortality from year to year. This correlated well with high population growth rate in 1974/75 and low growth in 1975/76 but not in the other years of the study. The very high population growth in 1976/77 could not be readily explained on the basis of any of the available parameters.

Immigrants into the study area were assessed from the number of new heavy adults (> 40g) caught in the control grid each month. The object was to distinguish genuine immigrants from mice which had been present in the study area all the time, but which had merely avoided capture. This, in turn, was to distinguish immigrants from mice which had been born

in situ. The analysis appeared to show that immigration was a continuous influence throughout the year. An average of about 25% of new mice caught each month was probably immigrants (range 23 - 34% each year).

Dispersal of marked mice from the control grid was studied by livetrapping in peripheral grid K. This was an attempt to solve the problem of whether mice which disappeared from the control grid were really dead (as assumed) or whether they might merely have moved elsewhere. Mice originally marked in the control grid were only defined as dispersers if their last recorded capture was in grid K and they had no recapture history of home range overlap with both grids. The majority of mice which moved from one grid to the other in fact simply had home ranges which overlapped both grids. Of 477 mice which disappeared from the control between February 1975 and February 1976, only 8% were identified as having dispersed on to grid K. This indicates quite a low level of dispersal which, in turn, substantiates the view that mice which disappear are dead. However, doubt still exists about this since during the same period immigration was measured at about 25%. Immigration and emigration are normally assumed to approximately balance. Hence, in this case either the method of measuring dispersal was inadequate, or else the study area was being colonised from elsewhere. Due to the great practical difficulties involved, it seems inevitable that there were inaccuracies in the measurement of dispersal. However, analysis of recaptures showed that about 40% of mice released each month had dis-

appeared by the following month. If one accepts that this is too high a proportion to have emigrated then it follows that some mortality factor must have been in operation. Since the autopsy of over 800 specimens yielded very rare symptoms of disease, it was considered that the most likely mortality agents were starvation and predation.

Analysis of stomach contents had shown that the diet of R.pumilio was primarily Acacia seeds. In most months, these comprised around 50% of the stomach contents, with a range from 27 - 81%. Green vegetation comprising epidermis, leaf and stem was usually second in importance, and in some winter months was the most important item. The supply of Acacia seed on the study area was assessed for a period of 16 months: (a) by sampling seedfall by means of plastic bags placed under the trees, and (b) by sampling the seeds available in the leaf litter by means of $0,25m^2$ quadrats. Measurements showed that ripe seeds fell from December to April and that abundant seeds were available in the leaf litter throughout the year. However, there was a distinct decline in the quantity of seed available in the litter during the winter and spring. The daily seed consumption of R.pumilio was calculated from experiments with captive mice. It appeared that in some months the mice in the study area could have eaten 19 - 40% of the seeds available in the leaf litter. Thus, although no food shortage was apparent during this study, it seems possible that, should the Acacia seed crop fail, a food shortage could develop.

The experimental approach to the investigation of food shortage is to supply additional food on an experimental area and to compare the effects on the population with a control. Supplementary food of high quality, in the form of commercial rat pellets, was supplied for 15 months on a grid (grid E) the same size as the control and adjacent to it. The results were ambiguous. Nevertheless, the experimental population did seem to show some response to the additional food. Although numbers on grid E declined during winter 1976, they always remained well above those on the control, and the population size at the end of the breeding season 1976 - 77 was 50% higher than on the control. The total biomass and mean body mass of mice on grid E was significantly heavier than on the control. There appeared to be preferential immigration into grid E, since about 42% more new mice were caught there than on the control. There was a significantly higher proportion of breeding females and breeding appeared to start earlier on the food grid, since one juvenile was caught there in August and four in September, whereas juveniles did not appear on the control until October. Conversely, both survival after first capture and survival from birth were worse on the food grid - more young per female were weaned on the control grid.

If predation was an important factor in the winter decline in population size each year, then one would not expect the provision of extra food to prevent it - unless the prey were actually weak and starving. The last mortality factor investigated was, therefore, predation. The Cape grey mon-

goose was the only common diurnal mammal predator (up to 1kg body mass). Between 0,6 and 2,3 mongooses were livetrapped per month, on average, in the study area. Data gathered on mongoose home range, from livetrapping, were inadequate but it was assumed that home ranges were not less than 1,5ha in area and that individual home ranges overlapped. An adult male mongoose kept in captivity in a large outdoor cage required about 40g of food per day, wet weight, to maintain its body mass. This amount agreed well with theoretical calculations of the energy requirements of a mammal of that weight. Analysis of mongoose scats showed that rodent hair was present in 72% of 316 scats and constituted the main item in 61%. By far the most abundant species was R.pumilio which occurred in 50% of the scats and was the main item in 42%. It was calculated that in the wild an adult mongoose could consume 23 - 44 mice per month, assuming that mice made up about half the diet. The higher figure would be the requirements of lactating females. The mean number of mice which disappeared per month from the combined control and food grids lay between 24 - 68 mice (area 1,1ha). It, therefore, appeared that from one to two mongooses active in the area could have been responsible for all the mice which disappeared. It is, therefore, suggested that the winter decline in numbers of mice each year was due to mongoose predation. However, since the density of R.pumilio observed in this study never fell below 10 mice/ha and since low density never lasted longer than one or two months and numbers of the fieldmice began to increase in the spring each year, it did not appear that mongoose predation was

exerting any control over the R.pumilio population. In particular, it appeared that predation could not maintain the population at low density, nor could it prevent increase of the mice once breeding began.

The fluctuations in density of R.pumilio documented in this study suggested comparison with the fluctuations of Microtus spp. which are thought to undergo regular periodic cycles of 3 - 4 year duration in the norther Hemisphere. Analysis of the fluctuations of R.pumilio showed them to be annual in character and analysis of the published cycles of microtines threw extreme doubt on the accepted interpretation of a periodicity of 3 - 4 years. I believe that an annual cycle of increase during the breeding season and decline during the non-breeding season will be found to be the best interpretation of most of the so-called periodic cycles.

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Acacia seed samples for me and Muffy Seiderer performed the bomb calorimetry for the energy values of *R.pumilio*. Dr. G. McClachlan of the South African Museum kindly identified various reptile remains for me in mongoose scats. Chris Stuart of Department of Nature Conservation, Robertson, sent me some special bait for attracting mongooses, which was much appreciated. Many people over the years, both students and staff, have helped with various aspects of the fieldwork for this project and I am grateful to them all, but I must make special mention of Kate Davies who, through her energetic work in the first half of 1975, greatly assisted in the investigation of dispersal. Grid K is named after her. Special thanks also go to Ann Gedye who prepared the figures. Last, but not least, I would like to thank my typist, Janet Longman, who has speedily, efficiently and with good humour set this dissertation into presentable form.

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* Original not seen.