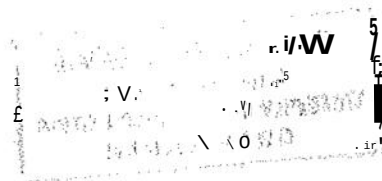


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THE ECOLOGY OF **PRAOMYS ALBIPES** (RUPPELL, 1842)
IN THE MENAGESHA STATE FOREST, ETHIOPIA

A THESIS SUBMITTED TO THE UNIVERSITY OF
MANCHESTER FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY
IN THE FACULTY OF SCIENCE

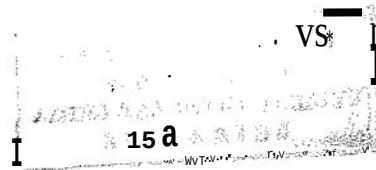
1994



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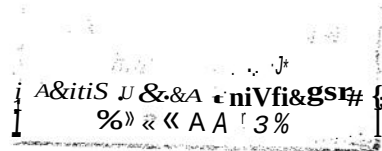
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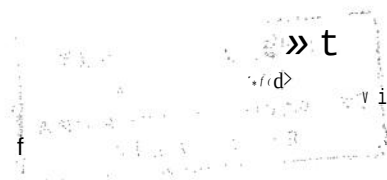


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ABSTRACT

The composition, abundance and distribution of the rodent fauna in the Menagesha State Forest, Ethiopia was investigated with particular emphasis on the ecology of the endemic **Praomys albipes**. Both snap and live-trapping surveys were conducted to assess the species composition, activity patterns, reproduction, embryo sizes, weight and feeding habits of **P.albipes**.

The snap-trapping surveys from November 1991 to July 1993 at different vegetation zones revealed the following rodents: **Praomys albipes**, **Pelomys harringtoni**, **Lophuromys flavopunctatus**, **Mus mahomet**, **Arvicanthis dembeensis**, **Rattus rattus**, **Otomys typus**, **Stenocephalemys griseicauda** and **Dendromus mystacalis**. A total of 293 rodents were captured during the snap-trapping surveys. **P.albipes** comprised 54.3% of the total catch followed by **Pelomys harringtoni** (15.4%), **L.flavopunctatus** (11.2%) and **M.mahomet** (10.9%). The remaining five species comprised only 8.2%.

P.albipes and **L.flavopunctatus** were distributed within an altitudinal range from 2200-3300m asl, occurring in bush, forest and **Erica** scrub. **Pelomys harringtoni** and **M.mahomet** were common in **Erica** scrub and bushy vegetation respectively. **P.albipes** is exclusively nocturnal. From snap-trapping, live-trapping and captive breeding programmes, reproductively active males with scrotal testes were observed throughout the year and the testes, once scrotal, remained so throughout life. Females breed

throughout the year with a peak at the beginning of the dry season (November). The number of embryos ranged from 2-8. Adult scrotal males and pregnant females weighed above 50g, subadults 30-39 and young ones below 29g. A steady increase in head and body length was recorded up to 40g. Analysis of diet from the stomach contents showed that berries and green leaves formed the largest proportion.

The density of rodents was assessed by conducting bimonthly live-trapping in a 1ha grid from May 1992 to July 1993. The following six species of rodents were recorded: **P.albipes**, **M.mahomet**, **L.flavopunctatus**, **O.typus**, **Pelomys harringtoni** and **Graphiurus murinus**. **P.albipes** comprised 64.3%, **M.mahomet** 24.3% and **L.flavopunctatus** 6.1%. The remaining three species comprised only 5.1% of the total. The total number of rodents observed on the live-trapping grid decreased towards the last trapping occasions. The monthly biomass ranged from 454-1546g with **P.albipes** contributing the largest sum. Recruitment of young or subadults was very low throughout the study period. More individuals were captured at the edge of the grid than at the centre, and forest blocks both at the edge and centre captured significantly more rodents than either the shrub or the grass blocks. Duration of residence for females was higher than for males. The mean home range length for females was 29.2m while for males, it was 65.3m. Males wandered about more than females.

Estimates of **P.albipes** population were obtained using direct enumeration, Hayne's, Fisher & Ford's, Jolly-Seber's and du Feu's methods.

From laboratory bred **P.albipes**, litter size ranged from 2-6 young with the mean weight of 3.0g at birth. The minimum conception and gestation time was 80 and 23 days respectively. A high rate of increase in weight was recorded in both males and females up to ten weeks while increase in size of ear and hindfoot was obtained up to nine weeks. The young are born naked and blind, with ear pinnae folded and toes fused. In the laboratory, **P.albipes** consumed almost all the berries and green leaves supplied from the wild.

I, Afework Bekele, declare that no portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

This thesis is dedicated to my wife, ZAP, for her continuous encouragement in initiating this research. Without her moral support, I could not have been in a position to commence and finalize this work.

PREFACE

After completing my first degree at Addis Ababa University (the then Haile Selassie I University) in 1972, I was employed as a graduate assistant in the Department of Biology, Addis Ababa University. I did my M.Sc. by research in the Department of Zoology, University of Manchester, from 1978-80 on the comparative functional morphology of jaw and cervical muscles in two rodent species. In 1980, I returned to Ethiopia to resume my teaching duties in Addis Ababa University. I have published papers on the distribution and taxonomy of some Ethiopian rodents. I have also participated in a number of symposia in India, Italy and the U.S.A. Besides my teaching profession, I have served as director of the Zoological Natural History Museum, Department of Biology, Addis Ababa University. At present, I am an instructor of vertebrate zoology and conservation courses in the Department of Biology, Addis Ababa University, Ethiopia.



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INTRODUCTION

The main purpose of my thesis is to investigate the ecology of **Praomys albipes**. This is an endemic rodent confined to the forests of Ethiopia. Relatively little work has been carried out on this rodent species as compared to the related species in other African countries.

Among the mammals of Africa, rodents are the most ubiquitous and numerous. Because of their diversity and overlap of characters, there has been no absolute agreement on their classification among mammalogists. The genera and species assigned to each grouping have been mostly controversial. This is especially true in the case of the species assigned in the genus **Praomys**. Based upon the similarity of cusp patterns on the cheek teeth, Ellerman (1941) lumped **Aethomys**, **Mastomys**, **Praomys**, **Thallomys**, **Myomyscus** and **Hylomyscus** under the genus **Rattus**. Later on, Matthey (1966), based upon chromosomal studies, removed the other genera from the **Rattus** complex. Davis (1965) grouped **Mastomys** as a subgenus of **Praomys** and tentatively assigned **Praomys fumatus** and **P. albipes** to the subgenus **Myomyscus**. Misonne (1971) grouped **Myomyscus**, **Mastomys** and **Hylomyscus** under the African soft-furred rats, genus **Praomys**. This classification was followed by Kingdon (1974), Delany (1975) and Honacki et al., (1982), but Rosevear (1969), Skinner & Smithers (1990), Nowak (1991) and Wilson & Reeder (1993) gave separate generic status

to each of these subgenera. Even then, the number of species assigned to the genus was not uniform. Nowak (1991) named eight species of **Praomys** across Africa with no mention of the distribution of any species in Ethiopia. Wilson & Reeder (1993) named 9 species in the genus **Praomys** but grouped **Praomys albipes** under **Myomys** as listed by Allen (1939); they also questioned the validity of the species they listed and indicated the urgent need for a careful systematic revision.

In order to overcome the problem of uncertain taxonomy, some of the species were lumped together temporarily pending further studies. One of these was the "natalensis-complex". This has been named successively as **Rattus natalensis**, **Praomys natalensis**, **Praomys (Mastomys) natalensis** and more recently as **Mastomys natalensis**.

An attempt to identify species in the "natalensis-complex" group on a karyotypic basis was carried out by Petter (1977) for West African sympatric multimammate rats. **Mastomys erythroleucus** has $2N=38$ and is mostly brown-coloured dorsally and grey-white ventrally. **Mastomys huberti** has $2N=32$ and is predominantly grey on both dorsal and ventral sides. Duplantier *et al.*, (1990, 1993) compared the genetic variability of **Mastomys** from Senegal using protein electrophoresis and recognized the three species as **M.erythroleucus**, **M.huberti** and **M.cf.natalensis**. The brief abstract of the paper given by Leirs *et al.*, (1993a) from

karyological studies on Tanzanian **Mastomys** shows all **M.natalensis** to have $2N=32$. Cytogenetic examination of the Zimbabwe **Mastomys natalensis** complex resulted in the recognition of two chromosomally distinct species ($2N=32,36$) occurring sympatrically (Lyons *et al.*, 1977; Gordon, 1978). Further, Lyons *et al.*, (1980) found that the $2N=32$ chromosomal forms from Zimbabwe exhibited a notable structural difference from the West African ones. Green *et al.*, (1980) carried out similar karyotype studies and electrophoresis of haemoglobin and found the same two distinct species occurring in South Africa. The $2N=36$ chromosomal form was assigned to **Mastomys coucha** and the $2N=32$ to **M.natalensis**. Robbins & Straeten (1989) described a new West African **Mastomys** species from Nigeria and Cameroon as **Mastomys verheyeni**. They also supported the naming of the South African forms but disputed the naming of West and Central African ones. They argued that the $2N=38$ specimens from Morocco, Senegal, Sierra Leone, Ivory Coast, Cameroon and Burundi showed distinct craniometric differences from each other. Pelage colours do not distinguish these chromosomal forms because they were collected from diverse habitats of West and Central Africa.

Qumsiyeh *et al.*, (1990) examined the **Praomys/Mastomys** complex by using G- & C-band chromosomal data and found **M.coucha** ($2N=32$), **P.fumatus** ($2N=38$), **P.hildebrandti** ($2N=32$), **P.jacksoni** ($2N=28$), **P.misonnei** ($2N=36$) and **P.cf.tullbergi** ($2N=35$). Their cytogenetic

data showed that there was no support for the dichotomy of **Praomys/Mastomys**, initially based on morphological traits, the similar chromosomal form from eastern Africa (**P.hildebrandti**) was distinct from southern Africa (**M.natalensis**) and there was a close association between **P.jacksoni** and **P.cf.tullbergi**. This was deduced by developing a coding system for the chromosomal characters to find the shortest tree among the autosomal rearrangements. Polyacrylamide gel electrophoresis of liver membrane proteins among the above species showed few differences in protein mobilities. Monoclonal antibodies produced against liver proteins of one species and tested by reactivity of other species confirmed the evolutionary similarity of species of this complex. They then concluded that future identification of species and evolutionary relationships among the African murids should take into account the morphological, chromosomal and immunological studies.

In Ethiopia, the genus **Praomys** used to be represented by the **P.natalensis** group, **P.fumatus** and **P.albipes** (Yalden *et al.*, 1976). Later on, Straeten & Dieterlen (1983) added **P.ruppi** to the list and by using canonical analysis confirmed that **P.albipes** was indeed a distinct species. **P.ruppi** was collected from the southwestern highlands of Ethiopia between altitudes of 2700-3200m. This species is bigger than **P.albipes** with a longer hindfoot and molar toothrow and a narrower interorbital region.

P.fumatus is a dry savanna species distributed across many countries of East and Northeast Africa and also including Arabia. Qumsiyeh **et al.**, (1990) revealed its karyotype, from Kenyan specimens, as $2N=38$. In Ethiopia, **P.fumatus** is confined to the south, where it is a dry country species recorded from 600-1700m. It is smaller in size than the other members of the genus, has a very long tail and is sandy brown dorsally and white beneath. More recently, from western and central parts of the country, **P.(M.)erythroleucus** and **P.(M.)huberti** have been identified from the "natalensis-complex" group using karyology, having $2N=38$ and $2N=32$ respectively (Orlov **et al.**, 1989). These species occur sympatrically in savanna and are common in agricultural fields. Lavrenchenko **et al.**, (1992) reviewed the different chromosomal forms in African multimammate rats and included 6 species in the group. They also used haemoglobin electrophoretic tests to identify the three Ethiopian **Mastomys** species as **M.erythroleucus**, **M.huberti** and **Mastomys** sp.2.

The other distinct species, widespread but confined to a forest habitat, is **Praomys albipes**. This species has a long tail and is larger than **P.fumatus**. It possesses five pairs of mammae and a dark patch on the upper metatarsal region. Karyotypic examination of this endemic species shows $2N=46$ with centromeric heterochromatin and additional heterochromatic arms in the X-chromosomes (Orlov **et al.**, 1989). **P.albipes** is described as the

most widespread and abundant of the Ethiopian rodents next to **Lophuromys flavopunctatus** (Yalden & Largen, 1992). The species occurs widely in the forest proper and at the periphery of forests, between altitudes of 1500 and 3300m. It has also been recorded at 1285masl (Dorst, 1972) and at 820masl in the humid densely-forested region of the southwest (Yalden *et al.*, 1976). Ingersol (1968) has collected the species on the Chercher Mountain ranges of southeast Ethiopia at altitudes of 2000 and 2700m asl.

Even though **P.albipes** is a very widespread and distinct species within Ethiopia, no work has been carried out on its ecology. However, extensive investigations have been conducted on the ecology of the closely related species in different regions of Africa, and, as a background to my studies, a summary account of the ecology of these related species is provided from different regions of Africa.

Among the rodents of tropical Africa, species of the **Praomys** (**Mastomys**) **natalensis** group are the most studied. They are widespread and easily accessible. In addition, their status as pests and reservoir hosts for a number of organisms that cause human diseases (plague, Lassa fever and pathogenic bacteria) have helped to focus attention on these species. Most of these studies concentrate on reproductive parameters. Western, Southern and East African regions are thoroughly covered. The following

paragraphs highlight some of the ecological studies carried out by different investigators on the above and related species on regional basis.

In West Africa, Brambell & Davis (1941) studied *M.erythroleucus* from Sierra Leone and concluded that adult males can be distinguished from immature animals by the weight of both testis and body. Males, once fecund, remained so throughout life and breeding in females was continuous, though there were short gaps during the dry season. Happold (1974, 1975, 1978) in his study of *Praomys tullbergi* from Nigeria described similar patterns of reproduction to its other West African relatives. He also found that the species was the commonest in the forest (83%) and bred throughout the year. In addition, he gave a detailed account of captive breeding for *P.tullbergi*. Hubert (1982) in a study of *M.erythroleucus* from Senegal described the large litter size and high neonatal mortality rate, and found reproduction to be closely related to the rainy season.

In Central Africa, Pirlot (1954) observed a continuation of breeding in *M.natalensis* throughout the dry season in eastern Zaire because of the less marked dry season and more extended rainfall. Dieterlen (1986) studied the 13 species of rodents in lowland rainforest of eastern Zaire and found that *P.jacksoni* was the second most abundant species.

More work on the reproduction, distribution and taxonomy of

Praomys/Mastomys has been conducted in Southern Africa. In South Africa, Oliff (1953) and Johnston & Oliff (1954) studied the multimammate rat in the laboratory. They provided information on longevity, mortality, fecundity, oestrous cycle and gestation period. Coetzee (1965) described the breeding season of the multimammate rat in the wild. Breeding occurred in most of the year with a break during the dry season, and the number of embryos per female was lower during the commencement of the breeding period. Meester & Hallett (1970), and Baker & Meester (1977) discussed reproduction and postnatal development of **M.natalensis** under laboratory conditions. They described the development of young and their mean weight gain; they reported the ability to mature and produce young at 77 days of age. Mass increase was highest from birth until day 5 and the highest mortality occurred during the neonatal period, mostly due to killing by parents. Sheppe (1972) used both snap and live-traps to estimate the population of rodents in a Zambian flood plain and found that **M.natalensis** was the most abundant species. The population was unstable with trap success ranging from 1-75% from dry to wet seasons. Swanepoel (1980) in his comparative study of **M.natalensis** in Zambian wheat fields and natural grassland observed a late summer breeding season in the natural grassland and a winter breeding season in wheat fields, even though the protein content of the diet was adequate for breeding in all

seasons. He speculated that breeding might be associated with the influence of green grassland and insects. Chidumayo (1984) described the populations of the multimammate rats in southern Zambia and found two peaks of abundance in the population - during the rainy season, caused by immigration, and in the early dry season, caused by reproduction. Populations inhabiting unstable habitats fluctuated due to destruction of cover. Bond *et al.*, (1980) surveyed small mammal distribution along an altitudinal gradient in South Africa and found *P.verreauxi* to be restricted to high and mid - elevations, even though fewer of the species were caught in those localities. Happold & Happold (1989, 1990) in their study of montane small mammals in Malawi collected *P.delectorum* in isolated mountain forest but less in scrub and none in woodland savanna.

In East Africa, Chapman *et al.*, (1959) observed large fluctuations in populations of the multimammate rat in Tanzania. Breeding reached a peak during the latter part of the rainy season and declined during the dry season. Delany (1964) surveyed the small mammal composition in different vegetation zones of Uganda and found that *Praomys morio* was frequent in moist montane forest. Delany (1966), in a study of rodents from the higher altitudes of Uganda, again found *P.morio* to be the dominant species in the forest. No insectivores were observed. The vegetation was an evergreen forest associated with *Juniperus*

procera, *Olea chrysophylla*, *Podocarpus gracilior* and *Teclea nobilis*. This vegetation was similar to the present study site - Menagesha Forest. Delany (1971,1975) found that among the 16 species of small mammals caught in Uganda forest, *P.morio* was the most frequent one, although the sample varied in size considerably from month to month. He also stated that both species, *Praomys morio* and *jacksoni* bred throughout the year. Cheesman^e & Delany (1979) made monthly estimates of the density of rodent populations in Ugandan tropical grassland and found that *M.natalensis* was the second most common species, with a mean duration of residence between 2 - 3 months. The live-trapping grid biomass was double that on the intensive removal grids. Neal (1977) studied the breeding biology and demographic pattern of *M.natalensis* and found two breeding seasons related to the bimodal pattern of rainfall. Dry season females were anoestrous and regression of testes was seen in adult males. Males matured earlier than females and litter size declined throughout the breeding season. Neal (1986) discussed the effects of climate, food and other factors on the timing and duration of reproduction in African small mammals and speculated that rainfall and food are the most important factors in maintaining breeding activity. Okia (1973) observed the breeding pattern of *P.morio* in an evergreen forest of southern Uganda. The species showed some form of seasonality in breeding which was related to rainfall.

Southern & Hook (1963) in their study of small mammals collected from Kenya and Uganda observed a high breeding population of *P.morio*. Delany & Roberts (1978) conducted live and snap-trapping in the Kenyan Rift Valley and found a considerable increase in *M.natalensis* during the rainy season, up to fifty fold, while breeding ceased during the later dry season. *Arvicanthis* and *Praomys* made 80% of the catch. Taylor & Green (1976) found that *M.natalensis* bred at the end of the rainy season when seeds and cereals were plentiful. The supply of additional wheat to this Kenyan highland population during the dry season did not induce unseasonal reproduction. They then concluded that the prolongation of the normal rainy season might generate excess food and cover, resulting in the extension of breeding season and consequently high population increase. Field (1975) analysed the stomach contents of *Praomys (Mastomys) natalensis* in Uganda and found that fruit formed an important part of the diet followed by termites, grass leaves and stems. Leirs *et al.*, (1990, 1993b) discussed the seasonal variation in growth and productivity of different generations in *M.natalensis* from Tanzania. They recognized three different generations with different growth stops, survival rates and breeding patterns; these differences were related to population fluctuations and rainfall.

The variation in the topography of Ethiopia, the separation and isolation of the numerous high plateaux have led to the

diversification of mammalian species. So far, 70 species of rodents have been recorded of which 15 are known to be endemic (Hillman, 1993). Most of the studies on small mammals of Ethiopia concentrate on faunal lists and distribution patterns. These have been catalogued by Yalden **et al.**, (1976). Despite the extensive plateaux comprising about 50% of the African highground above 2000m (Yalden, 1983), very little is known on the ecology of the mountain fauna of Ethiopia. So far, only a handful of ecological studies has been carried out on Ethiopian rodents. Müller's (1977) account on population ecology of **Arvicanthis abyssinicus** in the high grasslands of the Simien Mountains National Park describes the annual reproductive cycle, the density and home range of the species. Rupp's (1980) work on the rodents of Ethiopia presents a very wide survey of the distribution and habitat of the rodents collected from western, southern and central parts of the country, with emphasis on altitudinal zonation. **P. albipes** was the most common and widespread species among the rodents collected. More recently, Yalden (1988a,b) and Hutterer & Yalden (1990) have reinforced the above study by surveying high alpine moorland and dense forest in the Bale Mountains National Park, southern Ethiopia. Their study examines the species composition, distribution and altitudinal zonation of the species of small mammals. Collectively, these studies represent a very insignificant fraction when compared to the

diverse fauna of the country or the extensive studies in East and Southern African countries.

Many regions in Africa are not properly investigated and the tropical forests are the most understudied habitats (Delany, 1986). Although tropical forests do not occur widely in Ethiopia, there are still patches of forest blocks in isolated habitats. These patches are the remnants of a once continuous forest on Ethiopian highlands which covered above 37% of the total area. At present, according to the estimate of Ethiopian Mapping Authority (1988), less than 3% of the country is covered with forest. Deforestation in Ethiopia was recognised as a serious issue even a century ago (Pankhurst, 1989).

The highlands of Ethiopia are among the most densely populated agricultural regions of the country. The primitive method of farming followed for centuries, has resulted in habitat degradation at high altitudes (Gottelli & Sillero-Zuberi, 1992). Delany & Happold (1979) also mention the extreme modification of the vegetation over much of the Ethiopian plateaux due to the activities of people. Largen & Rasmussen (1993) stress the deleterious effect of the fast increase in human population and its associated destruction of the natural habitat to provide fuel, timber and cleared land for agriculture or grazing on the abundance and distribution of the flora and fauna of Ethiopia.

At present, the patches of remnant forests are mostly

localized in inaccessible localities. The Menagesha State Forest is one of the most accessible remaining forest habitat blocks in central Ethiopia. This area is part of the central plateau covering an altitudinal range from 2200-3385m asl. It has moreover a well documented history of both disturbance and conservation practices.

The conservation practice and history of the Menagesha State Forest date as far back as at least five centuries. Emperor Zera Yacob (1434 - 1468), realizing how serious was the loss of forest cover on the Wachacha range near Addis Ababa, gave orders to replant the area with seedlings and seeds taken from the nearby central region of Ethiopia. The forest has been protected by Imperial edict since 1600. Emperor Menelik II (1888 - 1912) assigned guards to protect the forest and proclaimed that no one was allowed to cut trees without his approval.

At the end of the nineteenth century, a sawmill was established within the forest by a German entrepreneur that later acted as a major destructive force on the forest. Due to the shortage of fire wood in the capital, Addis Ababa, there was a plan to move the capital to nearby Menagesha Forest (Pankhurst, 1989). Fortunately, the introduction of fast growing eucalyptus trees saved the capital from moving. Prior to the 1974 land reform act, government officials and local owners used to control the area, enhancing the rate of deforestation. In 1981,

the Menagesha Forest was accepted as one of the 13 national forest priority areas to ensure optimum protection of the natural forest and the planting of both indigenous and exotic conifers on degraded areas. The forest at present is managed by the Ministry of Natural Resources, Environmental Protection and Development. It is attended by foresters and guards stationed at Suba.

The Menagesha State Forest is located at about 43km southwest of Addis Ababa, coordinates $38^{\circ}30'$ to $38^{\circ}39'E$ and $08^{\circ}55'$ to $09^{\circ}04'N$. The geology of the area was described by Miller & Mohr (1966) as part of the extinct volcanic dome of Mount Wachacha with variable rock types from white to pale or green prophyritic trachytes. The average age of lava was estimated to be about 4.5 million years. The soils are derived from trachyte rocks and are characterized as dark brown to dark reddish brown with clay to sandy clay loam mixture (Belay Tegene, 1982).

The total area demarcated by the Ministry of Agriculture is 9248 hectares. At present, the natural forest covers about 2500ha. Friis (1992) in his general survey of Ethiopia described seven types of forests and grouped the Menagesha State Forest as one of the undifferentiated Afro-montane forests. These are **Juniperus - Podocarpus** forests with an element of broad-leaved species located on the central plateaux on both sides of the Rift Valley. The floristic composition of the forest was surveyed by

Breitenbach (1962), Breitenbach & Koukal (1962), Gilbert (1970), Henry (1973), Sebsibe Demissew (1980,1989), and Mesfin Tadesse (1992).

The vegetation shows the general pattern of montane zonation though the trees are mixed. At lower elevations (below 2400masl), *Podocarpus falcatus* is more dominant followed by *Juniperus procera* forest at mid-elevations. At about 2800masl, the vegetation abruptly changes to the heather zone and *Helichrysum* followed by more exposed rocks at the top (3385masl). Most of the higher elevation vegetation (*Hypericum lanceolatum*, *Erica arborea*, *Rosa abyssinica* and *Echinops steudineri*) occurs in uninhabitable areas as remnants and secondary growth. This upper zone vegetation has been seriously affected due to cultivation and grazing pressure. At mid-elevation *Juniperus procera* is still the most dominant vegetation of the forest but is shrinking in extent with time. It is highly valued as timber for the construction of houses because it is termite and fungus-resistant (Pohjonen & Pukkala,1992). It also produces a better quality wood. Due to its slow growth, reafforestation of the degraded area has concentrated on fast growing exotic conifers, but the experience of the Sahelian drought has changed the understanding of foresters, who now plant more *Juniperus* seedlings because they are drought-resistant.

To my knowledge, the fauna of the Menagesha State Forest has

not been documented. The present study, therefore, is an attempt to investigate the composition and ecology of the small mammal fauna in the isolated block which makes up the Menagesha State Forest. The study concentrates on the distribution, abundance and species composition of the rodent fauna with emphasis on the endemic ***Praomys albipes***. It compares the distribution pattern in the forest proper with that in nearby disturbed localities. The population dynamics of ***P.albipes*** have been studied in detail by using both snap and live-traps. These are supplemented by a captive breeding programme in order to record the development of young, growth rate, age at maturity, gestation time, longevity, litter size and weight. The study therefore attempts to answer some questions on the relative abundance of ***P.albipes***, patterns of distribution in relation to the vegetation, altitudinal zonation of the species, comparison of breeding seasons and other reproductive parameters both in the wild and laboratory, feeding habits, developmental stages under captive conditions and tries to compare the results with those of the related species in various regions of Africa.

2. MATERIALS AND METHODS

2.1 THE STUDY AREA

The present study was carried out in an isolated forest patch known as the Menagesha State Forest. It is located in central Ethiopia, about 43 km southwest of the capital, Addis Ababa, between longitudes $38^{\circ}30'$ to $38^{\circ}39'$ East and latitudes $08^{\circ}55'$ to $09^{\circ}04'$ North (Fig. 1). This natural forest has been protected by Imperial edict since the 1600s.

The area is part of the volcanic dome of Mt. Wachacha. The elevation extends from 2200 - 3385m asl. As part of the central highlands, the area experiences seven months of rain from March to September, with the highest concentration in July and August (Daniel Gamachu, 1977). The mean annual rainfall is estimated to be 1150mm and the mean annual temperature is from 11- 22°C with lower temperatures at higher altitudes. Informal recordings of mean minimum and maximum temperature are presented in Table 2. Data on rainfall of the forest are not available and have been frequently quoted to be more or less similar to the nearby weather station at Addis Ababa. The present investigator took the initiative in setting up a local station in the forest in collaboration with the station foresters. The two years data (1992-93) on the rainfall of the Menagesha State Forest were compared with the nearest meteorological station, Holeta town and Addis Ababa city, for the years 1981-93 (Table 1). The rainfall

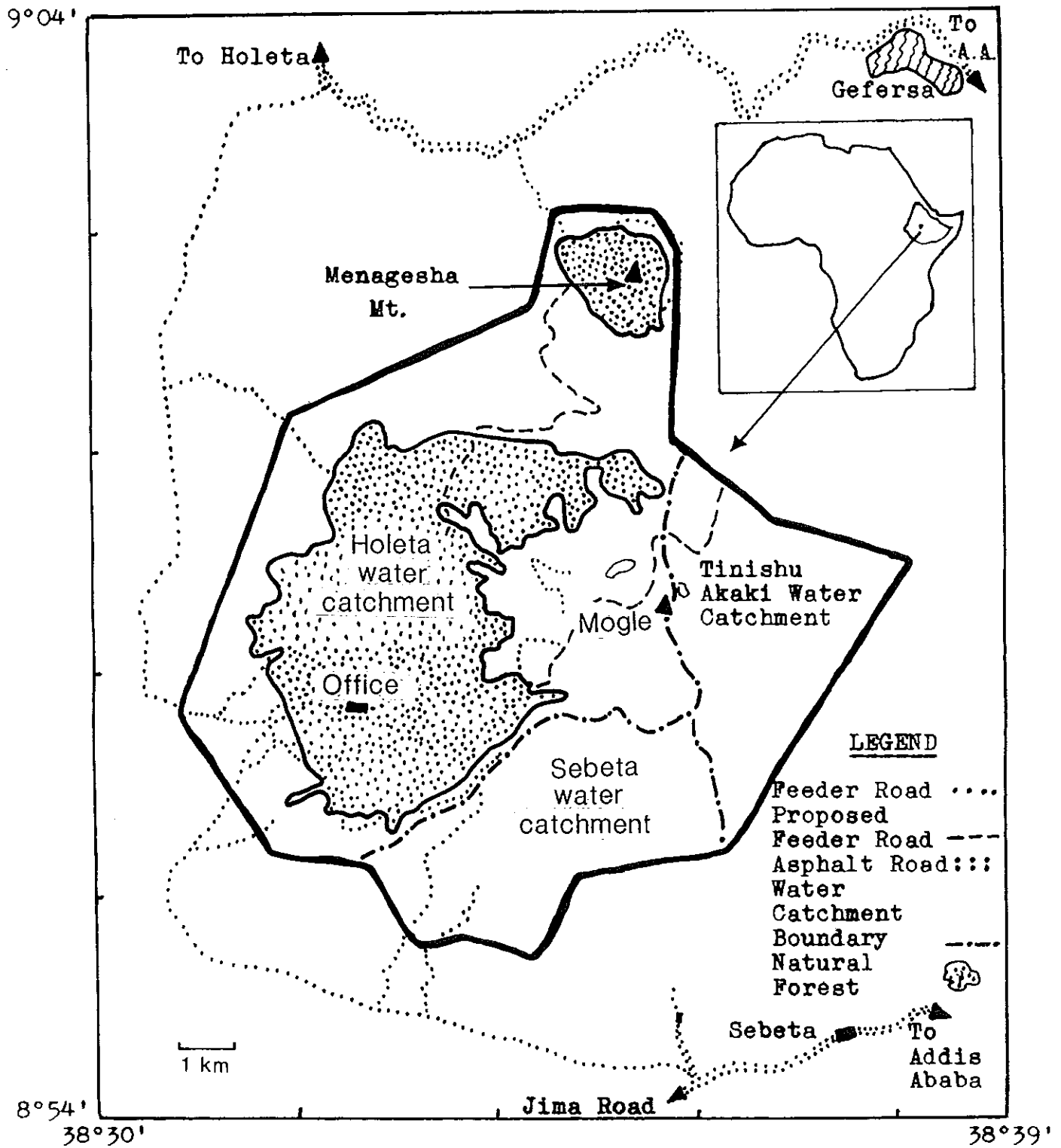


Figure 1. Map of the Menagesha State Forest.

Table 1. Rainfall data (mm) for the Menagesha State Forest (1992-93) compared with the nearest stations of Holeta and Addis Ababa for the years 1981-93.

Month	Menagesha			Holeta	Addis Ababa
	1992	1993	Mean	1981-93	1981-93
January	58.9	14.5	36.7	19.1	9.9
February	60.7	36.7	48.7	54.7	39.1
March	20.7	4.3	12.5	75.1	68.6
April	61.2	111.0	86.1	84.4	110.4
May	48.2	65.6	56.9	78.9	80.1
June	120.2	136.4	128.3	117.5	117.4
July	158.4	231.8	195.1	256.0	230.5
August	411.9	247.8	329.9	306.6	228.7
September	171.4	249.0	210.2	186.9	149.9
October	59.4	39.1	49.3	16.3	27.7
November	1.1	0.0	0.6	5.8	3.9
December	5.1	0.0	2.6	11.0	4.2
Total	1177.2	1136.2	1156.9	1212.3	1070.4

Table 2. Mean minimum and maximum temperature ($^{\circ}\text{C}$) of the Menagesha State Forest compared with the nearby localities of Holeta and Addis Ababa for the years 1992-93.

Menagesha			Holeta		Addis Ababa	
Month	Min.	Max.	Min.	Max.	Min.	Max.
January	12.9	23.2	5.7	22.7	8.5	23.0
February	12.2	23.4	8.0	22.3	9.5	23.4
March	13.1	25.7	6.3	25.0	9.8	26.1
April	13.7	25.9	8.6	23.5	11.1	24.9
May	13.4	25.1	8.2	23.6	10.7	25.0
June	12.4	24.6	8.0	22.1	10.1	23.2
July	11.9	21.7	9.1	19.5	11.4	21.2
August	12.0	21.7	9.6	19.3	11.1	20.4
September	11.1	21.4	7.6	19.5	9.9	21.1
October	11.1	23.3	5.9	21.0	8.2	22.4
November	9.9	23.0	3.1	21.7	5.9	22.6
December	8.9	23.3	2.8	22.6	6.0	23.3

and temperature data for Holeta and Addis Ababa were obtained from the Ethiopian Metreological Services Agency, Addis Ababa.

The Menagesha State Forest is grouped under undifferentiated Afro-montane forest by Friis (1992). *Juniperus procera*, *Podocarpus falcatus* and *Olea europaea* comprise the main vegetation while *Erica arborea* and *Helichrysum odoratissimum* with mountain grasses dominate the upper slopes. The boundary of the Menagesha State Forest was demarcated by the Ministry of Agriculture and covers an area of 9248 hectares (Anon. 1991), but the natural forest proper is estimated to be 2500ha. This figure is roughly one-third of the original size (Tadesse Worku, 1986). In an attempt to reafforest the degraded area, about 1000ha of artificial forest has been established so far. This new plantation is dominated by *Cupressus lusitanica*. The encroachment by farmers for timber, fire-wood, grazing and farming in recent years has become a big concern. This alarming destruction has caused much anxiety and initiatives are being taken to conserve the area as a historical site.

As part of the Wachacha mountain range, the Menagesha State Forest is highly valued for its water catchments. These are: Tinishu Akaki water catchment to the east, Sebeta water catchment to the south and Holeta water catchment to the north & west (Fig. 1). The proximity of the Menagesha State Forest to the capital city has also made it a centre of attraction to tourists and schools.

2.2 SNAP-TRAPPING

In order to assess the species composition, distribution and abundance of small mammals, surveys were conducted from November 1991 to July 1993 at roughly two monthly intervals. Peasant tukuls, gardens and wheat farms as well as bush at the periphery of the forest were surveyed to assess their species composition.

In the forest proper, new and old plantation sites as well as dense *Podocarpus* - *Juniperus* - *Olea* - *Erica* zones at altitudes from 2200 - 3385m asl have been covered. The selection of the sites was based upon possible representation of different habitats as well as easy accessibility. A total of 17 sites in the forest proper and 6 sites at the periphery or outside the forest have been surveyed (Fig. 2). Some of these sites were trapped frequently, at each trapping occasion, while the others were abandoned after one trapping occasion. A rough survey of the vegetation together with altitudes of the localities covered in the snap-trapping occasions (see Fig. 2) are described below:

A: Suba forest station, at 2440m asl with grassy patches, *Echinops steunderi*, *Solanecio gigas*, *Maytenus gracilipes*, *Cupressus lusitanica*, *Olea europaea*, *Podocarpus falcatus*, *Pinus radiata* and *Juniperus procera*.

B: At 2500m asl, deep gorge with more open grassy patches as well as *S.gigas*, *Kalanchoe densiflora* and *J.procera*.

C: At 2510m asl with *Rubus apetalus*, *S.gigas*, *Senecio*

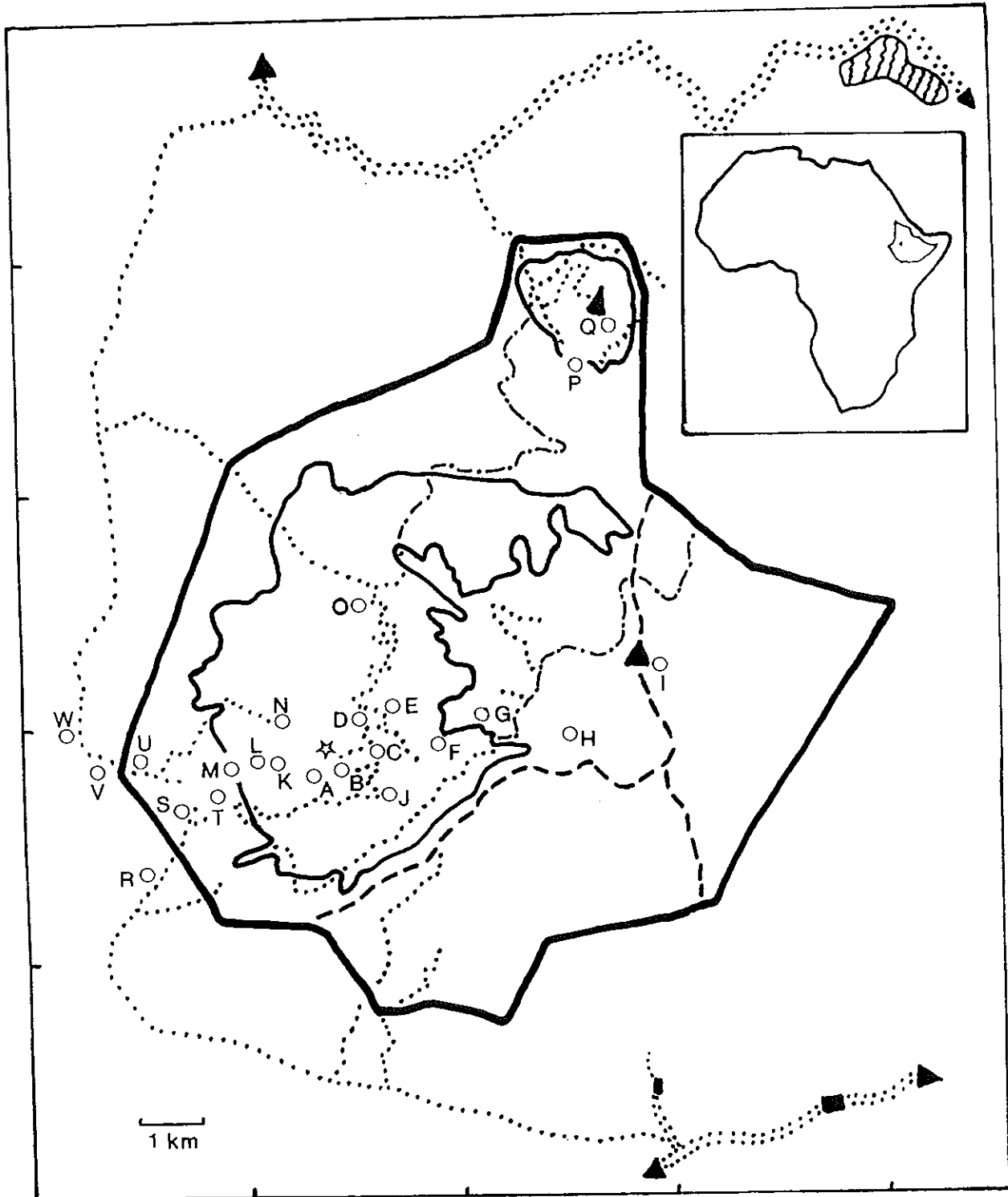


Figure 2. Location of the live (star) and snap-trapping (open circles) sites at the Menagesha State Forest (legend as Fig. 1).

ochrocarpus, *Myrsine africana*, *Acacia mearnsii*, *P.falcatus* and *J.procera*.

D: At 2540m asl with more open grassy patches and *J.procera*.

E: At 2580m asl with well covered herbs and grassy patches, *Dovyalis abyssinica*, *D.vericosa*, *R.apetalus*, *M.gracilipes*, *M.africana*, *P.falcatus*, *O.europaea* and *J.procera*.

F: At 2740m asl with *Erica arborea* forest, *M.africana* and stunted *J.procera*.

G: At 2860m asl near the hotel and tukuls with new plantations of *C.lusitanica* and *Pinus patula*; *Rosa abyssinica* and *E.steunderi*. This locality is very bare because of intensive grazing and farming.

H: Adere mountain at 3010m asl with grassy patches, *Erica arborea* and *Helichrysum odoratissimum* with stunted *J.procera*.

I: Mogle mountain, the highest peak at 3385m asl. *E.arborea* and *H.odoratissimum* comprise the dominant vegetation. Some very stunted *J.procera* also occur.

J: At 2470m asl with dense grass and herb patches, *O.europaea*, *M.gracilipes* and *R.apetalus*.

K: At 2350m asl with *Carissa edulis*, *J.procera*, *P.falcatus*, and *O.europaea*.

L: At 2330m asl with *J.procera*. It also includes an abandoned quarry with elephant grass.

M: At 2300m asl with *C.edulis*, *Croton macrostachys*, *Acacia decurrens* and a *J.procera* plantation.

N: At 2330m asl with *M.gracilipes*, *O.europaea* and *J.procera*.

O: At 2630m asl with stunted *J.procera*, grassy patches and dominant *E.arborea*.

P: At 2500m asl with *C.edulis*, *J.procera*, *Eucalyptus* plantation and crevices.

Q: At 2780m asl on the Menagesha mountain with *O.europaea*, *J.procera*, *P.falcatus* and stony crevices.

R: At 2200m asl with young *C.lusitanica* plantations, *C.macrostachys*, *C.edulis*, *Solanum incanum*, *Lippia adoensis*, *Measa lanceolata* and *Pennisetum trachyphyllum*.

S: At 2240m asl with *Eucalyptus globulus*, *Acacia abyssinica*, *Millettia ferruginea*, few *C.edulis* and a new plantation of *C.lusitanica*.

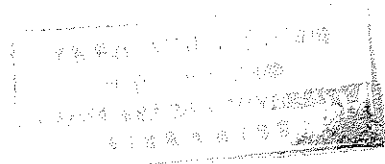
T: At 2280m asl in Suba village and the sawmill compound near the hay meadow.

U: At 2280m asl in a dense bush with *C.edulis*, *C.macrostachys* and young *C.lusitanica* plantation.

V: At 2250m asl around and inside the wheat fields.

W: At 2200m asl inside the village tukuls.

At each trap point, Victor mouse traps and the smaller Museum special traps were used alternately at 10m intervals. The mini-Victor mouse trap was also used occasionally for possible



trapping of shrews. After digging the soil, deep and wide tin containers with worm/meat bait and covered with litter were used to serve as pitfall traps for possible shrew trapping.

During the reconnaissance survey, onion as well as a piece of sponge soaked with vegetable oil were used alternately with peanut butter to assess the bait preference. In all the surveys, peanut butter was used as bait. Prebaiting and removal were carried out in the early morning and late afternoon, but traps set in agricultural plots were removed early morning. A total of 3209 trap nights were used during the survey. Sprung or stolen snap traps have not been considered.

The captured specimens were weighed, measured and sexed. The prepared skins and skulls were deposited in the Zoological Natural History Museum, Biology Department, Addis Ababa University.

Females were examined for pregnancy and lactation and males for testis size and location. For pregnant females, the number of embryos in each horn was noted. The stomach was preserved in 70% alcohol for further diet analysis.

2.3 LIVE-TRAPPING

A permanent 1ha live-trapping grid was established and utilized for 15 months from May 1992 to July 1993. Trapping took place at about two monthly intervals , each time for five consecutive days. The grid was located at 38°33'E and 08°56'N, at

an altitude of 2500m, in a gently sloping valley at 1.1km northeast of the forest station (Fig. 2).

The selection of the grid was based upon a good representation of the main vegetation zones in the forest proper. Prior to selection of the site, a thorough survey was made in different habitats using the same traps. This grid was selected because it combines trees with and without closed canopies, open habitats with shrubs, herbs, grasses and sedges in addition to flat and sloping surfaces. The 1ha grid was divided into 121 compartments based on the dominance of trees, shrubs or grasses (Fig. 3).

The floristic composition of the grid (except epiphytes) was determined by collecting plant specimens for identification in the National Herbarium, Biology Department, Addis Ababa University. The Flora of Ethiopia (Hedberg & Edwards, 1989) was used as a reference. The species, grouped under trees, shrubs, herbs, grasses or sedges, preceded by family name, were the following:

FERN

Herb

Family Adiantaceae

Adiantum thalictroides

GYMNOSPERMS

Trees

Family Cupressaceae

Juniperus procera

Podocarpaceae

Podocarpus falcatus

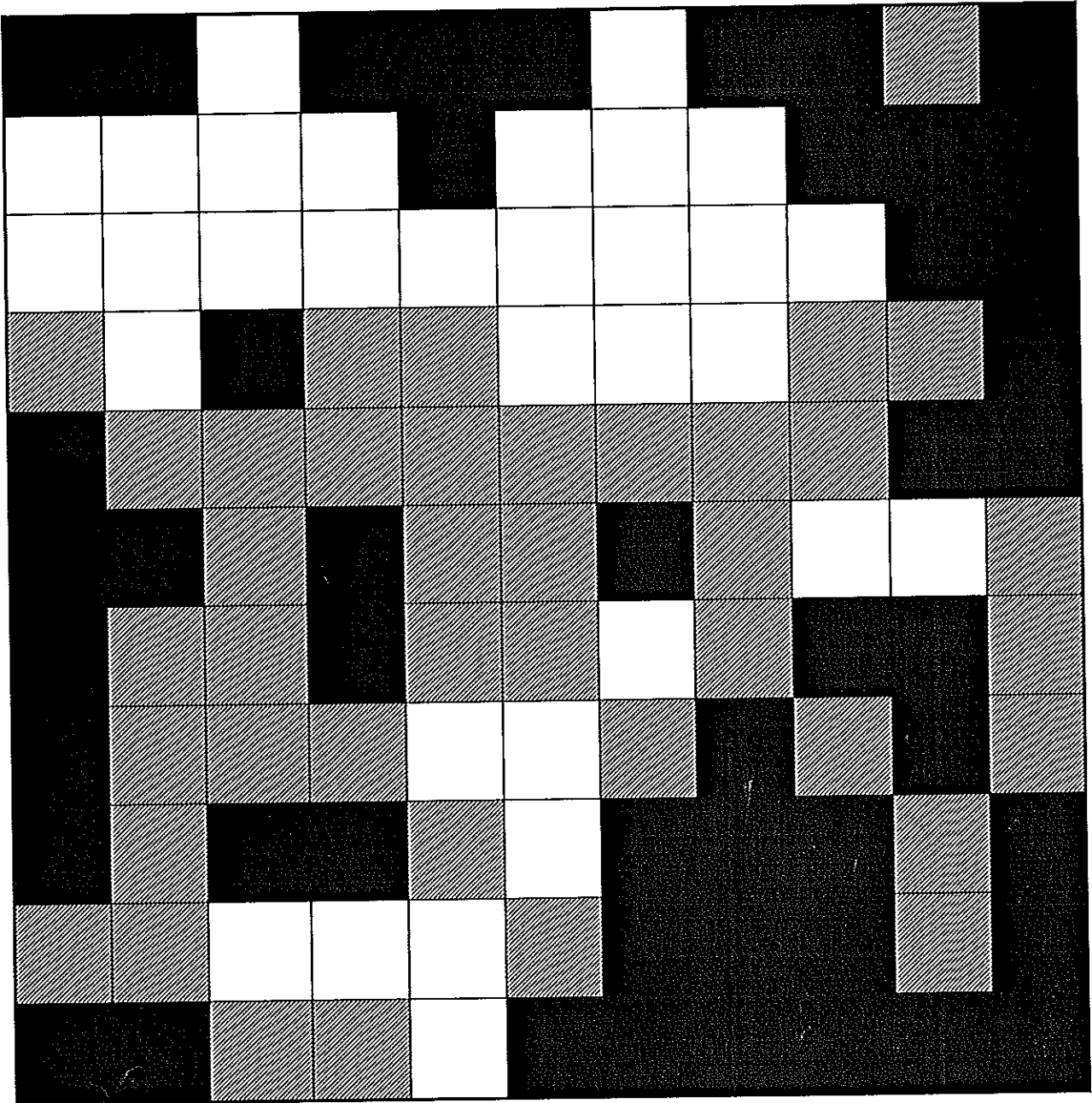


Figure 3. Principal vegetation cover in the compartments of the live-trapping grid (solid blocks = Trees, striped blocks = Shrub, and open blocks = Grass).

a) Dicotyledons

Trees

Family Araliaceae	<i>Schefflera abyssinica</i>
Buddlejaceae	<i>Nuxia congesta</i>
Melianthaceae	<i>Bersama abyssinica</i>
Mimosoideae	<i>Acacia mearnsii</i>
Myrtaceae	<i>Eucalyptus globulus</i>
Oleaceae	<i>Olea europaea</i> subsp. <i>cuspidata</i>
Oliniaceae	<i>Olinia rochetiana</i>
Rutaceae	<i>Teclea nobilis</i>
Sapindaceae	<i>Allophylus abyssinicus</i>

Shrubs

Family Anacardiaceae	<i>Rhus ruspolii</i>
Apocynaceae	<i>Carissa edulis</i>
Calastaceae	<i>Maytenus gracilipes</i>
Euphorbiaceae	<i>Euphorbia ampliphylla</i>
Flacourtaceae	<i>Dovyalis abyssinica</i>
	<i>Dovyalis vericosa</i>
	<i>Scolopia theifolia</i>
Myrsinaceae	<i>Myrsine africana</i>
Oleaceae	<i>Jasminum floribundum</i>
Papilionoideae	<i>Calpurnea aurea</i>
Rosaceae	<i>Rosa abyssinica</i>
	<i>Rubus apetalus</i>
Sapotaceae	<i>Spiniluma oxyacantha</i>

Herbs

Family Amaranthaceae	Achyranthes aspera
Acanthaceae	Hypoestes forskaolii
	Hypoestes triflora
Asclepiadaceae	Periploca linearifolia
Asteraceae	Helichrysum odoratissimum
	Senecio ochrocarpus
	Solanecio gigas
	Vernonia leopoldii
Boraginaceae	Cynoglossum lanceolatum
Crassulaceae	Kalanchoe densiflora
	Kalanchoe sp.
Menispermaceae	Stephania abyssinica
Rubiaceae	Galium spurium subsp. africanum
Urticaceae	Urera hypselodendron

b) Monocotyledons

Herb/Liana

Family Amaryllidaceae	Scadoxus multiflorus
Smilacaceae	Smilax krassiana

Sedges

Family Cyperaceae	Carex chlorosaccus
	Cyperus fischerianus

Grasses

Family Poaceae	Brachypodium flexum
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Digitaria abyssinica

Pennisetum trachyphyllum

Streblochaete longiarista

Sherman traps made of 0.02" aluminium sheet measuring 230 X 75 X 90mm were used throughout the study period. Peanut butter was used as bait. The grid comprised 11 rows and lines at 10m intervals covering an estimated area of 1 hectare. All the 121 points were marked by using yellow plastic tags. The grid was checked twice each day, from 0700 to 0900 hour and 1700 to 1800 hour.

A total of 4840 trap nights were used. The trapped animals were marked by toe-clipping and released after recording the location of capture, weight, species, identification code, sex and reproductive condition. Weight was recorded by Pesola spring balance to the nearest 1g. Animals caught in successive trappings were used to calculate the individual weight gain or loss between each trapping occasion. The captured animals were grouped as young, subadult or adult. Sexual condition of the males was noted, based upon the relative size and position of the testes. For females, condition of the vagina (whether closed or open), size of the nipples and the presence or absence of palpable embryos were noted.

On the occasion of the last grid survey, snap-traps were also used, at distances ranging from 20m to 400m encircling the

grid at 10m intervals, in an attempt to recapture animals that might have emigrated from the grid.

Populations were enumerated using the actual counts, direct enumeration of the total number caught on the grid in each trapping occasion, and for comparative purposes Hayne's (1949), du Feu's *et al.*, (1983), Jolly's (1965) and Fisher & Ford's (1947) estimates were used as well. A statistical package programme MEGA-STATS developed by Mike Hounscome, Manchester University, was used to obtain these estimates of the population of *P.albipes* in the live-trapping grid.

2.4 CAPTIVE BREEDING

Five pairs of *Praomys albipes* were captured in the forest with Sherman traps to found a breeding colony in the animal house of the Biology Department, Addis Ababa University. Each pair (one male and one female) was kept throughout the breeding cycle. Occasionally, the breeding male was removed at birth when the female was very aggressive or to identify whether the female had a postpartem oestrous or not.

Each cage was 42 X 20 X 23cm. The plastic cage was reinforced by additional wire mesh on the top and sides, to prevent the young from escaping. The floor of the cage was covered with saw dust. Wood shavings were used as a nesting material. The cage was cleaned twice a week. The minimum and maximum temperature of the room was recorded daily. Lights were

on during the whole day and off during the night.

Ample chicken feed, in the form of pellets, and water were supplied. The pellets were obtained in the form of flour from Kaliti Feed Processing Factory, Addis Ababa. The flour was prepared in the form of pellets and dried. The ingredients of the flour were corn, wheat bran and middling, bean, meat, bone, salt, lime, vitamins and minerals premix.

On selected animals, the consumption of food and water per day was recorded. Attempts were also made to identify the most favoured food by supplying them with wider choices of food from the wild. These were berries of *Carissa edulis*, *Juniperus procera*, *Olea europaea*, *Dovyalis abyssinica* in addition to the grasses. Survival rate, gestation and weaning time, age to maturity and sex ratio were determined from the laboratory bred animals.

Litter size and weight at birth were recorded as soon as the young were born. The weighing continued at weekly intervals until the rate of increase stagnated or fluctuated. Standard measurements for head & body, tail, hindfoot and ear length were taken to the nearest mm. The young were marked by toe-clipping one week after birth.

The weight was recorded by keeping the animal in a bag using either a Pesola spring balance or a triple beam balance to the nearest 0.1g. Maximum precautions were taken to minimize

disturbance and touching by hand during weighing and taking of measurements, especially during the early growth of the young.

Observations on physical developments were noted. These included: the approximate time for separation of toes, eruption of lower & upper incisors, unfolding of ear pinnae, opening of eyes and appearance of hair.

3. RESULTS

The outcome of the results obtained during the study period is given in the following three separate sections. The first section deals with the results obtained by snap-trapping surveys for the periods from November 1991 to July 1993. This section deals with the composition, abundance and distribution of the rodents in the Menagesha State Forest. In addition, activity, reproduction, embryo sizes, weight and the results of diet analysis in *P.albipes* are covered.

The second section deals with the results obtained by live-trapping surveys from May 1992 to July 1993. This section covers the species composition, biomass, reproduction, survival, habitat blocks, block capture, movement, berry estimate and population estimate of *P.albipes*.

The third section exclusively deals with the results obtained by captive breeding programme for *P.albipes* from March 1992 to December 1993. It covers the results on reproduction, size increase, physical development and intake of food in captive bred *P.albipes*.

3.1 SNAP-TRAPPING

3.1.1 Species Composition

Nine species of rodents were caught during the snap-trapping surveys of the different vegetation zones of the Menagesha State Forest from November 1991 to July 1993. A total of 293 specimens

were captured in 3209 trap nights (Table 3). The mean trap success was 9.1%. The highest trap success (26.9%) was recorded in July 1992 and the lowest (4.7%) in July 1993. The different species recorded in the Menagesha State Forest from the snap-trap surveys were: *Praomys albipes*, *Pelomys harringtoni*, *Lophuromys flavopunctatus*, *Mus mahomet*, *Arvicanthis dembeensis*, *Rattus rattus*, *Otomys typus*, *Stenocephalemys griseicauda* and *Dendromus mystacalis*. In addition to the above species, the mole-hills and tunnels of the underground dwelling *Tachyoryctes splendens* was very common in more open habitats from 2200-3000m asl. The quills of porcupine, *Hystrix cristata* were also observed dispersed in open habitats of the forest. A young shrew, *Crocidura* cf. *bicolor* was also caught by hand near the edge of the house in the forest station at 2440m asl.

3.1.2 Species Abundance

Except for March and July 1993, the most common capture for all trapping occasions was *P.albipes*. In the March 1993 collection, *Pelomys harringtoni* formed the largest catch while in July 1993, *M.mahomet* was the largest contributor. *P.albipes* comprised 159 of the total 293 rodents collected during all trapping occasions, which was 54.3% of the total rodents captured. *Pelomys harringtoni* comprised the second largest catch. A total of 45 (15.4%) individuals were captured in all trapping occasions. The males comprised 23 (51.1%) and the females 22

Table 3. Trap nights, species composition and abundance of rodents caught by snap-trapping surveys from different habitats.

Month	Species										Trap nights	% Trap success
	P.a	P.h	L.f	M.m	A.d	R.r	O.t	S.g	D.m	Total		
1991												
Nov.	18	1	4		3	5				31	405	7.7
Dec.	7		5							12	124	9.7
1992												
Mar.	14		3	4						21	199	10.6
May	5	1	3	3						12	60	20.0
July	30	2	4	2			1			39	145	26.9
Sep.	21									21	260	8.1
Nov.	17	2	4					2		25	290	8.6
1993												
Jan.	7	4			3	3				17	248	6.9
Mar.	9	18	3	3	4		1			38	320	11.9
May	21	11	5	6					1	44	458	9.6
July	10	6	2	14			1			33	700	4.7
Total	159	45	33	32	10	8	3	2	1	293	3209	9.1

P.a=P.albipes, P.h=Pelomys harringtoni, L.f=L.flavopunctatus, M.m=M.mahomet, A.d=A.dembeensis, R.r=R.rattus, O.t=O.typus, S.g=S.griseicauda, D.m.=D.mystacalis

(48.9%). **L.flavopunctatus** comprised the third largest catch. A total of 33 (11.2%) individuals were caught in all trapping occasions. 19 (57.6%) of these were males and 14 (42.4%) females. **M.mahomet** comprised the fourth commonest species. A total of 32 (10.9%) individuals were caught in all trapping occasions. Significantly more males (23, 71.8%) were caught than the females (9, 28.2%). The remaining five species of rodents comprised only 8.2% of the total captures. **P.albipes** was the only species captured on all trapping occasions, the other rodents did not show up on some trapping occasions. In September 1992, out of the 260 trap nights positioned in different habitats, only **P.albipes** was caught.

3.1.3 Species Distribution

P.albipes was the most widespread and abundant among the captured species. It not only comprised 54.3% of the total rodents captured, but it occurred widely in both bushy vegetation and in the forest (Table 4a). However, it was less common in **Erica** scrub and open grassy patches. In the Menagesha State Forest, it covered an altitudinal range from 2200-3300m asl, with frequent occurrences up to 2600m asl in the **Juniperus** and **Olea** zones. 61.0% of the total 159 **P.albipes** were captured in the forest habitat, 25.8% in the bush and only 13.2 in the **Erica** scrub (Table 4b). **P.albipes** comprised 97 (70.8%) of the total 137 rodents captured in the forest habitat while in the bush and in

Table 4a. The distribution of rodents from the snap-trap survey in the Menagesha State Forest across the vegetation zones.

Species	Catch	Altitudinal range (m)	Habitat-type
P.albipes	159	2200-3300	Bush, Forest, Erica
P.harringtoni	45	2200-3385	Bush, Open Forest, Erica
L.flavopunctatus	33	2200-3300	Bush, Open Forest, Erica
M.mahomet	32	2200-2580	Bush, Open Forest
A.dembeensis	10	2200-2300	Bush, Grass, Farm
R.rattus	8	2200-2860	Human habitations
O.typus	3	2500-3300	Open Forest, Erica
S.griseicauda	2	3010-3385	Erica
D.mystacalis	1	2200	Bush
T.splendens	-	2200-3010	Open Forest, Meadow

Table 4b. The distribution of rodents from snap-trap surveys in each habitat-type, altitude (m asl) and per cent trap success.

Species	Habitat/Altitude			Total Catch
	Bush <2300	Forest 2300-2800	Erica >2800	
P.albipes	41	97	21	159
P.harringtoni	3	8	34	45
L.flavopunctatus	14	11	8	33
M.mahomet	13	19		32
A.dembeensis	10			10
O.typus		2	1	3
S.griseicauda			2	2
D.mystacalis	1			1
Total	82	137	66	285
Trap-nights	868	1712	604	3184
% Trap Success	9.4	8.0	10.9	9.0

the *Erica* scrub, it comprised 50.0 and 31.8% respectively. *R.rattus*, *A.dembeensis* and *Pelomys harringtoni* could have been trapped more often had their habitats not been frequently avoided. *R.rattus* was plentiful in areas of human habitations (tukuls). *A.dembeensis* was very common in grassland, farmland and nearby scrub at 2200m asl below the forest. The abundance of this species could readily be recognized from its runways and burrows; sometimes hundreds undertook gregarious movements during the day time. *Pelomys harringtoni* occurred in restricted numbers in nearby bush and in open habitats in the forest where *Kalanchoe* vegetation dominates. However, it was very common in *Erica* scrub at higher altitudes where stony crevices occur. *L.flavopunctatus* was more widespread in bushy vegetation and open forests with grassy patches. Even though less abundant, it also occurred in *Erica* scrub at higher altitudes. *M.mahomet* was widespread in bushy vegetation. It also frequented open forests with grassy patches up to 2580m asl. *O.typus* occurred in open forests with grassy patches and in *Erica* scrub at higher altitudes. *S.griseicauda* was captured only in *Erica* scrub above 3000m asl. The single pregnant female *D.mystacalis* was captured in the bush outside the forest proper at 2200m asl.

Young *J.procera* and *C.lusitanica* plantations supported fewer species and individuals because their dense shade resulted in bare ground, no cover and no berries. At higher altitudes with

Erica and stunted **J.procera** habitat disturbed by human interference, fewer individuals and species were trapped (1.6%). However, at the highest altitudes with **Erica** scrub, where human interference is limited, more individuals and species were trapped. The per cent trap success (Table 4b) in the **Erica** scrub (10.9%) was almost double if trap-nights at sites disturbed by human interference were excluded.

3.1.4 Activity

All traps set in the forest were checked early morning and late afternoon. All of the captured **P.albipes** were from the early morning check, and no individual of **P.albipes** was caught from the late afternoon catch. Thus, **P.albipes** is exclusively nocturnal. In comparison, some individuals of **L.flavopunctatus**, **M.mahomet** and **Pelomys harringtoni** were also collected during the late afternoon check while **A.dembeensis** was exclusively diurnal. The rest of the rodents were collected from the morning check. Since some of the traps were checked at about 07.00 hours, some of these rodents collected during the early hours might be active at dawn. In the case of **P.albipes** some of the trap sites were checked at dawn and left for the late afternoon check. This also resulted in empty traps during the late afternoon check.

3.1.5 Reproduction

Composition of wild caught rodents from different habitats based on sex and age groups is given in Tables 5 & 6. Out of the

Table 5. Composition of different age groups in snap-trapped *P.albipes*. Adult males are divided between those with scrotal and abdominal testes.

		Males				Females		
Month		Scrot.	Abdo.	Subad.	Young	Preg.	Adult	Subad. Young
1991	Nov.	8		1	1	2	5	1
	Dec.	1		2	1		1	2
1992	Mar.	5	2		1	1	3	1
	May	1			1		2	1
	July	13	2	2		3	5	3
	Sep.	8			3	4	5	1
	Nov.	6				9	1	1
1993	Jan.	2	1			2	1	1
	Mar.	3	1		1	2		1
	May	7		2	2	5	1	2
	July	4		1	1	2	1	1
Total		58	6	8	11	30	25	9

Table 6. Composition of snap-trapped male (M) and female (F) rodents excluding *P.albipes*.

Month	Species														Total catch
	P.h		L.f		M.m		A.d		R.r		O.t	S.g		D.m	
	M	F	M	F	M	F	M	F	M	F	M	M	F	F	
1991															
Nov.		1		4			2	1	1	4					13
Dec.				5											5
1992															
Mar.			2	1	3	1									7
May		1	1	2	2	1									7
July	2		3	1	1	1					1				9
Sep.															0
Nov.	1	1	3	1								1	1		8
1993															
Jan.	3	1					1	2	1	2					10
Mar.	11	7	1	2	2	1	2	2			1				29
May	5	6	3	2	6									1	23
July	1	5	1	1	9	5					1				23
Total	45		33		32		10		8		3	2		1	134

P.h=*Pelomys harringtoni*, L.f=*L.flavopunctatus*, M.m=*M.mahomet*,
A.d=*A.dembeensis*, R.r=*R.rattus*, O.t=*O.typus*, S.g=*S.griseicauda*,
D.m=*D.mystacalis*

total 159 individuals of **P.albipes** captured in all trapping occasions, 83 (52.2%) were males and 76 (47.8%) were females. The difference in the capture of the number of males to females was not significant ($X^2_1 = 0.30$, n.s.). Out of the 83 males, 58 (70%) were reproductively active with scrotal testes, 6 (7.2%) were adults with abdominal testes and 19 (22.8%) subadult or young. Out of the 76 females, 39.4% were pregnant, 32.9% were quiescent females and 27.6% comprised subadults or young. The recruitment rate for the young or subadult is very low for both males and females. The November 1992, September 1992 and May 1993 captures of high numbers of pregnant females correspond with the high number of males with scrotal testes, but the November 1991 and July 1992 high number of scrotal males did not correspond with high pregnancy rate. The highest percentage of pregnant females (81.8%) were recorded for November 1992. Despite the very sharp season in pregnancy rate, no sharp increase in young or subadult recruitment rate was observed during successive trapping occasions (Table 5). All trapping occasions in 1993 show 50% or more pregnant females. This might be in response to the lower size of the population, but the low number of captures should also be taken into consideration before arriving at this conclusion. In **P.albipes**, reproductively active males with scrotal testes were observed throughout the study period.

The largest number of **P.albipes** was caught in July 1992.

76.4% of the males captured during this period were reproductively active with scrotal testes. At the same time, 80% of the males captured in November 1991 and 100% of the males captured in November 1992 were adults with scrotal testes. 72.7% of the males captured in September 1992 were also adults with scrotal testes. Pregnant females were recorded in most months of the study period with a peak in pregnancy during November 1992; 81.8% of the females captured in November 1992 were pregnant. In May and September 1992, 50% and 40% of the females captured were pregnant respectively. The availability of either young or subadult *P.albipes* throughout the study period confirms that the species breeds throughout the year.

The relationship between reproduction and rainfall is shown in Fig. 4. The rainfall data (Table 1) show the small rainy season from March-May followed by the long rains from June to September. November is a dry season when, following the rainy season, fruits will be frequently available. The highest pregnancy rate in November might be associated with the highest season of fruit availability. The association between pregnancy rate and high level of rainfall using the arcsine transformed data was not significant. Pearson's Correlation Coefficient shows low negative association between peak pregnancy rate and rainfall ($r = -0.30$, n.s. for the same month's rainfall and $r = -0.03$, n.s. for the previous month's rainfall).

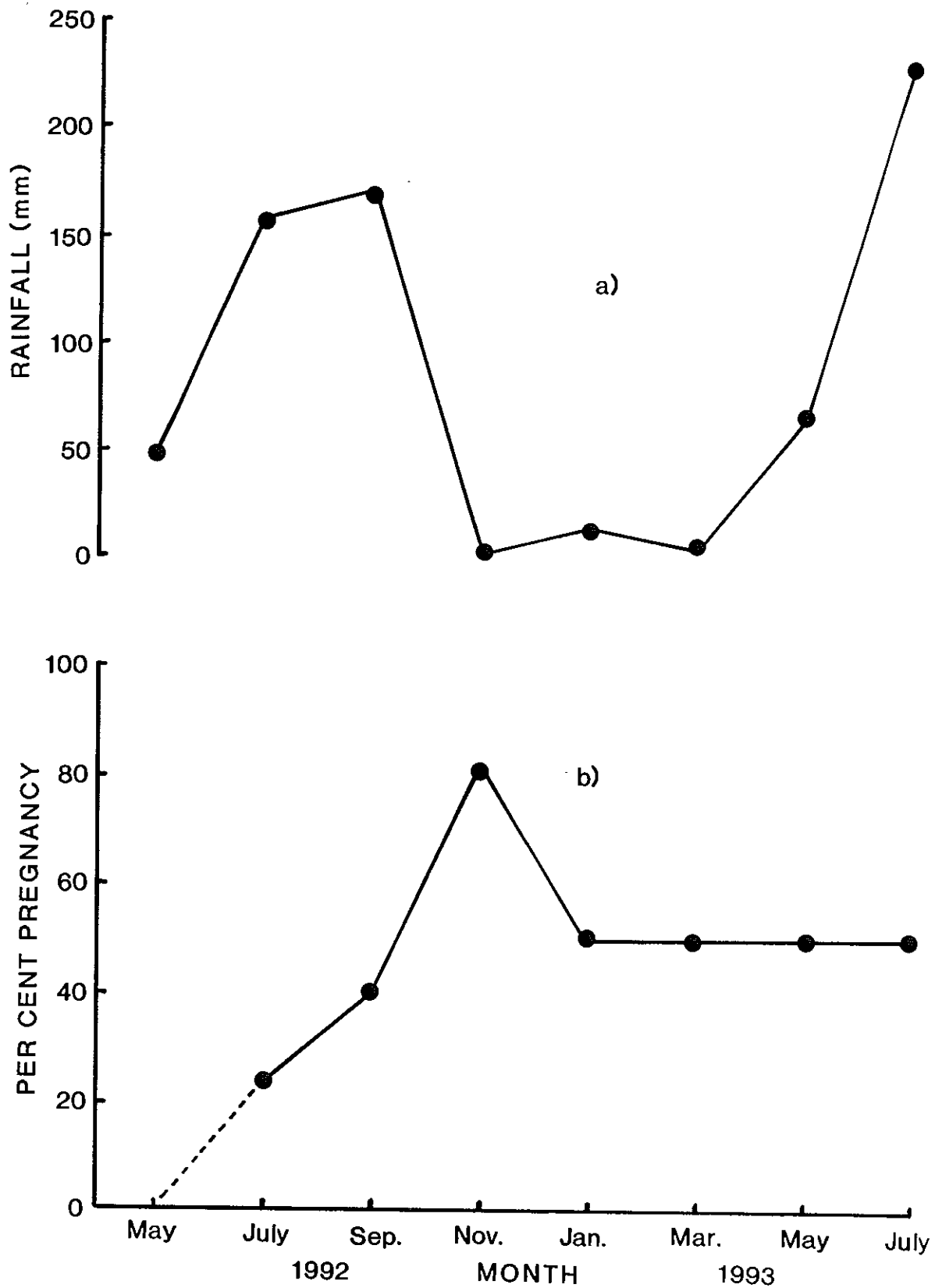


Figure 4. Relationship between rainfall at Menagesha (a) and per cent pregnancy (b) in *P. albipes* from the snap-trapping surveys.

3.1.6 Embryo Size

The number of embryos in 18 wild caught pregnant females of **P.albipes** is given in Table 7. The number of embryos in each pregnant female ranged from 2-8. The most frequent embryo number was 4. The mean embryos per female including the resorbing ones was 4.89 ± 1.45 . However, if the resorbing embryos are excluded, the mean embryos per pregnant female is 4.67 ± 1.19 . The position of implantation sites (47,41) did not vary significantly between left and right horns ($X^2_1 = 0.28$, n.s). Resorbing embryos were recorded in some of the larger litters, but not in those with fewer than 4 embryos.

3.1.7 Weight

The weight of **P.albipes** recorded during the trapping occasions is shown in Figs. 5 and 6. Adult scrotal males and pregnant females mostly weigh above 50g. Male adults with abdominal testes and quiescent females weigh between 40-50g. Subadults in both sexes weigh between 30-39g while young ones are mostly below 29g. The least weight of the youngest **P.albipes** caught in the snap-trap survey was 18g. The highest weight recorded was 80g for a pregnant female and 88g for a scrotal male. In **P.albipes**, males once scrotal remain so throughout life, with active sperm in the checked epididymis. Testis size (volume) for scrotal males was $> 15 \times 9$ mm and for abdominal males $< 14 \times 7$ mm. Heaviest individuals had largest testes sizes. These are believed to be the oldest individuals.

Table 7. Number of embryos, frequency and implantation sites (left & right) in snap-trapped pregnant *P.albipes* (each asterisk indicates one resorbing embryo).

No. of embryo	Frequency	Implantation sites (L+R)	Total
2	1	0+2	2
3	1	2+1	3
4	6	2+2, 2+2, 1+3, 3+1, 3+1, 4+0	24
5	4	2+3, 3+2, 3+2, 4*+1	20
6	4	3+3, 3+3, 4+2, 1+5	24
7	1	3+4*	7
8	1	4*+4*	8
Total	35	47+41	88

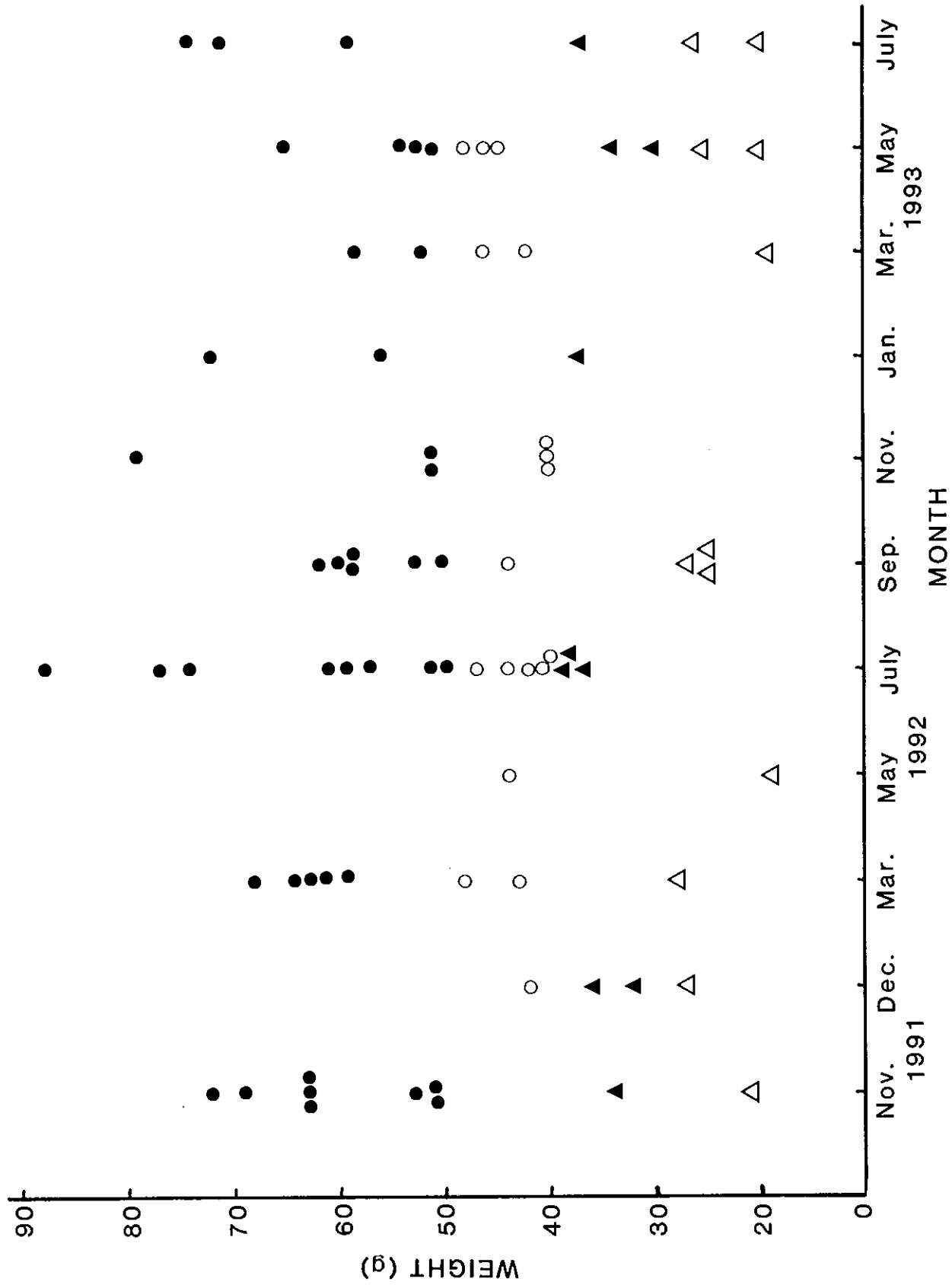


Figure 5. Relationship between weight and reproductive condition in male *P. albiges* over the snap-trapping period (solid circles-scrotal males, open circles-subadult, solid triangles-subadult, and open triangles-young).

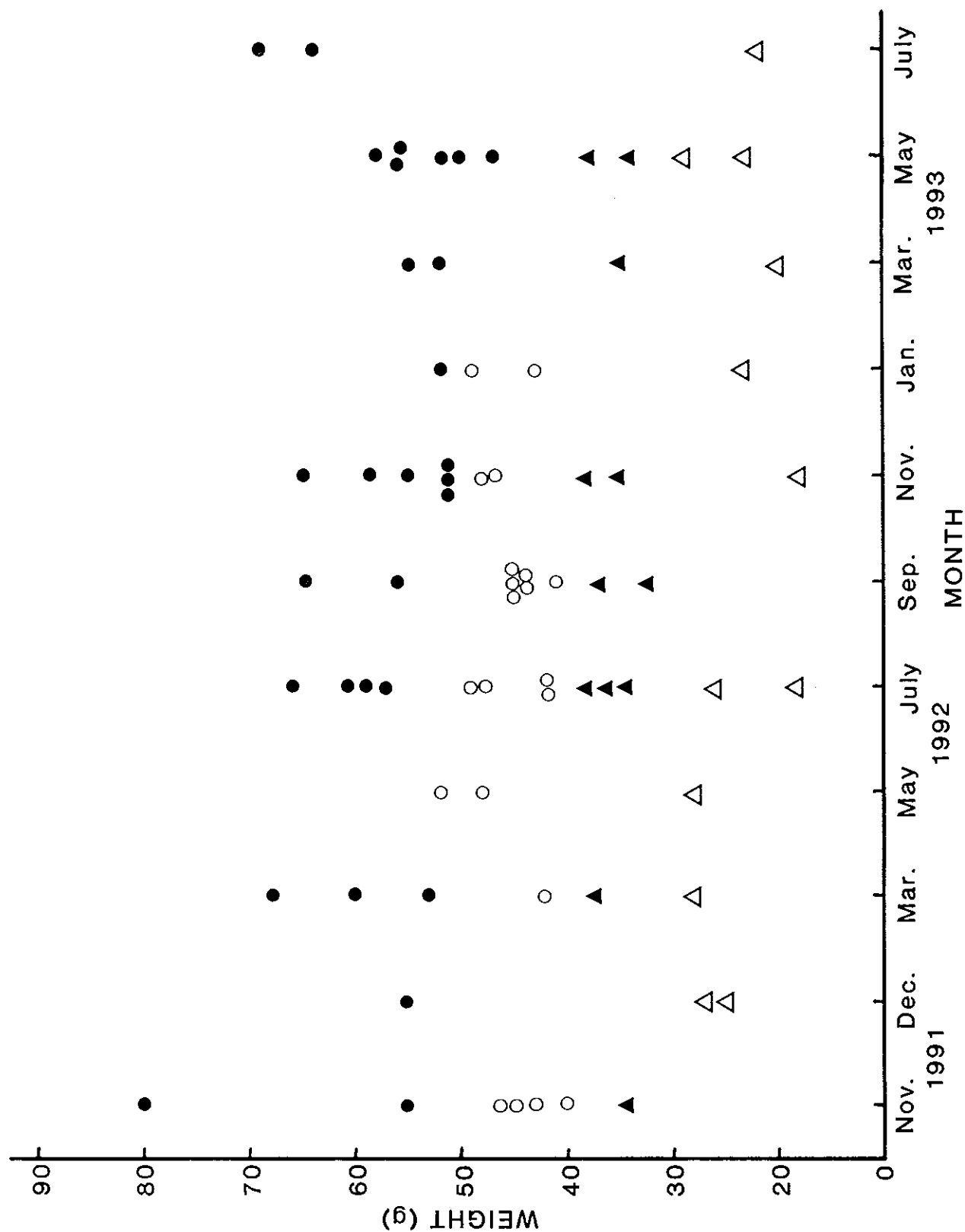


Figure 6. Relationship between weight and reproductive condition in female *P. albigipes* over the snap-trapping period (solid circles-pregnant females, open circles-adult, solid triangles-subadult, and open triangles-young).

3.1.8 Body Size

Weight against head & body length from the snap-trap survey is shown in Figs. 7 & 8. There is an increase in size against *age* in **P.albipes**. In both males and females, a steady increase in size is obvious until about 40g in weight. This increase seems to extend in males up to 50g. Males seem to show slight increase in size even after 50g. Females show wider fluctuations after 50g.

For comparative purposes, mean adult body measurements for all captured species in the Menagesha State Forest are given in Table 8. For **P.albipes**, because of adequate samples, the mean weight and body measurements are given separately for each sex. The weight figures for female **P.albipes** includes pregnant individuals as well. Males, therefore, weigh slightly more than females. These values will be further compared with the values obtained in different localities of Ethiopia by Yalden (1988a,b) and Rupp (1980) in the discussion section. The higher weight recorded for **D.mystacalis** and **G.murinus** is for pregnant females.

3.1.9 Diet Analysis

A total of 113 stomachs of **P.albipes** covering different seasons were checked for the composition of food contents. The identification of the stomach contents was mostly based on the berry coat colour. This was perfected by collecting berries and leaves from the wild and feeding the captive **P.albipes**

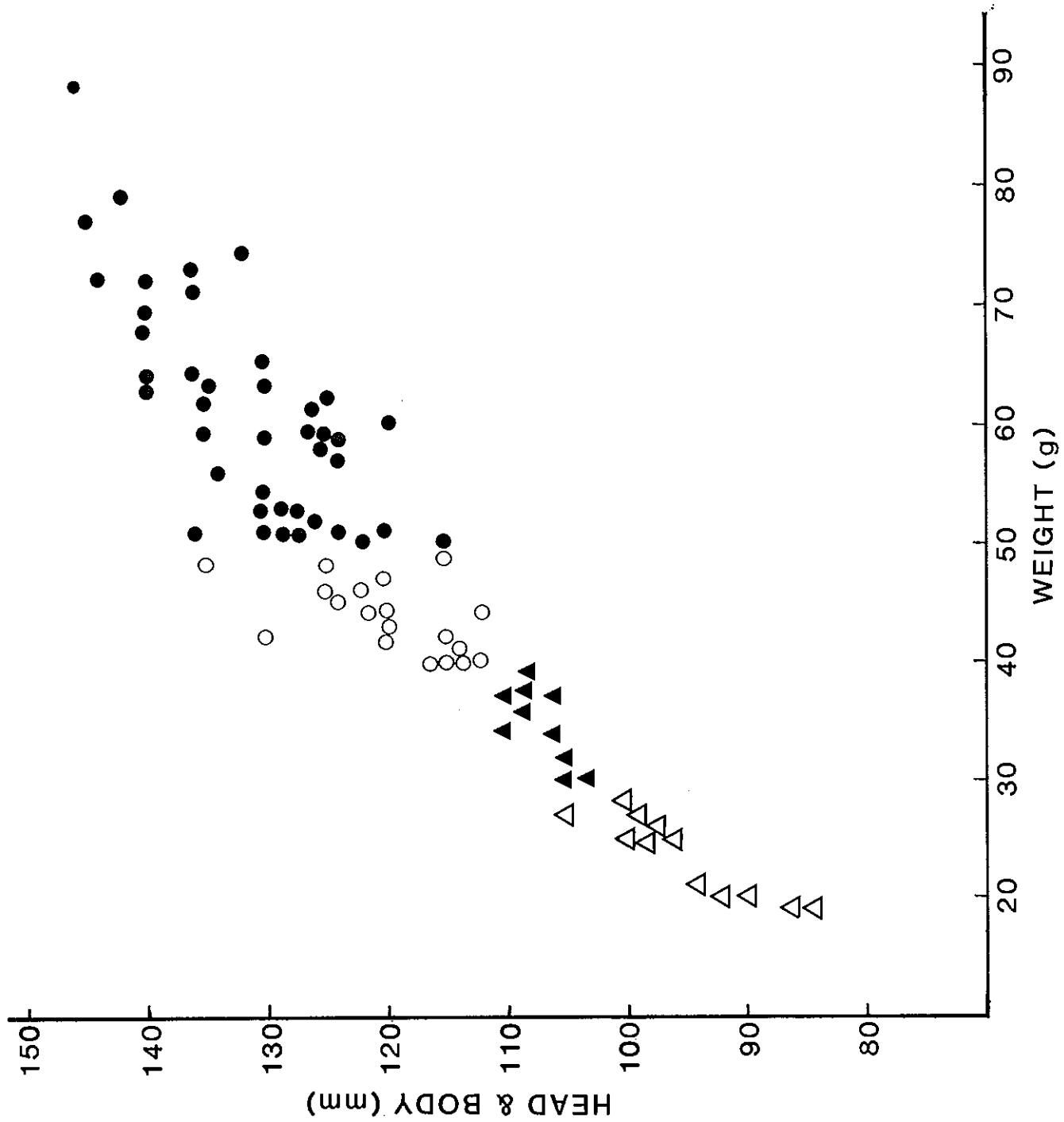


Figure 7. Weight (g) against head & body (mm) in different age groups of male **P. albipes** from the snap-trapping survey.

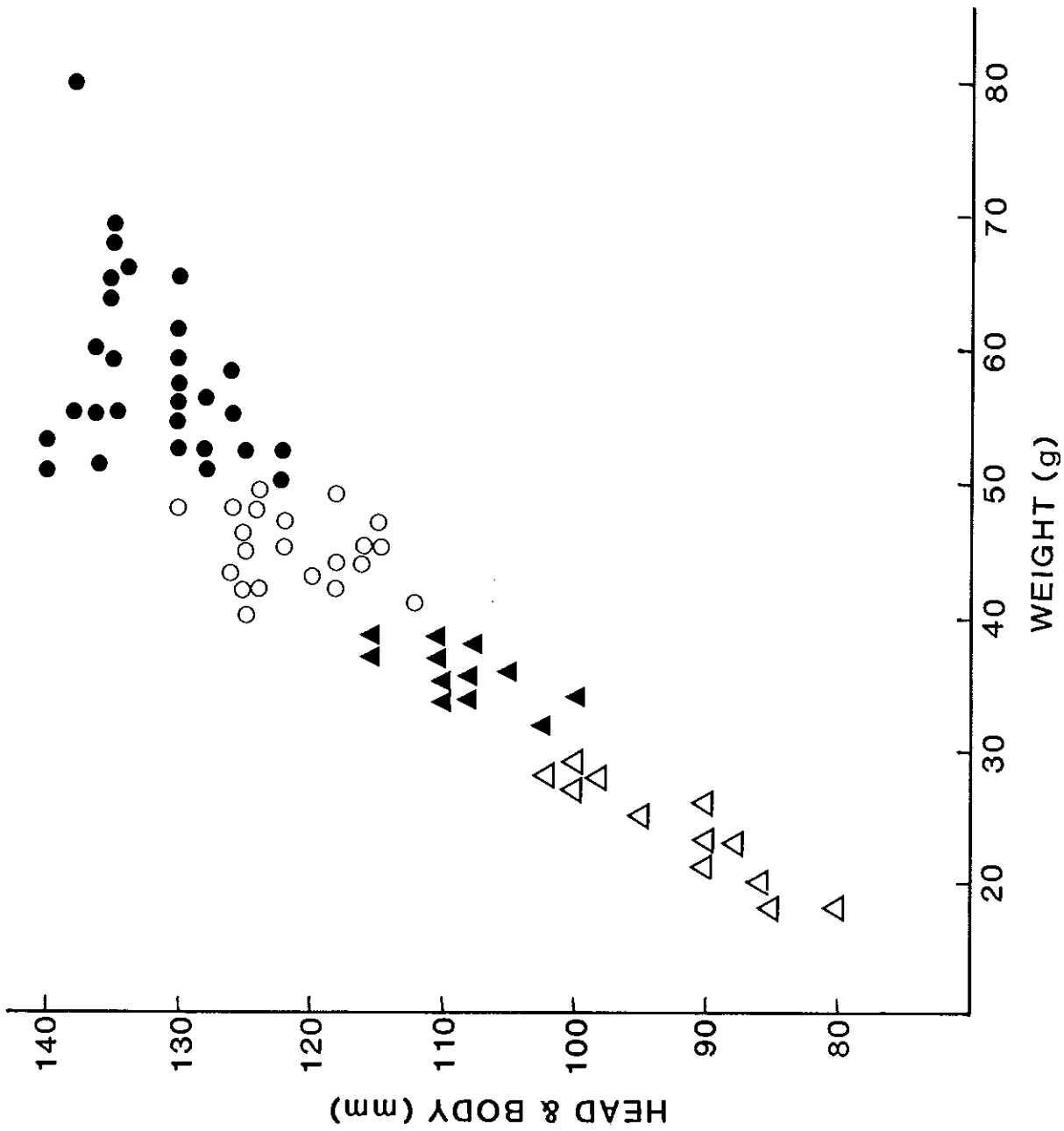


Figure 8. Weight (g) against head & body (mm) in different age groups of female *P. albipes* from the snap-trapping survey.

Table 8. Adult weight (g) and body measurements (mm) of rodents snap-trapped in the Menagesha State Forest. The sexes are presented separately for *P.albipes*, but neither weight nor tail length are significantly different ($t=1.6$, $P<0.11$ and $t=1.3$, $P<0.21$ respectively), $\pm S.D.$

Species	No.	Weight	HB	TL	HF	EA
P.a.	M=60	55.6 $\pm$ 11.1	127.7 $\pm$ 8.8	156.5 $\pm$ 8.7	26.8 $\pm$ 0.7	21.5 $\pm$ 1.0
	F=50	52.5 $\pm$ 8.5	127.4 $\pm$ 7.1	158.5 $\pm$ 7.9	26.7 $\pm$ 0.6	22.3 $\pm$ 0.7
	All	54.2 $\pm$ 10.1	127.5 $\pm$ 8.1	157.4 $\pm$ 8.5	26.8 $\pm$ 0.7	21.9 $\pm$ 1.0
P.h.	21	64.9 $\pm$ 11.9	136.3 $\pm$ 7.8	128.3 $\pm$ 6.8	27.6 $\pm$ 1.0	17.4 $\pm$ 0.7
M.m.	28	10.2 $\pm$ 1.8	66.4 $\pm$ 4.7	45.8 $\pm$ 2.8	13.9 $\pm$ 0.7	11.1 $\pm$ 0.7
L.f.	27	63.5 $\pm$ 10.9	131.4 $\pm$ 7.4	62.8 $\pm$ 3.5	21.2 $\pm$ 1.1	17.3 $\pm$ 0.8
A.d.	6	79.3 $\pm$ 9.7	130.8 $\pm$ 8.6	96.4 $\pm$ 5.9	27.0 $\pm$ 1.4	15.2 $\pm$ 0.8
R.r.	6	53.7 $\pm$ 20.5	121.7 $\pm$ 16.9	135.0 $\pm$ 13.9	24.3 $\pm$ 1.9	17.8 $\pm$ 2.2
S.g.	2	87.5	147.0	129.0	25.0	19.0
O.t.	2	96.0	150.0	63.0	26.0	20.0
D.m.	1	18.0	75.0	102.0	19.0	15.0
G.m.	1	40.0	82.0	70.0	17.0	16.0

P.a.=*P.albipes*, P.h.=*Pelomys harringtoni*, M.m.=*M.mahomet*,
L.f.=*L.flavopunctatus*, A.d.=*A.dembeensis*, R.r.=*R.rattus*,
S.g.=*S.griseicauda*, O.t.=*O.typus*, D.m.=*D.mystacalis*,
G.m.=*G.murinus*.

exclusively with each item, sacrificing the animals to observe the stomach contents.

The preliminary diet analysis on 53 stomachs outside the forest proper (bush) showed that the berries of **Carissa edulis** occurred in 50 and green leaves in 20 of the stomachs checked. The berries of **Rosa abyssinica** were found in 6, seeds and animal matter in 2 each. Nematodes ranging in number from 1 to 4 were observed in 8 stomachs.

From the forest proper, a total of 60 stomachs were examined for their food content. The berries of **Olea** were observed in 36, **Juniperus** in 34, **Rosa** in 15, **Rubus** in 8 and green leaves in 38 stomachs. Animal matter and seeds were each observed on one occasion only. Nematodes ranging in number from 1-10 were found in 17 of the stomachs examined.

These preliminary observations show that the berries of **Olea** and **Juniperus** in the forest and **Carissa** in the bush, together with green leaves, appear to be the major food items consumed by **P. albipes**. Some of the stomachs contained peanut butter from the trap and rubbish material. Some of this rubbish was the juices/fruits of berries. The absence of invertebrates, especially insects, was striking since termites were plentiful. From my personal observations in the field, **Olea** berries were observed seasonally while the berries of **Carissa** and **Juniperus** occurred throughout the year. Under old **Juniperus** trees, berries

are observed scattered on the ground with a peak during the rainy season. Plenty of **Carissa** berries were observed all the year round on the plant and very few on the ground. Although not observed, there is a possibility that **P.albipes** might collect these berries either by climbing or pulling down the branch of the shrub to the ground as a result of its weight. The shortness of this shrub and its dense cover, coupled with the longer tail of **P.albipes**, might support this argument. Yalden (1988b) has also captured a single individual on the branches of a tree. The examination of these stomachs for their food content is a preliminary observation and not an exhaustive one; I do not claim that it is a complete analysis. More studies in depth need to be carried out including data from other localities as well.

3.2 LIVE-TRAPPING

3.2.1 Species Composition

The density of rodents was assessed by conducting bimonthly live-trapping in a 1ha grid of the Menagesha State Forest from May, 1992 to July, 1993. A total of 390 captures of 281 individuals was made in 4840 trap nights. Six species of rodents were recorded. These were: *P.albipes*, *M.mahomet*, *L.flavopunctatus*, *O.typus*, *Pelomys harringtoni* and *Graphiurus murinus* (Table 9). *P.albipes* was by far the most abundant species, followed by *M.mahomet* and *L.flavopunctatus*. A total of 115 rodents were recorded as new captures. *P.albipes* comprised 74 (64.3%) of the total rodents captured in the live-trapping grid. However, the number of *P.albipes* declined across the last four trapping occasions while the number of *M.mahomet* increased.

M.mahomet comprised 28 (24.3%) and *L.flavopunctatus* 8 (6.1%) of the total rodents captured. However, the remaining three species (*O.typus*, *Pelomys harringtoni* and *G.murinus*) comprised only 5.3% of the total. The total number of rodents observed on the live-trapping grid decreased at each live-trapping occasion. This decrease was highly pronounced during the 1993 catches. The recruitment rate for the young, subadults and adults was also low in the 1993 catch. Unless the immigration rate increases, the grid population is likely to remain low at least for a couple of months.

Table 9. Number of rodents on the live-trapping grid on different trapping occasions (the numbers include new captures, given in parentheses).

Month	Praomys	Mus	Lophuromys	Otomys	Pelomys	Graphiurus	

1992 May	(33)		(1)		(1)		
July	22(4)	(1)	(1)	(2)			
Sep.	24(12)	(1)	(1)				
Nov.	15(6)	(1)	(2)				
1993 Jan.	12(8)	7(6)					
Mar.	8(4)	8(6)	(2)				
May	6(3)	(4)	(1)				(1)
July	6(4)	12(9)			(1)		

Total new	74	28	8	2	2		1

3.2.2 Biomass

The monthly biomass of captured rodents in the 1ha live-trapping grid varied from 454-1546g (Table 10). In all trapping occasions, **P.albipes** formed the largest biomass (Fig. 9). The monthly biomass for **P.albipes** varied from 260-1397g. The number of individuals captured at each trapping occasion varied from 12-35 and for **P.albipes**, from 6-33. **P.albipes** was the only species captured on all trapping occasions. Although **M.mahomet** were captured more abundantly during the last four trapping occasions, their contribution to the over-all biomass was limited due to their size. The 8 individuals of **L.flavopunctatus** contributed more to the over-all biomass than the 28 **M.mahomet**.

3.2.3 Reproduction

A total of 126 **P.albipes** were recorded at different live-trapping occasions. Some of these individuals were recaptured from previous trapping occasions. Including these recaptured individuals, captures totalled 66 (52.4%) males and 60 (47.6%) females, which was not significantly different from 1:1 ratio ($X^2_1=0.29$, n.s.). However, the total new captures for **P.albipes** throughout the study period was 74. Out of the total new captures, 40 (54%) were males and 34 (46%) were females ($X^2_1=0.48$, n.s.). The composition of different age groups shows that **P.albipes** breeds throughout the year with the highest pregnancy rates in September and November (Table 11). The

Table 10. Biomass (g/ha) of rodents on the 1ha live-trapping grid
(number of specimens is in parentheses).

Month	All Species	<i>Praomys</i>	<i>Mus</i>	<i>Lophur.</i>	<i>Pelomys</i>	<i>Otomys</i>	<i>Graphi.</i>
1992							
May	1546	1397(33)		93(1)	56(1)		
July	1229	978(22)	11(1)	48(1)		192(2)	
Sep.	1394	1296(24)	18(1)	80(1)			
Nov.	953	832(15)	12(1)	109(2)			
1993							
Jan.	611	551(12)	60(7)				
Mar.	564	390(8)	73(8)	101(2)			
May	454	303(6)	37(4)	88(1)			26(1)
July	483	260(6)	142(12)		81(1)		

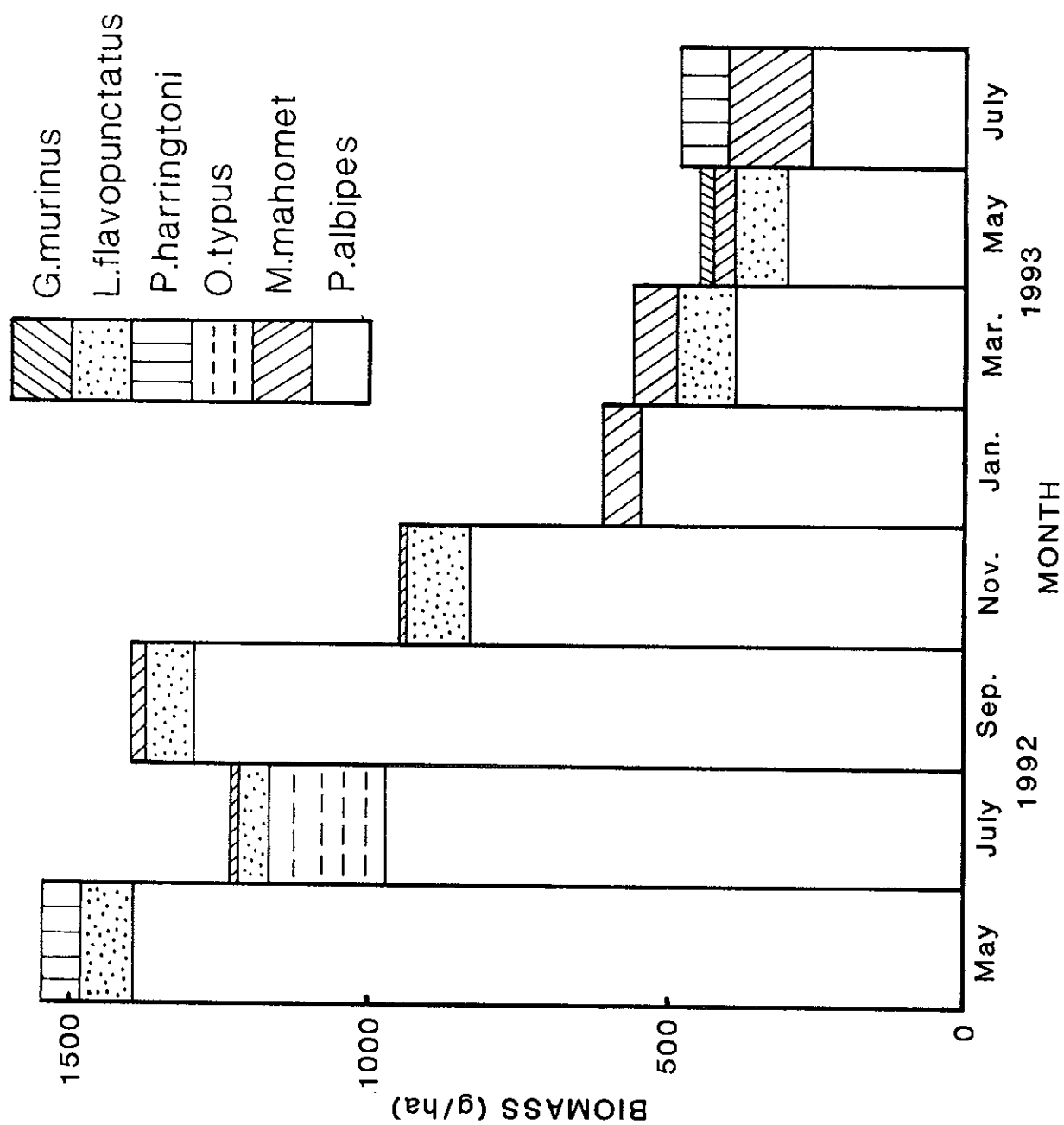


Figure 9. Biomass (g/ha) of rodents on the live-trapping grid.

Table 11. Composition of different age groups of *P.albipes* from the live-trapping grid. Adult males are divided between those with scrotal and abdominal testes.

		Males				Females			
Month		Scrot.	Abdo.	Suba.	Young	Preg.	Adult	Suba.	Young
1992	May	6	10	3		2	4	5	3
	July	8	6			4	1	3	
	Sep.	9				11	3	1	
	Nov.	6	1			8			
1993	Jan.	4		1	1	3	1		2
	Mar.	3				3		2	
	May	2		1		2		1	
	July	2			3				1
Total		40	17	5	4	33	9	12	6

pregnancy rate for November 1992 was 100% and for September 1992, it was 73.3%. At each trapping occasion at least two animals were recorded as lactating. Relationships between pregnancy rate and rainfall are shown in Fig. 10. Highest pregnancy rates were obtained during the end of the rainy and beginning of the dry seasons. The association between peak pregnancy rate and rainfall using arcsine transformed data was not significant. Pearson's Correlation Coefficient showed a low negative association between peak pregnancy and for the same month's rainfall ($r = -0.17$, n.s.) and a low positive association for the previous month's rainfall ($r = 0.13$, n.s.). Like the snap-trap survey results, the peak in pregnancy was associated with the season of highest fruit availability. Comparison between the pregnancy rates from snap and live-trapping surveys using the arcsine transformed data of Pearson's Correlation Coefficient showed a significant high positive correlation ($r = 0.89$, $P=0.007$).

Reproductively active, scrotal males were recorded throughout the study period with a peak in September and July, 1992. Pregnant females were recorded in most of the trapping occasions with peaks in September and November. Males with scrotal testes and pregnant females constituted more than 50% of the total captured age groups in each sex throughout the study period. Out of the total 60 females, 33 (55%) were pregnant. Adult females comprised 70% and young or subadult formed only

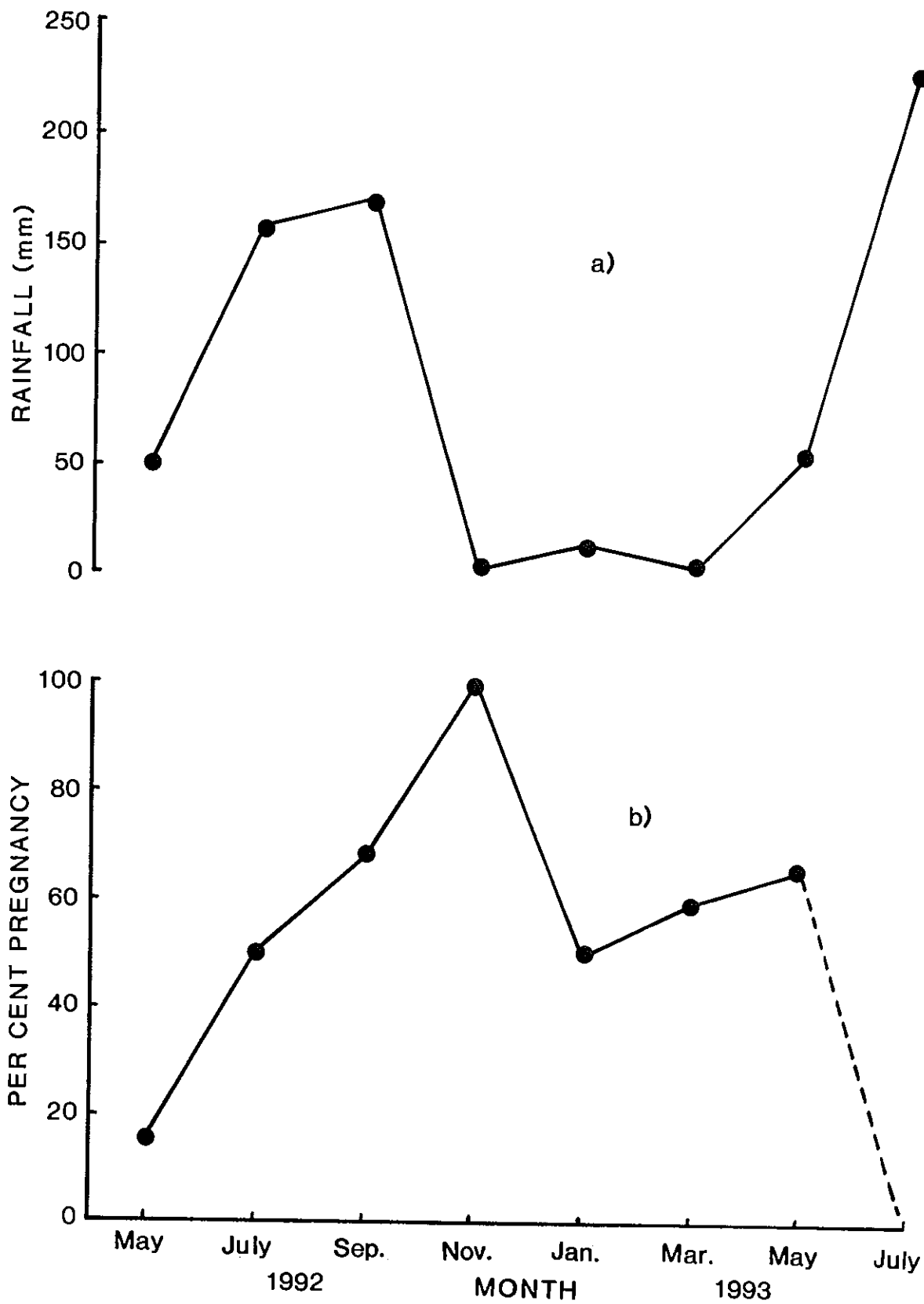


Figure 10. Relationship between rainfall at Menagesha (a) and per cent pregnancy (b) in *P. albipes* from the live-trapping grid.

30%. Out of the 66 males, 40 (60.6%) had scrotal testes. 57 (86.4%) were adults and only 9 (13.6%) were young or subadult. So, out of the total 126 individuals, young and subadults comprised only 26 (20.6%). The recruitment rate of the young **P.albipes** in the 1ha live-trapping grid was also low, further confirming the results obtained in the snap-trapping surveys.

3.2.4 Weight

Weight records for the first four trapping occasions for both male and female **P.albipes** show weight gains and reflect the increase in reproductive activity (Fig. 11). However, weight loss was also recorded for some individuals. Variations in the weights of **P.albipes** from the live-trapping grid on different trapping occasions are given in Table 12. In both males and females, heavier animals were observed during September and November. Males weighed more than females. The differences in weights between males and females for May 1992 ($t=2.6$, $P<0.02$) and for the total ($t=2.24$, $P<0.02$) were significant, but variations among different age groups in the same sample were high. In addition, small sample sizes could also have biased these results.

3.2.5 Survival

During the live-trapping surveys, out of the 115 rodents recorded as new captures, 15 (13%) died as a result of army ant and severe cold. Interference by larger mammals was low and no animal died as a result of damage to the live traps. Duration of

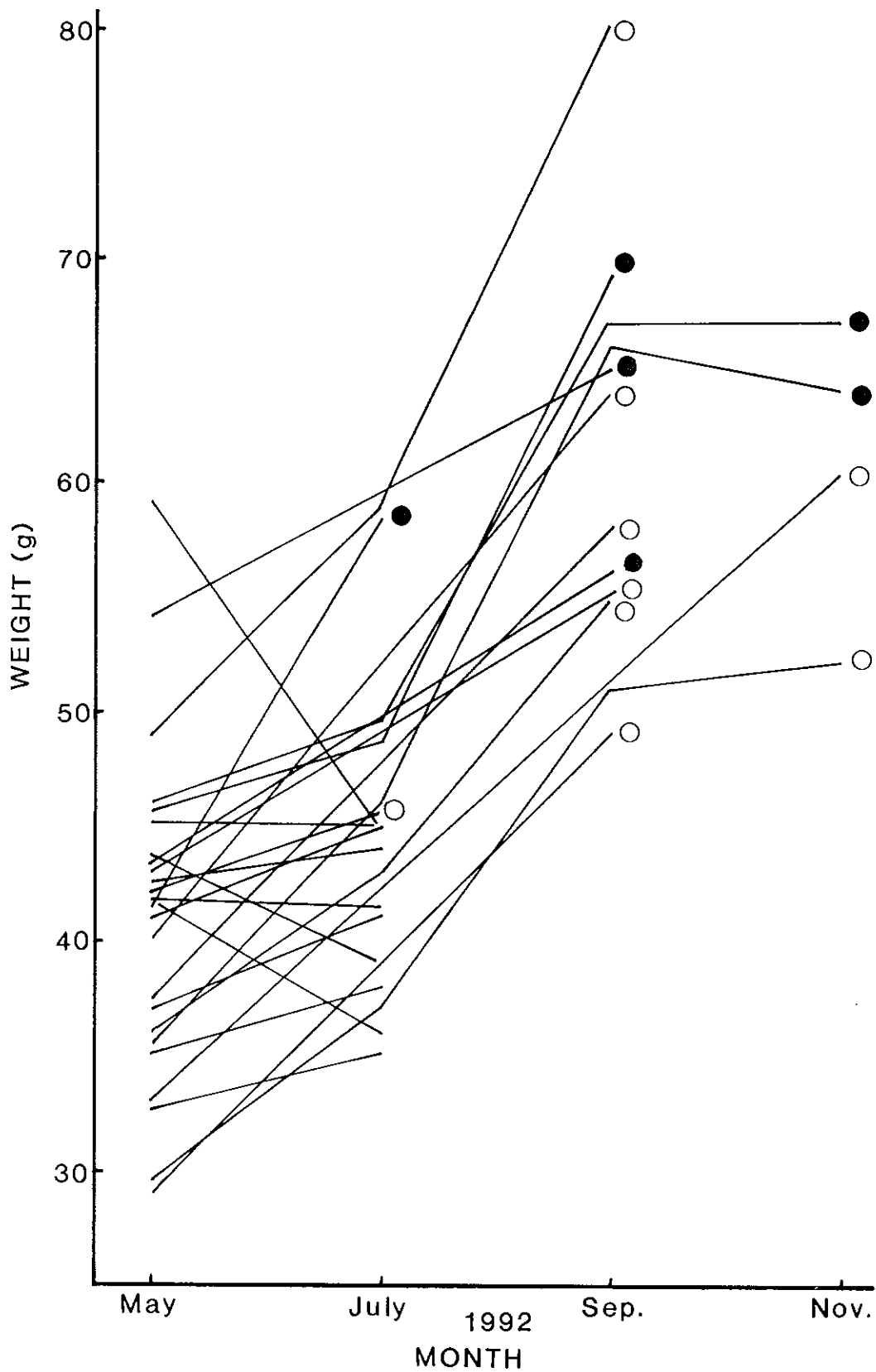


Figure 11. Weight changes for individual *P. albipes* recaptured on the live-trapping grid. Latest captures of pregnant females (open circles) and scrotal males (solid circles) are indicated.

Table 12. Mean weight (g) and S.D. of male and female *P.albipes* in the live-trapping grid on different trapping occasions (N=sample size).

		Month	N	Male	N	Female
1992		May	19	46.1±11.1	14	37.3±7.6
		July	14	45.9±6.2	8	41.9±7.7
		Sept.	9	58.0±9.4	15	51.6±11.4
		Nov.	7	59.1±9.5	8	52.3±5.3
1993		Jan.	6	47.3±21.0	6	44.5±13.1
		Mar.	3	54.7±7.0	5	45.2±11.0
		May	3	52.7±14.4	3	48.0±11.1
		July	5	47.2±20.1	1	24.0
Total			66	49.9±12.4	60	45.2±11.0

residence (survival) was recorded following the first trapping occasion. Out of the 33 individuals captured and released in the first trapping occasion, 18 survived for 2 months (54.5%), 12 survived to 4 months (36.4%), 6 survived for 6 months (18.2%), 2 survived for 8 months (6.1%) and only 1 survived over a year (3.0%). This represents the minimum known survival time since true survival should consider animals emigrating as well as the duration of residence before capture.

The above survival rate was compared with that calculated by the Fisher & Ford (1947) method of population estimation. The survival rate estimated by Fisher & Ford method was 0.56 (56%) averaged over the study period. This estimate predicts that 56% (19) survived for 2 months, 31% (10) for 4 months, 18% (6) for 6 months, 9.8% (3) for 8 months, 6% (2) for 10 months and 3% (1) survived to one year. Except for the estimate of survival to the third trapping occasion, the Fisher & Ford method closely matches the actual figures. Since this method was based on the supplied data of captures and recaptures, the result was not surprising. However, it showed that survival was distributed evenly between trapping occasions, and so is the mortality. This supported the view that population size was not affected either by a change in seasons or food availability. The survival rate was also estimated by Fisher & Ford method for males and females separately. The survival rate averaged over the study period for

males was 42% and for females, it was 58%. So, in the present live-trapping grid, duration of residence for females was higher than for males.

3.2.6 Habitat Blocks

The 1ha live-trapping grid was divided into 121 blocks (plots) in order to identify the habitat preference of *P.albipes*. Each block size was estimated to cover 10 X 10m, centered on a trap site. These were classified as forest, shrub or grass depending upon the type of vegetation (Fig. 3). To identify whether there is an edge effect in the trapping success of the animals captured, the blocks were further grouped into edge and centre (Table 13). The total number of edge blocks was 40 and the centre blocks 81. The forest blocks at the edge numbered 27 and at the centre 22 (Table 15). The shrub blocks at the edge were 8 and at the centre 32 while the grass blocks at the edge and centre were 5 and 27 respectively.

3.2.7 Block Capture

In the 40 edge blocks, 193 captures of 128 individuals of *P.albipes* were made in 1600 trap nights, whereas in 81 centre blocks, 121 captures of 100 individuals were made in 3240 trap nights (Tables 13 - 16). This shows that significantly more individuals were captured at the edge of the grid than at the centre ($X^2_1 = 54.8$, $P < 0.001$).

Captures of individuals among all the habitat blocks (Table

Table 13. The observed and expected captures of individuals between the edge and centre blocks in the live-trapping grid.

Site	Observed	Expected	No. of blocks
Edge	128	75.4	40
Centre	100	152.6	81
Total	228	228.0	121

$X^2_1 = 54.8, P < 0.001$

Table 14. The observed and expected captures of individuals among the habitat blocks in the live-trapping grid.

Block type	Observed	Expected	No. of blocks
Forest	140	92.3	49
Shrub	49	75.4	40
Grass	39	60.3	32
Total	228	228.0	121

$X^2_2 = 16.8, P < 0.001$

Table 15. Capture success for individuals of *P.albipes* between the edge and centre based on habitat blocks (number of blocks is in parentheses).

Site	Forest	Shrub	Grass	Total	X^2_2	P
Edge	103 (27)	11 (8)	14 (5)	128	11.8	<0.01
Centre	37 (22)	38 (32)	25 (27)	100	5.3	n.s.
Total	140	49	39	228		
$X^2_1 = 19.4$						
P = <0.001						
		0.2	12.1			
		n.s.	<0.001			

Table 16. Total capture events (i.e. including recaptures) of *P.albipes* between the edge and centre, based on habitat blocks in the live-trapping grid (number of blocks in parentheses).

Site	Forest	Shrub	Grass	Total
Edge	161(27)	13(8)	19(5)	193
Centre	45(22)	46(32)	30(27)	121
Total	206	59	49	314

14) show that forest blocks caught significantly more captures than either shrub or grass blocks ($X^2_2 = 16.8$, $P < 0.001$).

Table 15 shows that trap success or capture rate for individuals of *P.albipes* at the edge of the forest blocks was significantly higher than the centre blocks. However, there was no significant difference in the capture of individuals at the edge or centre of shrub blocks, but the grass blocks at the edge captured significantly more individuals than the centre.

The data from Tables 15 and 16 were used to construct Figure 12. Figure 12 shows that forest blocks at the edge and centre captured more individuals than the grass or shrub blocks. The recapture rate for the forest blocks at the edge was highest, followed by grass and shrub blocks, while the recapture rate at the centre did not vary significantly across the three habitats, but shrub blocks captured more individuals than the grass blocks.

3.2.8 Movement

Within the five days at each trapping occasion, both males and females were mostly trapped within small home ranges. Females were mostly caught within the radius of 20m. 75% of the males were captured at more than 50m home range length from the first trapping site while 30% were confined within the a radius of 20m. Only one scrotal male was trapped at sites more than 80m apart in consecutive day's trapping (wanderer). Females also stayed in the same area between different trapping occasions, while males

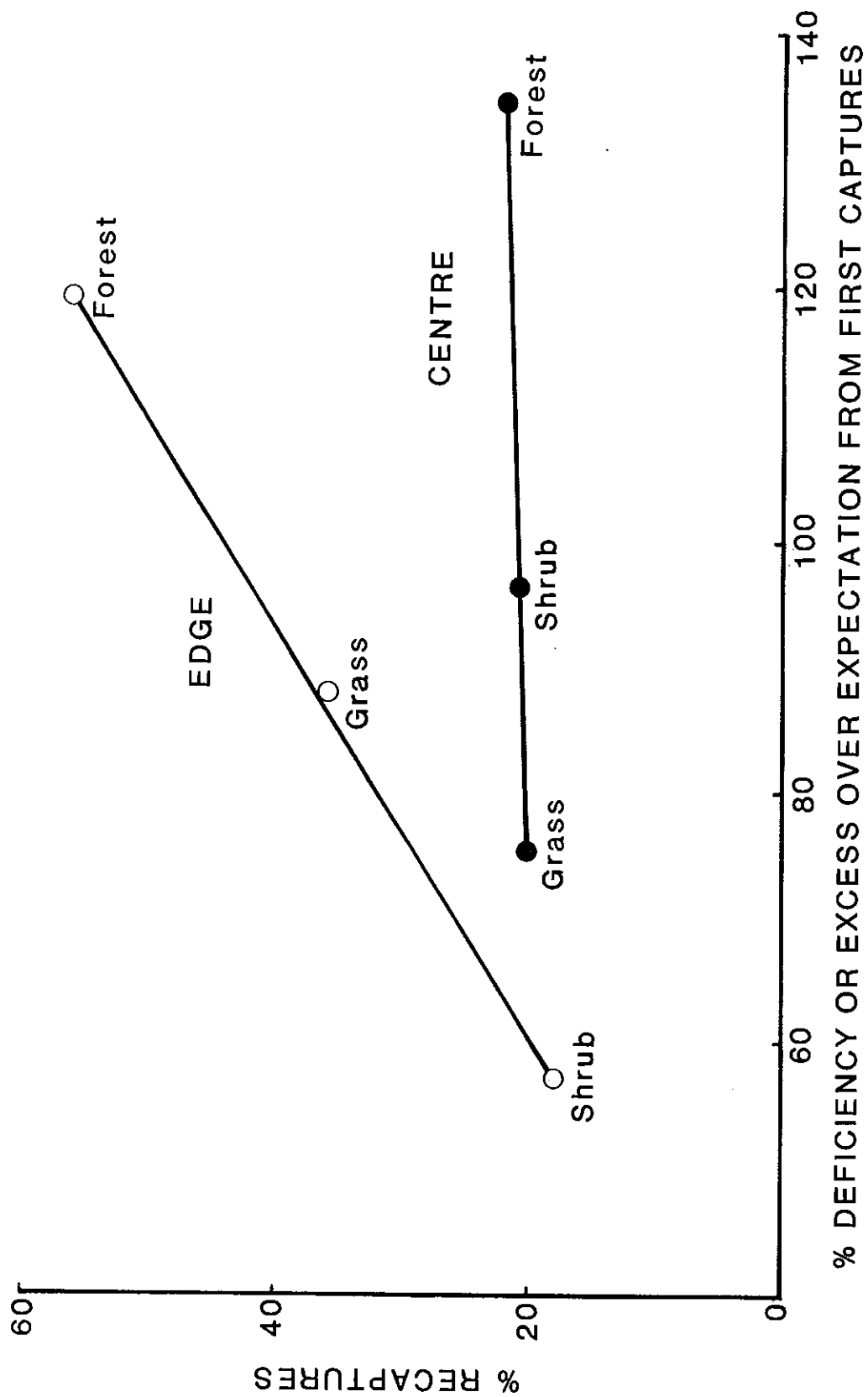


Figure 12. Per cent recaptures against per cent deficiency or excess over expectation from first captures of *P. albipes* in both edge (open circles) and centre (solid circles) blocks of the live-trapping grid.

kept on changing their home ranges at each trapping occasion. Although males were more mobile than the females, this did not significantly affect the sex ratio (66:60). Home range lengths given below are for individuals captured during four or more trapping occasions. The home range lengths from the live-trapping data confirm that females are less mobile than males (Figs. 13 and 14). In *P.albipes*, the mean home range length in metres for 13 females was 29.2 ± 12.9 while for 13 males, it was 65.3 ± 31.2 . Males wander about significantly more than females ($t=3.86$, $P<0.001$). In the final snap-trapping surveys encircling the grid, two previously marked males were captured, at 200 and 300m apart at opposite ends from the grid area, whereas no females were trapped outside the grid area. This confirms the argument that males are more mobile than the females.

3.2.9 Berry Estimation

Juniperus berry fall on the grid ground was observed throughout the year, with a peak in September (Table 17). These berries occurred throughout the year in habitats where old *Juniperus* were found. The amount of fall on the ground depended upon the number of birds active in consuming the berries on the branches as well as the amount of rainfall prior to that particular date.

During the study period, the mouths of many abandoned burrows were observed with clusters of seeds of either *Olea* or

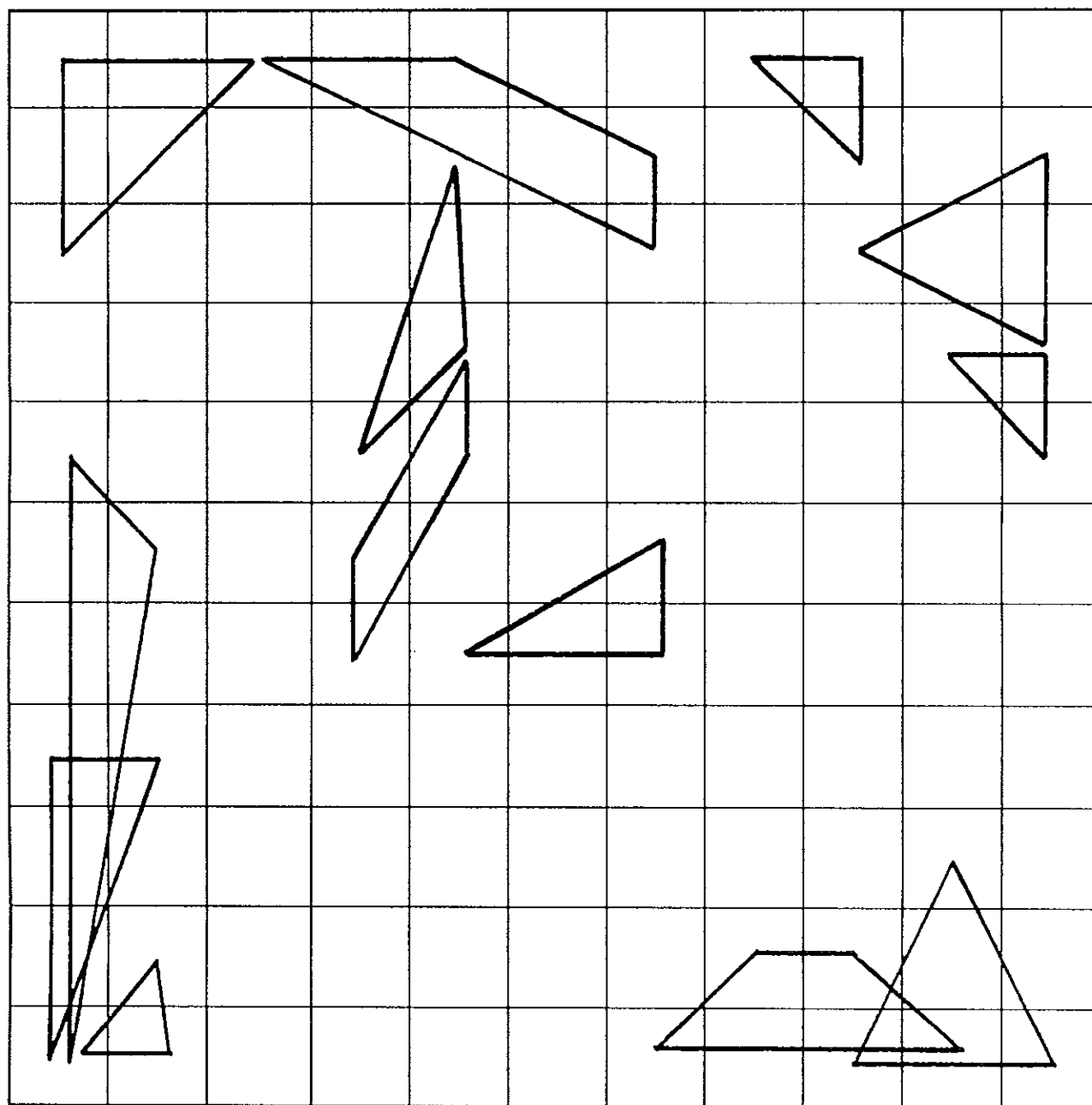


Figure 13. Home ranges of female ***P. albipes*** in the 1ha live-trapping grid at Menagesha State Forest.

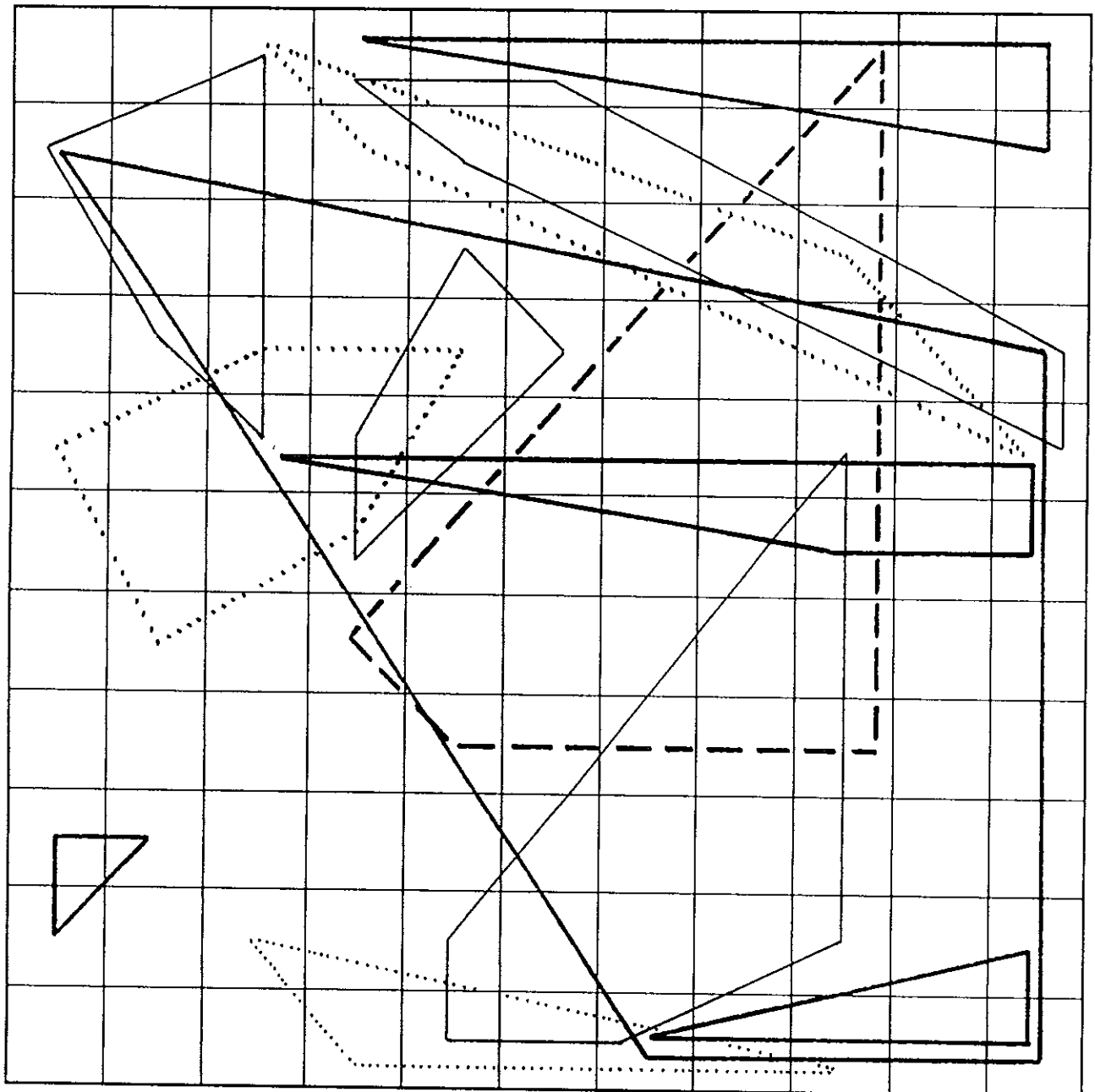


Figure 14. Home ranges of male ***P. albipes*** in the 1ha live-trapping grid at Menagesha State Forest.

Table 17. *Juniperus* berry fall over the year; 2 polythene squares each 1m² emptied over four successive days in each month, $\pm S.D.$

Sites	1992			1993		
	September	November	January	March	May	July
A	30.0 $\pm$ 9.1	13.3 $\pm$ 3.3	2.3 $\pm$ 2.1	15.8 $\pm$ 5.9	16.8 $\pm$ 9.1	22.0 $\pm$ 26.2
B	18.5 $\pm$ 6.4	3.3 $\pm$ 1.0	7.0 $\pm$ 7.4	20.8 $\pm$ 14.4	18.3 $\pm$ 14.7	13.8 $\pm$ 15.0

Juniperus. **Juniperus** berries were observed throughout the year on the ground. Some of these berries were found decayed on the ground. This availability of berries on the ground where old **Juniperus** trees occur might suggest that berry food is not a limiting factor in controlling the size of population in **P.albipes**, but some of these berries were unripe and might not be preferred by the animal.

3.2.10 Population Estimates

Population estimates of **P.albipes** in the live-trapping grid are given in Tables 18 & 19. Actual numbers caught were compared with estimates of direct enumeration (Minimum Number Alive), du Feu, Hayne, Fisher & Ford and Jolly-Seber methods.

The accurate estimation of population sizes of small mammal populations is difficult. The different methods that are available are based on some assumptions that are rarely satisfied. Some of these assumptions include: correct record of captures as marked or unmarked, no loss of individual marks, marking should not affect the animal's chance of survival or subsequent capture, either the population should be closed (no gain or loss during sampling) or an open population with equal effects on both marked and unmarked animals, equal chance of capture in both marked and unmarked animals, and marked and unmarked animals mix freely or equally.

The actual catch was compared using the five methods of

Table 18. Population estimates of *P.albipes* on the live-trapping grid using du Feu's method, $\pm S.E.$

Month	Captures	Recaptures	Capture events	Estimated population
1992 May	33	55	88	36 $\pm$ 2
July	22	39	61	24 $\pm$ 2
Sept.	24	36	60	27 $\pm$ 2
Nov.	15	18	33	18 $\pm$ 2
1993 Jan.	12	17	29	13 $\pm$ 2
Mar.	8	8	16	10 $\pm$ 2
May	6	8	14	7 $\pm$ 1
July	6	7	13	7 $\pm$ 1

Table 19. Comparative population estimates of *P.albipes* from the live-trapping grid by different methods. Each actual catch represents captures at bimonthly intervals (MNA=Minimum Number Alive).

Actual Catch	MNA	Hayne	du Feu	Fisher & Ford	Jolly & Seber
33	33	32	36±2	-	-
22	28	21	24±2	22	42
24	26	25	27±2	26	31
15	17	16	18±2	19	31
12	12	9	13±2	29	12
8	8	7	10±2	19	8
6	6	6	7±1	11	6
6	6	6	7±1	15	-

population estimates. Both enumeration and du Feu's methods slightly over estimated the population compared to the actual catch. The estimate obtained by du Feu's method varied in line with the actual captures. Even though it is a simple method to employ, with few mathematical manipulations, it assumes a closed population; this may be a reasonable assumption within the 5 days of a trapping occasion.

Hayne's method also varied in synchrony with the actual catch, except that it underestimated the population in the fifth trapping occasion. The main reason for this underestimate is that 50% of the population were caught at the last trapping session during that trapping period.

The estimates obtained by Fisher & Ford and Jolly-Seber methods were variable (Table 19). The estimates obtained by Fisher & Ford method were discrepant except for the third trapping occasion. The population estimates using Jolly-Seber method for trapping occasions 5-7 were the same as the actual catch, but the estimates for the other trapping occasions were higher. Based upon this method, the biomass estimated for **P.albipes** for July 1992 trapping occasion should have been 1890g as opposed to the actual total of 978g.

3.3 CAPTIVE BREEDING

3.3.1 Reproduction

Pregnancies were recorded throughout the year in laboratory bred *P.albipes*. Fig. 15 shows the number of litters produced at monthly intervals out of 15 adult pairs. The peak months of birth were November, followed by April and September (Fig. 15). Out of the five pairs of *P.albipes* brought live from the wild for captive breeding, two males and a female were found to be sterile. Upon autopsy of the males, the scrotal testes were observed to be very dark. About 30% of the captive bred individuals were not able to produce young even after a year. However, once females had started breeding, they kept on producing young almost every month with few breaks.

3.3.2 Young Production

From 4 successive female founders and their female offspring, I managed to get a total of 174 young in 42 litters. Litter size ranged from 2-6 young. The most frequent litter size was 5 (Table 20). The mean litter size was 4.1 ± 1.3 . The mean weight (g) at birth was 3.0 ± 0.5 (Table 21). Although the mean weight of young from the smallest litters was high, the mean weight for litter sizes 3 and 6 was the same. For comparative purposes, the mean weights of young, litter and embryo sizes in addition to the gestation period in related species of *Praomys*, from different sources, are given in Table 22. *P.albipes* shows

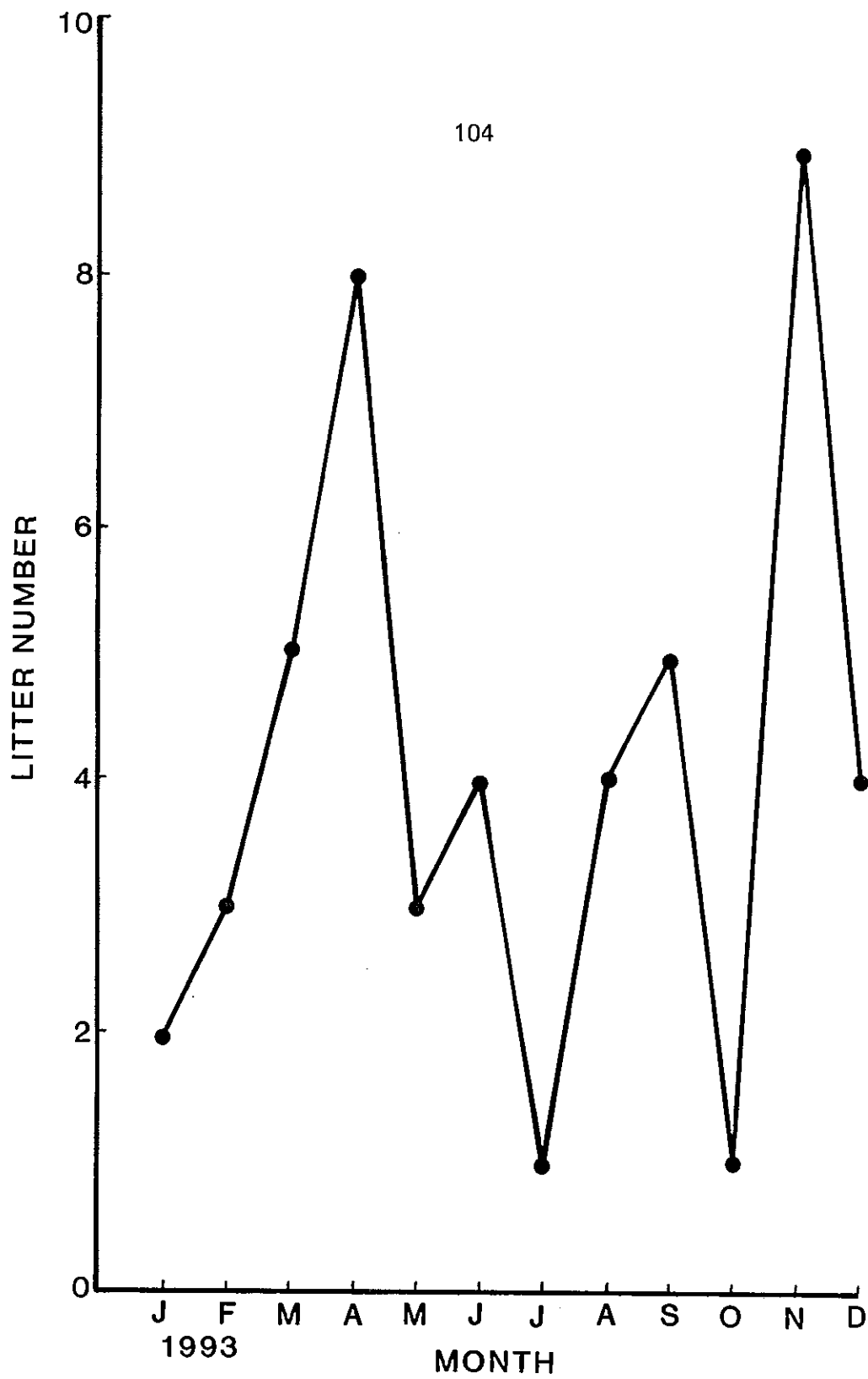


Figure 15. Number of litters in *P. albipes* born in captivity on monthly basis.

Table 20. Relationship between litter size and survival rate in captive bred *P.albipes*. Neonatal mortality is taken up to seven days and young mortality up to one month.

Litter size	Frequency	Total young	Neonatal mortality	Mortality in young	Per cent survival
2	8	16	4	1	68.7
3	4	12	2	0	83.3
4	8	32	7	3	68.7
5	18	90	15	13	68.9
6	4	24	5	0	79.2

Table 21. Relationship between litter size and weight in captive bred neonatal young.

Litter size	Number of young	Mean weight $\pm$ S.D.
2	16	3.2 $\pm$ 0.5
3	9	2.8 $\pm$ 0.2
4	28	3.1 $\pm$ 0.7
5	85	3.0 $\pm$ 0.3
6	24	2.8 $\pm$ 0.3
Totals	162	3.0 $\pm$ 0.5

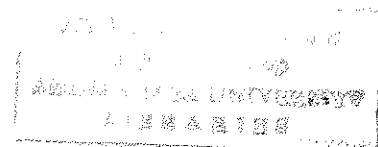


Table 22. Comparison of gestation period, mean number of embryo, size of litter and weight of young (g) among the African species of *Praomys* from different sources. Data for *M.natalensis* complex were included for comparative purposes.

Species	Gestation period	Number of embryos	Size of litter	Weight of young	Source
<i>P.albipes</i>	23 days	4.7	4.1	3.0	a
<i>P.jacksoni</i>	26 days	-	3.4	3.0	b
<i>P.morio</i>	36 days	3.3	3.3	3.0	c
<i>P.tullbergi</i>	24 days	3.6	3.0	2.7	d
<i>M.natalensis</i>	23 days	12.6	11.3	2.2	e

a) This thesis b) Delany (1975) and Dieterlen (1986)
 c) Delany (1971) d) Happold (1978) e) Baker & Meester
 (1977), Johnston & Oliff (1954), Meester (1960) and Neal (1977).

a larger embryo and litter size than its closest relatives. Out of the 174 young born in captivity, 141 were positively sexed within five days. The rest were consumed by their parents. Isolation of the young ones temporarily for weighing and measuring resulted in a very high response from the mother but not from the father. In the process of protection by the mother, moving young to their nest by mouth-dragging, some of the very young ones were injured. This resulted in cannibalism. All the young, adult female and male shared the same nest. The mother became aggressive towards the male as soon as the young ones were born, but this lasted only for half a day. The number of male to female young produced was 73:68 or 51.8 to 48.2%. It was not significantly different from the 1:1 ratio. Some of the young ones, those which were eaten by the parents before being sexed, were not included in the calculation of the sex ratio. The mortality of young up to one month old was 28.7%.

3.3.3 Breeding Pattern

In order to determine the minimum age of reproduction, young females with reproductively active males and young males with adult females were kept in separate cages. The minimum conception time recorded was 80 days (Table 23), but many females did not respond until about 120 days. The minimum gestation time recorded was 23 days, and most produced young within a month after their previous litter. Post-partem oestrous was observed in some. This

Table 23. Age at first litter, conception time and number of young in first litters of four captive bred female **P.albipes**.

Cage number	Age in days	Conception time	Number of young /litter
3	130	100	4
6	121	91	5
7	111	81	5
8	110	80	4

Table 24. Duration of reproductive life from first to last litter, number of litters produced in that time, total young produced and mortality of the young in four captive female **P.albipes**.

Cage number	Duration (days)	Litters produced	Total young	Mortality
3	246	8 (6, 5x5, 4, 4)	39	6
6	244	5 (5, 5, 4, 3, 2)	19	6
7	368	9 (5x5, 6, 6, 6, 3)	46	8
8	167	5 (5, 4, 4, 4, 3)	20	7

was performed by isolating the male from the female one day after the production of young. The number of days between two successive litters was taken as the litter interval. The litter interval varied depending upon the time of conception.

Males become sexually mature or reproductively active as soon as the testes descend to the scrotum. The time recorded for scrotal testes was between 10-12 weeks. The testes, once scrotal, remain so throughout life.

The highest reproductive performance recorded by a single adult female was 46 young within 368 days (Table 24). Mortality rates varied from 15.4 to 35%. The mortality of young was lowest in cages 3 and 7. These two cages produced more young than any other. Allowing for the different lengths of reproductive life, cage 3 produced young at a higher rate than the others.

3.3.4 Size Increase

In both sexes, weight gain was highest (more than double) during the first week of growth. This equal gain in weight in both males and females was observed up to 10 weeks. After about 11 weeks, males performed slightly better than females (Fig. 16). A high rate of increase in weight was recorded in both males and females up to ten weeks. After about ten weeks, the growth rate became slower.

Increase in the size of ear and hindfoot was recorded up to the ninth week (Fig. 17). Accurate measurement was difficult

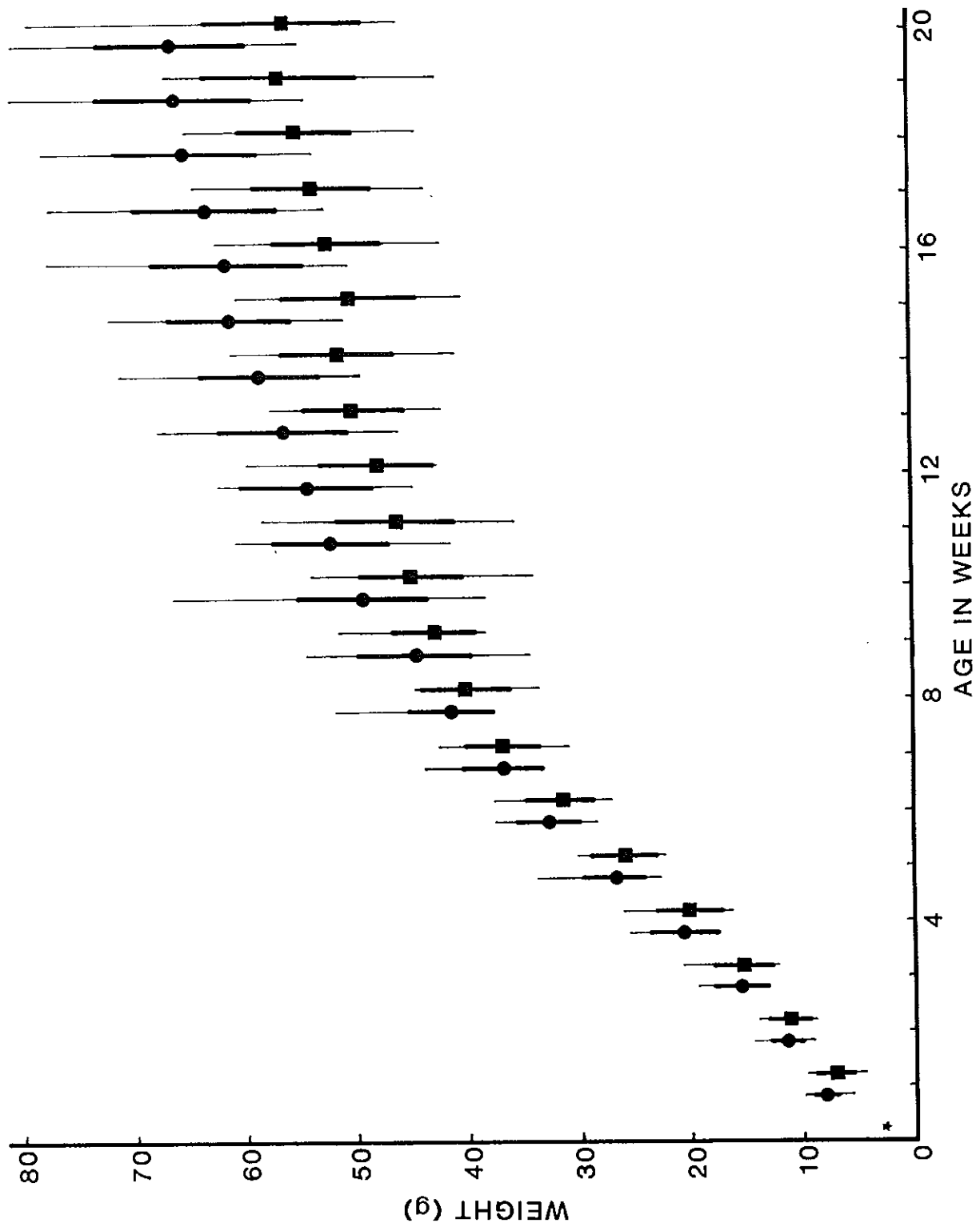


Figure 16. Weight (g) of captive bred male and female *P. albipes* up to 20 weeks (circles-mean weight of males, squares-mean weight of females, heavy line-S.D., thin line-range, and star-mean weight at birth).

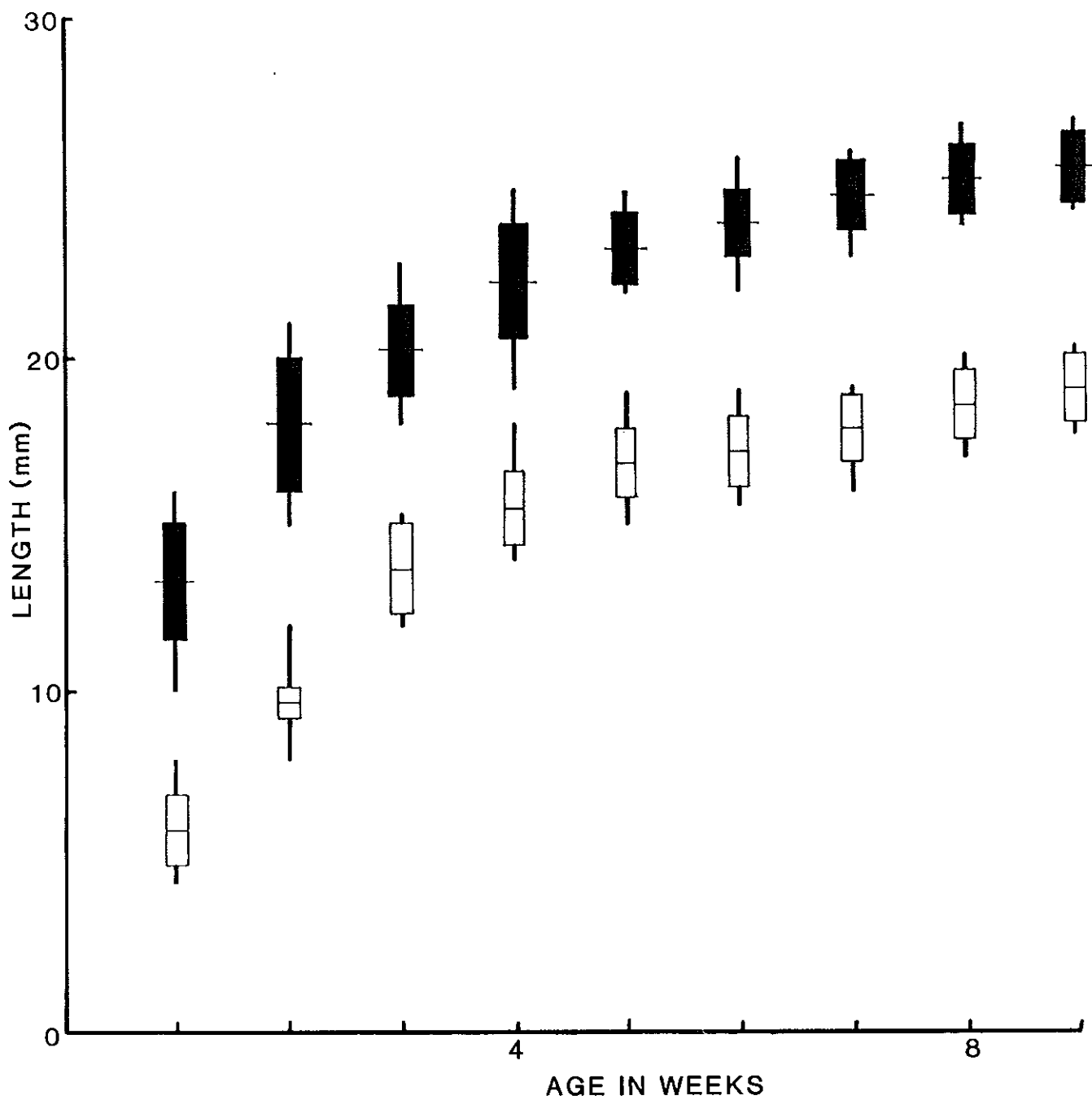


Figure 17. Growth in hindfoot (solid bar) and ear (open bar) in captive bred *P. albipes* from week 1-9 (cross line-mean, thick bar-S.D., thin line-range).

because of the activity of these animals. This increase in the size of hindfoot and ear was highest during the first 4 weeks. It slowed down after the fourth week. Increase in the length of tail and head & body was continuous until adult size was reached. Slow growth in tail and head & body lengths continues even after the adult stage is reached.

3.3.5 Physical Development

The young are born naked and pink coloured without any sign of pigmentation. Ventrally, some of the abdominal organs are visible through the skin. At birth, the ear pinnae are folded and sealed and the pups are without hearing responses. The eyes are closed. The toes are fleshy and fused. The pinnae unfold within 4-5 days and the toes separate within 5-7 days (Table 25). Within a few days, black pigmentation develops followed by fine soft and dark pelage dorsally and grey-white fur ventrally which appear within 7-10 days. Moulting of the young hair occurs gradually up to one month. At about 3 months, the rusty grey pelage is completely formed, but this transition stage is continuous and it is difficult to specify the exact date. The eyes open within 13-18 days. Lower incisors erupt earlier than the upper ones. Eruption time for lower incisors is between 10-12 days and for upper incisors, it is between 13-15 days. Young start nibbling and licking food between 16-24 days. Although it was very difficult to record exactly the weaning time, it is roughly 24-29 days.

Table 25. Observed time (days) for different developmental stages in captive bred *P.albipes* (numbers indicate individuals observed).

Days	Pinnae unfold	Toes separate	Hair appears	Eyes open	L.incisors erupt	U.incisors erupt
4	■12					
5	■17	■5				
6		■23				
7		■1	■3			
8			■20			
9			■1			
10			■6		■11	
11					■16	
12					■2	
13				■1		■13
14				■3		■15
15				■10		■2
16				■11		
17				■4		■1
18				■2		

3.3.6 Food Intake

Consumption of different food items (berries and pellets) by captive bred **P.albipes** is given in Table 26. Preliminary tests for food preference were carried out by supplying a known weight of berries, green leaves and pellets. In the laboratory, **P.albipes** consumes almost all the berries and green leaves supplied from the wild. The amount of food consumed on a daily basis shows only the food types taken by the animal, and says little about food preferences (because the animals were not given a choice) nor about the nutritional value of these different foods.

Table 26. Daily food consumption (g of berries or pellets) by a pair of captive bred **P.albipes** (each food item supplied separately).

Juniperus	Carissa	Olea	Dovyalis	Rubus	Rosa	Pellets
13.1	39.5	24.9	25.1	29.8	50.8	12.2
15.0	16.8	25.8	25.2	31.6	11.0	13.5
26.1	38.8	26.5	23.1	10.5	31.7	20.5
10.4	12.3	19.5	42.0	27.4	8.8	23.3

4. DISCUSSION

P.albipes is one of the Ethiopian endemic rodents, and one that is widely distributed over a wide range of forest habitats. Although this species is ubiquitous in its distribution, it is never very abundant. This chapter discusses the results obtained during the course of study from November 1991 to July 1993, in and around the Menagesha State Forest, central Ethiopia. Data obtained from captive breeding programme, snap and live-trapping were used to assess and compare the results with similar studies both in Ethiopia and abroad. This chapter looks at the size comparison of **P.albipes**, attempts to examine the community ecology of rodents in general and specifically, the ecology and population dynamics of **P.albipes** in the Menagesha State Forest.

4.1 Size of P.albipes

4.1.1 Weight Comparisons

In the present study, the mean adult weight of **P.albipes** was estimated to be $54.2g \pm 10.1$ from the snap-trapping surveys. The lumping of all age groups in the live-trapping survey yielded 49.9g for males and 45.2g for females. Weights for **P.albipes** were presented in Tables 8 & 12. The mean weight in the snap-trap surveys (Table 8) was restricted to adult **P.albipes** because of adequate sample sizes. In the live-trap survey, the weight was derived by lumping different age groups because of small sample sizes. As a result, lower mean weights and higher standard

deviations were observed in the live-trap data while higher mean weights were obtained in the snap-trap data both for males and females. In both cases, males weighed slightly more than females although the difference was not significant. Similar weight variations between the males and females were also recorded for **P.morio** in Uganda (Delany,1971) and for **P.tullbergi** in Nigeria (Happold,1975). In weighing females, pregnant ones were not excluded. So, it is possible that the extra weight of embryos, embryonic membranes and uterine fluids has increased the actual weight recorded. In other words, the actual difference from the weights of males should be higher than shown in the table.

The mean adult weight in the present study was compared with similar studies on **P.albipes** in Ethiopia. Yalden (1988b) obtained 49g while Rupp (1980) recorded 55.0-73.6g from various localities of Ethiopia. In the present study, the mean adult weight for **P.albipes** was between the results obtained by the above two investigators, but if all age groups were considered, the mean weight was slightly below that of 49g obtained by Yalden (1988b). The mean weights of **P.albipes** from the live-trapping grid show the highest values in November and September (Table 12). These months include the end of the wet and beginning of the dry seasons. Availability of berries was expected to be highest during these months. The high figure for November and September was associated with more numerous scrotal males and pregnant

females. Although the overall mean weight comparison showed that males weighed significantly more than females, the variations in weights among the different age groups in the same month, higher standard deviations and small sample sizes, especially in the 1993 trapping occasions, make comparison of weights at different months very difficult and not significant statistically. The 24g weight shown at the bottom of Table 12 was for a young *P.albipes*, the only female individual captured during the last live-trapping occasion. The mean weights of *P.albipes* for May 1992, January and July 1993 (Table 12) were low because the population included more young or subadults, but the low mean figure for July 1992 was due to the loss of weight by some of the adults (Fig. 11).

The highest weight recorded in both snap and live-trap surveys for a pregnant female was 80g. The highest record for males was 81g in the live and 88g in the snap-trapping surveys. The highest record obtained for captive bred females was 79.8g and for males, it was 86.1g. The highest weight recorded by Rupp (1980) was 83g. Delany & Monro (1985, 1986) obtained a difference of 10g higher in captive bred *Arvicanthis niloticus* and emphasized the limitations of applying the data obtained in the laboratory to the wild populations. In the present study, I did not find significant differences in the weights of the age groups among the captive, snap and live-trapping grid, but in the captive breeding programme, old male and female adults mostly

weighed above 60g. Variations in food availability , greater activity in an unrestricted environment and fierce competition might slow down the growth of a given animal in the wild. It is true that in the captive bred individuals, activity is limited and food is ample if acceptable to the animal, so there might be less wastage of energy and a build up of mass or fat. This did not happen in the present captive breeding programme, and one might argue that this was because the choice of food was limited or the nutrient content of the pellets might be low. This argument was not supported because during autopsy for different experimental purposes, most of these adult individuals were carrying excess fatty tissue. Happold (1975) obtained body weights of 38.0g for male and 34.9g for female *P.tullbergi* from Nigeria, with reproductively active females as low as 27g. Delany (1971) obtained a body weight of 85g for *P.morio*. So, the weight recorded for *P.albipes* was intermediate between these two species.

In the present study, weight was used to recognize age groups; the young age group of *P.albipes* weighed less than 30g, subadults less than 40g, adult males with abdominal testes and quiescent females were less than 50g, while scrotal males and pregnant females were greater than 50g. These weight categories closely match in the records of both snap and live-trapping surveys. The demarcation lines between the weights of young,

subadults, reproductively inactive and active adults as below 30, 40 and 50g were not precise, and the actual weight in each age group can vary depending upon food availability during a particular season, so there can be an overlap in weight at the higher limit of one age group and the lower limit of the next age group. Irrespective of these limitations, Figs. 5 and 6 show a good demarcation between the different age groups of **P.albipes**.

The record of weight changes in **P.albipes** from the live-trapping grid shows that weight gain from May-July, 1992 was low and some animals even lost weight (Figure 11). Weight gain was highest from July-September, 1992. This was the big rainy season. No animal lost weight during this time. This was expected because September was the month where the wet season ends and so more berries and green leaves were available. Although some individuals were not trapped, loss of weight was also observed in some adults captured in November. Similar growth stops were recorded for **P.natalensis** at the end of the dry season in Tanzania by Leirs *et al.*, (1990,1993b). Retardation of growth in **A.niloticus** was also observed during the dry season by Delany & Monro (1985). Neal (1977) observed a seasonal fluctuation of adult body weights in the same species in East Africa. These weights increased during the rainy season and decreased by 25% during the dry seasons. Field (1975) observed low body weights, below the average weight at maturity, in individuals born at the

beginning of ^{the} wet season. Under favourable conditions, individuals can mature earlier than the average.

Growth of captive bred **P.albipes** showed similar trends of increase for both males and females up to eight weeks (Fig. 16). After 8 weeks, males showed higher rates of increase but the difference was not significant. Animals reached about 30g at about 6 weeks, 40g at about 9 weeks. The rate of increase slowed down after 10 weeks (adult stage). This trend goes in line with the data recorded in the snap-trap survey where growth in head & body was highest up to 40g, more or less the adult stage, and slows down after that. The time taken to reach about 40g in the captive **P.albipes** should not be assumed to be the same as for wild animals, for the reasons explained previously.

4.1.2 Body Measurements

The mean adult body measurements (Table 8) all fall between the ranges enumerated by Rupp (1980). Slightly higher values were obtained than by Yalden (1988b). Happold (1974) gave body measurements^(mm) for head & body 103, tail 145, hindfoot 22 and ear 17.5 for **P. tullbergi**. These measurements are significantly lower than the ones recorded for **P.albipes** (Table 8), confirming that **P.albipes** is a different species from **P.tullbergi**. There was no observed difference in size increase in the ear and hindfoot between male and female **P.albipes**. Increase in the size of ear and hindfoot was highest up to 4 weeks. Growth is minimal after

the eighth week. Delany (1971) observed faster growth in the length of hindfoot up to 3 weeks of age in *P.morio*. Hindfoot length in rodents is a better indication of size for taxonomic purposes because of its relatively rapid growth, as others have also found.

4.1.3 Physical Development

The physical development of captive bred *P.albipes* was compared to similar studies for *P.morio* in Uganda and *P.tullbergi* in Nigeria. In all cases, the young were born blind and naked (hairless), with ear pinnae sealed, the outer meatus and toes fused. Although most of the durations specified for physical developments match, slight variations occurred. In the present study the timing observed for pinnae unfolding was between 4 and 5 days, while in *P.tullbergi* it was 2-3 days. In *P.tullbergi*, incisor teeth were observed at the fourth day. In the present study, lower incisors erupted earlier than the upper (10-12 days). Similar times of incisor eruption was also reported by Baker & Meester (1977) for *M.natalensis*, but those young were born with sparse hair.

The weaning time recorded in the present study was similar to that for *P.tullbergi*. However, the nibbling or licking time observed for *P.albipes* was between 16 and 24 days, whereas nibbling time recorded for *P.tullbergi* was 11 days, although the young did not swallow solid food until several days later.

4.2 Community Ecology of Rodents

4.2.1 Species Abundance

Praomys albipes, previously a poorly known endemic rodent confined to the forests of Ethiopia, turns out to be the dominant element among the Ethiopian rodents in the Menagesha State Forest. **P.albipes** comprised 57.1% of the total records in the combined live and snap-trapping sites of the Menagesha State Forest. **P.albipes**, although not very abundant, was found to be ubiquitous in the Menagesha State Forest over the altitudinal range of 2200-3385m asl. 57.1% was a very high percentage figure, compared to similar collections in different regions of Ethiopia by different investigators. At the same time, it also showed that population size for the other species of rodents was limited. Yalden (1988a), in the Harennna Forest, Bale Mountains National Park, Ethiopia, found **P.albipes** to be the largest contributor (33%) and ranged from 1510-3200m asl. **P.albipes** also comprised 25% of Rupp's (1980) collection from the south and western parts of Ethiopia. **P.albipes** has been recorded at altitudes as low as 820m asl in southwestern Ethiopia (Yalden, et al., 1976). The higher altitudinal range for **P.albipes** in the Menagesha State Forest arose because, as part of the central plateau, the base of the mountain range starts from 2200m asl.

In both the collections of Yalden (1988a) and Rupp (1980), **L.flavopunctatus** was the second most abundant species. If higher

altitude collections were considered, Rupp (1980) obtained 31.3% **P.albipes** and 24.1% **L.flavopunctatus**. By contrast, in the present study, when both snap and live-trapping surveys were combined, **M.mahomet** was the second highest component (14.7%) followed by **Pelomys harringtoni** (11.2%) and **L.flavopunctatus** (10.0%). Yalden (1988b) obtained 19.3% **L.flavopunctatus** which formed the second largest component. Yalden & Largen (1992) stress that **L.flavopunctatus** is the most abundant and widespread of the Ethiopian rodents. Although the species was widely distributed in both scrub and forest cover, in the Menagesha State Forest, the number of **L.flavopunctatus** was limited.

The mean trap success of 9.1% obtained in this study was very low compared to similar studies in Ethiopia. Yalden (1988a,b) in the Haremma Forest, southern Ethiopia, recorded a mean success rate of 18.7% and a trap success of 38.9% in **Erica** scrub. Rupp (1980) obtained a 35% trap success. In the present study, the highest trap success recorded was 26.9% for the July 1992 trapping occasion (Table 3). The 10.9% trap success (Table 4b) obtained in the **Erica** scrub includes sites with low and high human interference. My lowest trap success (1.6%) was observed in the **Erica** forest between altitudinal ranges of 2800-2960m asl, near to human habitation. Only 5 **P.albipes** were caught out of a total of 304 trap nights. These sites were intensively grazed by livestock, resulting in less ground cover. However, the

Erica scrub at 3000-3385m asl, where human interference was limited, yielded better trap success (20.3%) and species diversity; 61 rodents comprising 5 species were captured out of a total of 300 trap nights. **Pelomys harringtoni** formed the largest component in these altitudinal ranges. Yalden (1988b) recorded similar low trapping success in the **Erica** forest disturbed by human habitation and highest trap success in the undisturbed **Erica** scrub above the disturbed zone, but **Pelomys harringtoni** was not recorded in the Haremma Forest. Happold (1978) emphasized the unusually low number of **P.tullbergi** in Nigerian forest disturbed by human interference.

The trap success rate was variable in different countries of Africa. Happold & Happold (1989) in their study of montane Malawi small mammals recorded a trap success rate from 3-34%.

4.2.2 Species Composition

In the present study, the recorded composition of the rodent fauna of the Menagesha State Forest was 12 species (including **T.splendens** and **H.cristata**). Similar studies in different countries of Africa reveal variable species diversity. Delany (1966) in his study of the composition of small mammals on Mount Moroto (Uganda), recorded only 3 species of rodents and no insectivores. The ground vegetation was disturbed by human interference. The main vegetation pattern was similar to the present study site. In the present study, although the diversity

of the species was better than the above study, no insectivore was trapped. Only one young shrew was caught, by hand, in the grassy patch forming the garden of the forest station. Attempts to trap more shrews in the same site by using mini-Victor trap and local pit-fall traps in the forest did not succeed.

Delany (1964) recorded 50 species of small mammals in the grasslands and forests of Uganda. de Castro (1985) in a study of the distribution and abundance of small mammals in the eastern Cantabrian Mountains (Spain) recorded 24 species. Cerqueira *et al.*, (1993) in a continuous 5 year study in shrubby woodland of eastern Brazil, obtained seven species of small mammals with a trap success 6.02% in 1ha grid. Sampling along altitudinal gradients in two mountain localities of South Africa recorded 6 species of rodents and 2 of shrews (Bond *et al.*, 1980). Happold & Happold (1989) in the montane region of Malawi recorded 8 species of rodents and 1 shrew. Happold (1974) in western Nigerian forest recorded 14 species of rodents.

Similar studies in Ethiopia by Yalden (1988b) and Hutterer & Yalden (1990) recorded seven species of rodents and 4 shrews while Rupp (1980) obtained 10 rodents and 8 shrews (see also Hutterer, 1981). The present study recorded 12 species of rodents (two of which are sight records). These figures suggest that like the other forested regions of Ethiopia, the Menagesha State Forest has an impoverished fauna. Some of the expected Ethiopian

forest rodents like *Oenomys hypoxanthus*, *Lemniscomys striatus*, *Grammomys dolichurus* and *Dasymys incomtus* were not observed. Although the species diversity obtained in the Menagesha State Forest is comparable to similar studies in other regions of Ethiopia, it is less diverse compared to some forests of East and Central Africa. This view complements the suggestion put forward by Diamond & Hamilton (1980) about the poor forest fauna of Ethiopia as a result of reduction in the size of forests during the cold and dry periods of the Pleistocene. In addition, some of the species might have been affected due to habitat manipulation by humans prior to the introduction of conservation practices five centuries ago and the continuation of this encroachment at the present time as well.

4.2.3 Altitudinal Distribution

In the present study, *P.albipes* is distributed at altitudinal ranges between 2200-3300m asl in either bush, forest or *Erica* scrub. The distribution of rodents along the gradients of vegetation in the Menagesha State Forest was compared to similar studies in Ethiopia. As part of the central plateau, the lowest altitude of the Menagesha State Forest is 2200m asl. The range of altitudinal distribution of *P.albipes* falls within those described by Yalden (1988b) and Rupp (1980). But, in addition to the forest sites, *P.albipes* also frequents scrub or bushy vegetation outside the forest proper. The scrub area dominated

by **C.edulis** is the preferred habitat outside the forest.

Pelomys harringtoni was not collected from the Hareenna Forest, but Rupp (1980) collected the species from various localities of western Ethiopia from 1800-3200m asl. In the present study, **Pelomys harringtoni** comprised the largest collection in the **Erica** scrub above 3000m asl. Stony crevices at these altitudes were the preferred habitats.

L.flavopunctatus was widely distributed in scrub and open habitats in the forest, but in the present study, it was less abundant than in other studies in Ethiopia.

The distribution of **M.mahomet** in grassy patches, bush and open habitats was similar to the previous study by Yalden (1988a,b), but in the Menagesha State Forest, this species was restricted below 2580m asl. No **M.mahomet** was trapped above the specified altitude in the Menagesha State Forest.

A.dembeensis was unusually common at 2200m asl near grassland or farmland. **R.rattus** was ubiquitous in areas of human habitations. Rupp (1980) recorded trapping this species in the forest as well. In the present study, only one animal was captured in the garden of the forest station.

The record of **O.typus** in the present study was within the range of Rupp's collection. **S.griseicauda** was collected in the **Erica** scrub above 3000m asl conciding with Rupp's trapping. The altitudinal range reported by Yalden (1988a) was 2400-2920m asl.

The single pregnant female *D.mystacalis* was collected in *C.edulis*-dominant shrub. At the same time, the single pregnant female *G.murinus* was collected at 2500m asl in the grid near an old *Juniperus* tree. *T.splendens* was not collected, but its presence was readily recognized by its soil piles and it was common in the open forest and meadow. This species is very widespread in different parts of Ethiopia.

4.3 Ecology of *P.albipes*

4.3.1 Population Estimates

The limitations of population estimation have been discussed by Flowerdew (1976), Caughley (1977), Southwood (1978), Blower *et al.*, (1981) and Montgomery (1985,1987). In the study of population estimates, it is unlikely that all the criteria assumed in the mark-release-recapture methods are satisfied. Bronner & Meester (1987) compared the various methods of population estimation and concluded that actual numbers caught and direct enumeration methods represented population size most accurately because of their overall similarity. Chees^eman & Delany (1979) consider variations in estimating population numbers by different methods and accept the figure obtained by direct enumeration due to long periods of study (18 months). However, Hilborn *et al.*, (1976) obtained low population sizes by using the enumeration method, and Montgomery (1987), after discussing the shortcomings of direct enumeration, stressed the usefulness of the Jolly-Seber method.

In the present study, attempts were made to give population estimates by using several different methods. The direct enumeration method (minimum number alive or Calendar of Captures) assessed the number of animals alive at a given time including the temporary absentees. Flowerdew (1976) recommended this method if the trapping interval was once a month with longer trapping sessions than five days. In the present study, the trapping intervals were bimonthly and trapping sessions only five days. At the same time the actual catches fell towards the end of the study.

Both du Feu **et al.**, (1983) and Hayne's (1949) methods assume closed populations in the estimate of animal numbers, constant probability of capture and that marking should not affect the chance of recapture. Trapping sessions were carried out each for five days. The data at each trapping occasion were lumped together in order to estimate the population size using Fisher & Ford and Jolly-Seber methods. The population estimates using Fisher & Ford and Jolly-Seber methods were of course higher than the actual catch or direct enumeration method. Even then, the total population size was lower than those observed in many habitats. In estimating population numbers, only **P.albipes** was considered, so the total rodent population would be higher if the other species were taken into consideration.

Since so many factors determine the number of captures, I

do not claim that during the present study all animals dwelling in the area have been captured. Sidorowicz (1960) argues that rain increases the number of animals captured in the forest. In the present study, however, the low population was obtained during the last trapping occasion of the heavy rainy season. Gurnell (1976) observed the capture of fewer animals during cold and wet seasons because of their reduced activity. The species type, age, sex, drought, heat and moonlight for nocturnal animals were also some of the factors involved in affecting the capture of animals. In the present study, about 5% of the traps checked were found sprung either due to rain or baboons or other predators like the white tailed mongoose. No allowance was given in the estimation of numbers.

Bait preferences of the animals might also play a role in the number of captures. Beer (1964) found peanut butter to give the best results for shrews and rodents. In the present study, attempts were made to assess the bait preferences of rodents in the Menagesha State Forest. During the early preliminary surveys, onion, vegetable oil on a sponge and peanut butter were used separately. Peanut butter was used throughout the study period because of its availability and preference by the rodents. Meat was used in an attempt to trap shrews.

4.3.2 Biomass

In the present study, I estimated a monthly biomass of mixed

rodents on the live-trapping grid from ranging 454-1546g/ha and the density of individuals varied from 12-35/ha. These figures seem low compared to similar studies in different localities of Ethiopia; in particular, Müller (1979) in the Simien Mountains National Park at 3700m asl obtained 4900 - 16,500g/ha for **Arvicanthis abyssinicus**. This result is associated with the population dynamics of the species. **Arvicanthis** is a prolific breeder with a litter size of 4.9, a higher growth rate and younger age at maturity. But, the above estimates were obtained from grasslands as opposed to forest habitats. Yalden (1988b) reported 1258-1565g/ha in the Haremma Forest in August 1986, a comparable biomass to my figures. Similar studies in Africa show figures in a variable range. Happold (1975) in Nigerian forests obtained 5-50 rodents/ha. Happold & Happold (1989) estimated the densities of small mammals in montane areas of Malawi from 20-29/ha while in woodland this density varied from 3-17 individuals/ha with a seasonal fluctuation in biomass from 143 - 575g/ha. Cheesman & Delany (1979) in grasslands of Uganda recorded a rodent biomass from 672 to 2221g/ha. Hanney (1964) obtained a low density of 4.7 animals for the harsh-furred rat in Malawi. Gliwicz (1985) in the savanna of Mozambique obtained densities of 9-33/ha.

Biomass estimates for small mammals in the lowland forests of Zaire are unusually high; Dieterlen (1967) found densities of

236-361 rodents/ha. Fleming (1971) in his small mammal study in Panama obtained a biomass of 4025-6304g/ha. Comparison of densities was difficult due to the variation of weights in different species of small mammals.

Comparison of biomass estimates is complicated due to variations of habitats and different rodent faunas. At the same time, trapping also underestimates the numbers available. Some of the species, with arboreal or fossorial life-styles, might not be accessible to capture. At the same time, like all other studies, it also assumes that all small mammals are trapped during that occasion. Biomass estimates are thus only a gross approximation. Grasslands in Africa support a higher biomass of rodents than forests. In savanna areas, the grass is mostly available for mammals while in forests most of the energy is concentrated in the trees, which in most cases is unavailable for animals.

In the present study in the Menagesha State Forest, I found rodents to be less abundant both in species type and number than similar studies in forest habitats of Uganda and Zaire. As a result, their contribution to overall biomass is low.

4.3.3 Habitat Preference

The results in the Tables 13-16 and Figure 12 show that there is a significant association on the live-trapping grid between *P.albipes* and the forest habitat as opposed to the grass

or shrub blocks. This relationship was further complicated by the additional significant edge effect, which can also be readily demonstrated by comparing the blocks. The one-third (40) of the blocks at the edge of the grid captured more than 56% of *P.albipes*, compared to the 81 blocks in the centre which only captured 44%.

Taking these two features, if the 3 habitat types on the live-trapping grid were compared just for the edge blocks, trap success for the forest blocks was significantly higher than the the shrub or grass blocks. In other words, more individuals were caught in the forest edge. At the same time, grass blocks at the edge also captured more individuals than the shrub, but less than in the centre. The capture of more individuals in the grass blocks at the edge than the shrub should not be surprising because the blocks assigned to grass include other herbs as well. In addition, the occurrence of more green leaves and herb cover in the grass blocks might have been attractive to the species. This has been suggested by the diet analysis which frequently recorded green leaves in the stomach (see section 3.1.9). At the same time, some shrub blocks had barren ground, with no vegetation cover, and only produced fruit at a particular season.

The per cent recapture rates for the six compartments (three at the edge and three at the centre) were compared with the per cent deficiency or excess of first captures over the expectation

of random capture across the grid by manipulating the data from Tables 15 and 16 to obtain the results in Figure 12. Figure 12 shows that the total capture events in forest blocks were markedly higher than the shrub or grass blocks and emphasises the very high recapture rate for the forest/edge blocks. These results are in line with the observations of Yalden (1988a,b), confirming that *P.albipes* is indeed essentially a forest animal, and extend the results from the snap-trapping survey (Table 4b); not only does *P.albipes* prefer the forested parts of Menagesha, but within the forest prefers the most tree-covered blocks.

In the present study, the area covered by the live-trapping survey was strictly 1ha, but the confirmation of edge effect indicates that the effective trapping area was bigger than 1ha. Thus, the density or biomass of rodents should be less than the actual figure calculated (Table 10). It is however, difficult to estimate by how much the density or biomass should be reduced. If the radius at each trapping site was considered to be 5m, then the total grid area would be 1.21ha. Based on this figure, it would be possible to recalculate the biomass. This trapping radius is only an approximation and it is difficult to work out the actual estimate of the increase in the area. In the present study, males of *P.albipes* showed longer home range lengths than females (Figs. 13 and 14). Radio-tracking studies carried out by Wolton (1985) and Attuquayefio *et al.*, (1986) on wood mice

Apodemus sylvaticus showed that home range movement and sizes varied depending upon the habitat type and sex. During the breeding season, males doubled their home ranges compared to the females. Although radio-tracking is an expensive project, further work should be carried out to assess the movement and home range sizes of **P.albipes** precisely.

4.3.4 Food Preference

The food preference in captive bred **P.albipes** was tested by supplying the animal with a known weight of different food items from the wild as well as with the standard pellets. **P.albipes** consumed all of the food items, but in different proportions. However, this was a gross estimation of food intake without considering its calorific value.

Accurate estimation of the diet should consider per cent occurrence (identification), per cent amount (volume) and calorific values. In the present study, gross identification of food items was conducted in 113 stomach samples. Most of these food items were less chewed, making them easier to identify. The preliminary work of supplying captive animals with a known food item from the wild and sacrificing them to observe the stomach contents helped a lot in the positive identification of some of the major food items.

In the present study, the nutrient content of the food items was not studied. Some food items should be more nutritious than

others. Fatty foods are better than watery ones and dry cereal seeds are more nutritious than watery ones. So, estimating the calorific content of some of the wild berries and pellets, might in the future answer some of the queries like how much **P.albipes** needs and what limits the food supply of the animal, its growth, breeding pattern and even population size. The identity and importance of the green food needs investigation. More detailed work on the quantity and quality of these food items from different localities should be carried out, probably as a small scale student project.

4.4 Population Dynamics of P.albipes

4.4.1 Embryo and Litter Sizes

In the present study from both snap-trapping and the captive breeding programme, high mean embryo (4.7) and litter (4.1) sizes were obtained. From the captive bred animals, a gestation period of 23 days was also recorded.

The data obtained from the snap-trap surveys on embryo size and from the captive breeding programme on litter size were compared with similar studies in related species from West, Central and East Africa (Table 22). The gestation time (23 days) for **P.albipes** was among the lowest of the species compared. The mean litter and embryo sizes in **P.albipes** were higher than all of the related species studied. Although gestation time for **M.natalensis** was similar to that of **P.albipes**, weight of young,

litter and embryo sizes were different.

In the calculation of mean embryo sizes for **P.albipes**, resorbing embryos were excluded since they did not contribute in the number of viable young. Implantation sites in the left and right horns did not significantly differ (47:41). Delany (1971), in his study of **P.morio** in the forests of Uganda, observed significant differences in the implantation sites between the right (134) and left (89) horns.

In the present study, the most frequent litter size in the captive bred **P.albipes** was 5 as compared to 4 from the wild embryo counts. Happold (1978) in his study of **P.tullbergi** from Nigeria obtained a litter size of 3 as the most frequent, while Delany (1971) recorded 4 as the most frequent litter size for **P.morio**. In the present study, the mean weight of young from the smallest litter size (2) was high, but overall variability and small sample sizes confound these results. Overall, new-born young weighed $3.0g \pm 0.5$. Delany (1971) recorded the mean weight of young in a litter size of 2 to be similar to those in litters of 4 in **P.morio**.

In the present study, extreme differences were observed in the weights of young from similar litter sizes from the same mother. So, it was not possible to conclude that young from low litter sizes weighed more than those from higher litter sizes. The weight of young can vary depending upon the condition of the

mother. It is possible that well fed mothers can give birth to heavier individuals than underfed mothers. In the present study, pellets were supplied in excess at all times, and all had equal access to the food supply, so the variation in the weight of young among the same litter, small sample size and the similar mean weight between litter sizes of 3 and 6 suggest that there is no systematic difference among litter sizes.

The 23-30 days gestation period recorded for *P.albipes* was within the range recorded by *P.jacksoni*, but lower than that of *P.morio*. Exact gestation time was recorded by removing the male from the female within 24 hours of giving birth. This practice was repeated in 6 individuals. Four of these females gave birth at 22 day intervals, while the other 2 did not respond. In undisturbed cages, repeated births were recorded at intervals of 23-30 days. The 30 days interval might indicate that the female was pregnant during the second oestrous cycle as observed by Happold (1978) for *P.tullbergi*.

Age at the time of first conception was calculated by subtracting the highest gestation time from female age. Although the earliest conception time recorded for *P.albipes* was 80 days, this varied considerably among individuals. Most females bred after 5 months. Similar studies for *P.tullbergi* from Nigeria showed a conception time of 62-115 days. The earliest date for production of a litter in *P.morio* was 95 days with a conception

time at about 2 months old.

There were wide variations in the number of young produced by the female *P.albipes*. But, most females once they produced young, did so continuously. Continuous production of small litters was also observed in some. The size of the first litter born was not necessarily associated with small litter size subsequently.

The reproductive life, from the first litter to the last as shown in Table 23, indicated the maximum number of young produced during that time for the selected females, but many females did not attain that many. In fact, because of so many factors, low productivity should be expected in the wild, and the data only show the possible maximum production number per female at a given time provided that other factors did not interrupt the system. In the wild, the reproductive potential will not be realized because of variations in food availability, mortality or predators.

4.4.2 Population Decline

During the study period, the population of *P.albipes* declined drastically, especially in the last four live-trapping occasions. Not all age groups were represented in all trapping occasions because of low sample sizes, as seen in Tables 5 and 11, but in combination, these two tables show that *P.albipes* breeds throughout the year with peaks in September and November.

Comparisons between pregnancy rates from both snap and live-trapping data showed a significant level of association, but the association between rainfall and peak pregnancy was not significant. However, rainfall is one of the major factors in increasing food production in a given habitat, but its effect is observed at the end or beginning of the successive season. In the present study, peaks in pregnancy rate are associated with the end of wet season or the beginning of dry season when the berry supply was plentiful. At the same time, as indicated in Table 17, berry availability was also highest in September.

The captive breeding programme also showed that *P.albipes* breeds throughout the year with a peak in November, but not in September. However, factors that might control the breeding pattern, especially rainfall and its effect on food availability, were not represented in the laboratory, so this comparison is doubtful.

My study shows that *P.albipes* breeds throughout the year as do that of *P.morio* and *P.tullbergi*, but has a higher litter size than either *P.morio* or *P.tullbergi* and shorter gestation period than *P.morio*. The net effect of all these factors should be a fast turnover and greater population size. However, both the live and snap-trapping surveys show that the species was never abundant and in fact declined towards the last trapping occasions despite the presence of both young and subadult age groups in

most trapping occasions. Was the population decline in **P.albipes** in the Menagesha State Forest a natural phenomenon? Was it associated with availability of rainfall, food, temperature, predator, disturbance by the present investigator or cannibalism?

In the Menagesha State Forest, small and long rains occupy most months of the year. The dry season was from November to February. Even during these months, small amounts of rain were expected. This extended rainfall should result in the production of more food, extended periods of reproduction and higher female fecundity. The overall effect of these should result in a greater production of young per female per year with a wide spread of age ranges throughout the year. The mean rainfall for the 1981-1993 for the nearest station (Holeta) shows 75.1 for March. The figure for Menagesha for ~~the same~~ month during 1993 (Table 1) was only 4.3m. Thus, a smaller amount of rainfall than usual fell at the end of the dry and beginning of small rain seasons. This extended dry season up to March might have played a role in the decline of the population of **P.albipes**. Probably low juvenile survival or a higher mortality rate might have contributed to it. The cause of mortality was not known. Certainly the volume of the rain at the beginning of 1993 was only 40% of that in the equivalent 1992 season (Table 1).

The cause of decline in population ought not to be food, because, as mentioned earlier, berries and green leaves were

available throughout the study period, even though the quantity varied from season to season. Some of these berries might be too unripe to be taken by the animals. Table 17 shows a very low berry fall in January 1993 (dry season).

The causes of population fluctuations in rodents are very variable. Different investigators have argued for climate, food abundance, food quality, predation, vegetative cover, endocrine organs and genetic quality. Cerqueira *et al.*, (1993) detected no regular pattern of seasonal population fluctuations, but observed pluriannual patterns of fluctuations in their 5 year study of small mammals in eastern Brazil. Andersson & Jonasson (1986) in their studies of microtine rodents in Sweden observed strong fluctuations, up to 100 fold, in density. But, food quantity and nutrient levels were not the main factors for the fluctuations of these microtine rodents. So, it is possible that other factors might have played a role in the decline of the population of **P.albipes**. From the live, snap and captive breeding data, it was confirmed that **P.albipes** breeds throughout the year. The presence of active scrotal male throughout the study period suggests that factors influencing breeding were controlled by the females and not by males.

The productivity of a given habitat was associated with the numbers of animals occupying that area. Berries and green leaves were available throughout, although their nutritive quality was not assessed.

Different investigators have proposed that photoperiod, water content of the food, hormones in germinating vegetation, cover, temperature and rainfall influence breeding activity in small mammals. Food was considered the main factor that determined breeding cycles. Happold & Happold (1990) obtained low numbers of animals because of a shorter rainy season. This resulted in strong fluctuations in food resources, reduced opportunity for reproduction and overall low productivity. In African savanna, higher biomass of large mammals was correlated with higher annual rainfall (Delany & Happold, 1979). This might be true for small mammals as well.

Many studies of African small mammals show that breeding commenced at the end of wet season or at the beginning of dry season. This was no doubt associated with food availability, but food availability was not the only factor in initiating breeding. This was demonstrated by Taylor & Green (1976) who supplied excess food for *M.natalensis*. This did not initiate reproduction, but resulted in excess fat deposits. Sharpe & Miller (1990) observed the timing of initiation of breeding in *Peromyscus maniculatus* to be related to nest-site habitat. Availability of breeding site might play a role in determining breeding. In the present study site, especially in the grid, burrows were observed to be plentiful. Most of these burrows were abandoned ones, because setting traps at the mouth of the burrow caught few

P.albipes. At the same time, very old **Juniperus** and **Olea** seeds were observed at the entrances of the burrows. The presence of unusually high number of burrows might indicate that the area was occupied at least in the recent past when the population was high. During the live-trapping surveys, it was observed that the released individuals hid themselves in any burrow very rapidly.

It is also argued that it is not the availability of food, but the nutritional level maintained in the diet of an animal that enhances breeding. Field (1975) observed that 16% protein in the diet of a small mammal was sufficient to support both reproduction and growth. However, Swanepoel (1980), showed from the analysis of **M.natalensis** stomach contents, there was no difference in the diet between the breeding and non-breeding seasons.

Oestrogen content in the grass has been proposed to stimulate breeding in rodents. Leirs **et al.**, (1993c) in their abstract on **M.natalensis** from Tanzania, confirmed that both temperature and food supply were not the limiting factors in initiating reproduction. From laboratory studies, they showed that sprouting grass has a stimulating effect on reproduction and breeding was triggered by supplying new vegetation. Happold (1978) stressed the importance of an adequate supply of leaves for reproduction in captivity. **P.tullbergi** did not breed during the first year because forest leaves were not provided, but when

leaves were made available, they bred within a few weeks. Grass was available during most months of the year in the Menagesha State Forest, but the level of oestrogen in the grass was not determined, and since new shoots possess more oestrogen, this could be a factor.

P.albipes has large litters and breeds throughout the year. The potential number that could be produced should be higher than obtained during the first live-trapping occasion. The present study revealed that population density was never high, and moreover declined during the study periods. The dry season and low food availability were not the factors producing the decline in population, because the lowest number was observed during the wet season when green leaves were abundant and at a time of year when the population was at a high level during the previous year. The low mean weight in July 1992 might also suggest that the population was not doing well even during the wet season.

Neal (1986) stressed the effect of temperature at higher altitudes in causing a delay in reproduction. During the present study periods, the informal recordings at Menagesha show that temperatures were never extreme (Table 2); minimum and maximum temperatures fluctuated by only 4°C from month to month. Temperature might play a role at extreme altitudes like for **Arvicanthis abyssinicus** inhabiting the moorland of Simien at 3700m asl. Müller (1977) observed reproduction in this species

during the dry warm season and obtained a very high biomass. **A.abysinicus** had a litter size of 4.9. Since it is an opportunistic breeder with fast growth to maturity, the turnover should be high and so is the biomass.

Trapping disturbance by the present investigator might initially look like the cause for the decline in **P.albipes**. The death of five pregnant females might seem significant because with an average litter size of four, the population would increase by 20 if all survived. Moreover, these would be likely to reach reproductive age within five months. Although this mortality might seem likely to affect the population, the following arguments suggest that in fact it was not significant. The deaths of five pregnant females were spread during the course of the study period and through time the turnover was expected to be high. Given the small size of the grid (1ha) in relation to the size of the forest, the unoccupied space left by accidental mortality ought to have been filled by immigrants from neighbouring sites. At the same time, with a mean litter size over four and the short gestation period accompanied with continuous reproduction, the replacement level after the population decline should be fast because of low competition for food and space. Extrapolating from the first live-trapping occasion, there should have been an increase in population during the interval to the next trapping session, even after making

allowance for the calculated 50% mortality. The high number of pregnant females in September and November 1992 should have resulted in population build-up. In fact, from 11 pregnancies recorded in September 1992 (Table 11), no young or subadult was captured in the November live-trapping occasion. At the same time, out of the 8 pregnancies recorded in November 1992, only 4 young or subadult were caught in January 1993 as opposed to the theoretical 32. These data indicate that the ageing population was not being replaced at a constant rate and the recruitment of young or subadult to the population was very low. Probably the mortality rate for the young was very high. The snap-trap surveys (Table 5) also show that few young were being recruited compared to the total population size. Out of the 76 female *P.albipes* captured during the snap-trapping surveys, only 21 (27.6%) were young or subadult. Out of the 83 males, only 19 (22.9%) were young or subadult. In general, of the total 159 *P.albipes* captured during the snap-trapping surveys, young or subadult contributed 40 (25.2%). Similar figures were also observed in the live-trapping grid. Out of the 60 females, 18 (30%) were young or subadult. Out of the 66 males, 9 (13.6%) were either young or subadult. In other words, out of the total 126 individuals of *P.albipes* captured in the live-trapping grid, only 26 (20.6%) represented the young or subadult population. So, these data indicate that the recruitment rate of the young was very low, resulting in the population decline.

Emigration (dispersal) was not considered as a factor causing the decline because animals should disperse randomly, so being as likely to enter as leave the grid. During the last trapping occasion, an area up to 400m encircling the grid was snap-trapped, but this resulted only in the capture of two marked adult males and produced the lowest trap night efficiency of any snap-trapping session (4.7%, see Table 3). Thus, the size of the *P.albipes* population outside the grid was also very low in mid-1993 compared with the equivalent period in 1992.

From the live-trapping surveys, I observed that the mobility rate for females was lower than males (Figs. 13 and 14). Duration of residence (survival rate) for females was higher than for males. These factors should have helped to produce a faster turnover.

During initiation of the captive breeding programme, four pairs of live *P.albipes* were captured from different habitats of the forest and brought to the laboratory to form the founder colony. Through time, I observed that two males and a female were sterile. At the same time, about 30% of the young reared in the laboratory failed to produce young even though they were kept up to one year old. It was possible that, due to some unexplained cause, the sterility rate was high, resulting in a low reproductive output.

In the captive breeding programme, mortality of the young

due to cannibalism was more than 25%. It was possible that similar high mortality of young in the wild might also have played a role in reducing the population. Happold (1978) also observed both females and males consuming their young in *P.tullbergi*. So low survival rate of the different age groups either due to cannibalism or predation might play a role in controlling the population of *P.albipes*.

During the night time, owls were very frequently heard (Scops owl-*Otus scops* and Barn owl-*Tyto alba*). At the same time, *P.albipes* although a ubiquitous species, by no means were abundant in a given area by comparison with *M.natalensis* or *A.dembeensis*.

Data from snap and live-trapping surveys augmented by a captive breeding programme showed that *P.albipes* breeds throughout the year. From both snap and live-trapping surveys, seasonal peak pregnancies were recorded at the beginning of the dry season (November). Following this, a sharp increase in young or subadult recruitment was expected in January 1993. However, the data in Tables 5 & 11 show a very negligible recruitment rate for young or subadult. In fact, Table 5 shows a very poor level of recruitment throughout the year. Although more pregnant females were recorded, high young or subadult mortality due to various reasons must have caused in low recruitment rate, resulting in a decline in the population size.

P.albipes is also widely distributed in different localities and habitats of Ethiopia, including sites where **Juniperus** and **Olea** do not occur. The food items consumed by this species are therefore also likely to include different species. At the same time, the pattern of rainfall varies from region to region. The composition of the rodent fauna is also variable. Competition for a similar niche e.g. from **Praomys ruppi** or **Stenocephalemys** species is also likely to affect the distribution and abundance of the species. Is **P.albipes** behaving in the same manner in different regions of Ethiopia as in the Menagesha State Forest? If not, what strategy does the species follow in these regions? How do the patterns of rainfall, food type and distribution, competition among the species and environmental degradation affect the species? Further long term and continuous investigation should be carried out both in the present study site and in different regions of Ethiopia. The effect of food on the abundance of the species should be carried out by supplementing its food. More work on the mechanisms involved in population dynamics of the species needs should be conducted, perhaps as small scale student project. Comparative studies from different localities will have to be compiled in order to come up with a comprehensive understanding of the population dynamics of **P.albipes**.

5. CONCLUSIONS

P.albipes is an endemic rodent species widely distributed in many forest habitats of Ethiopia. In the Menagesha State Forest, it is ubiquitous and mostly dominant across a wide range of altitudes. It breeds throughout the year with peaks during the end of the rainy and beginning of the dry seasons. Once the adult stage is reached, males with scrotal testes become reproductively active and remain so throughout life. The litter sizes range from 2-6 and gestation period is 23 days. The adult stage is attained within 3 months at about 40g in weight. Preliminary diet analysis shows that berries and green leaves comprise important food items for the species. Despite its catholic diet and high reproductive potential, the population in this study area does not seem very abundant. Moreover, the species is concentrated in areas of forests where human interference is low. Unfortunately, these forest habitats in Ethiopia are shrinking from day to day due to human population pressure. At the same time, the social, political and economic turmoil in the country is aggravating deforestation at a faster rate. The Ethiopian Mapping Authority (1988) estimated that at present about 3% of the country is covered with forest as opposed to the former 37%. At the present time, temporary absence of law and order has intensified the destruction of relict forests in isolated localities. The Menagesha State Forest is no exception to this destruction. This

once protected state forest is being destroyed by the surrounding farmers. Urgent conservation measures should be taken before mass destruction occurs.

The highland forests are not only important water catchment areas, but also help in reducing erosion, serve as genetic resources, for honey production, for traditional medicines, pollination, food production, fuelwood and timber production. Unfortunately, most of the 52 million people of Ethiopia are concentrated in central highlands where the present remnant forests occur.

Primitive farming methods coupled with population pressure are likely to affect even the remaining relict forests. More clearance of forests for farming, timber and firewood is likely to continue unless preventive measures are taken. The present emphasis on maintaining biodiversity from the Rio-Earth Summit should give priority to preserving these relict forests before it is too late.

These forests are important areas serving as a refugium because of the shrinking population size of some forest mammals. This shrinkage is likely to affect the population of *P.albipes* as well as other forest mammals. So far, there is no harmony between the responsible authorities and the farmers that live in these areas. Proper conservation education has not been given to increase the awareness of the farmers. Most of the farmers are

not aware of the damage that they are inflicting on the environment. Their immediate attention is to fulfil their immediate needs. In the past, force was being used by the relevant authorities in order to protect these areas and deter the farmers. But, these measures were found to be ineffective especially at times of political turmoil where revenge was taken by the farmers in revolt against the system. More forests and new plantation sites have been destroyed and more game animals have been killed in the last three years.

To alleviate these problems, conservation of forest habitats on a sustainable basis should be given priority. Community-based management should be introduced in order to reconcile government authorities and farmers. A feeling of belonging should come from the farmers. Some living organisms might be more susceptible to human interference than others, affecting the species richness of a given habitat. In some cases, the immediate solution to preserve the fragile biodiversity of a given habitat might be to allocate a portion of the habitat free from human interference. The Menagesha State Forest, because of its historical significance, should be given priority.

In order to alleviate some of the causes for environmental degradation, measures should be taken by the relevant authorities in the introduction of efficient farming technology, high quality seed and livestock. The country has immense potential of untapped

geothermal energy and hydroelectric power resources. To minimize dependency on fire-wood, priority should be given to change the life-style of the people towards electrification and the use of solar power energy. Otherwise, the present trend is likely to continue with adverse effects on the remaining fragile ecosystem.

Recently, hunting of wild animals has been prohibited in Ethiopia, but putting the proclamation into practice has always been a problem in Ethiopia. In order to solve these problems, the wise usage and sustainable development of the natural resources should be encouraged by the concerned authorities. The farmers also should have a say in the execution of the policy and share the benefit to develop some of the necessary infrastructures in their localities. Then a feeling of belonging and responsibility could easily develop.

In Ethiopia, the Wildlife and Forestry departments were once grouped under the Natural Resources Conservation and Development Main Department, Ministry of Agriculture. At present, a new separate Ministry of Natural Resources, Environmental Protection and Development has been established. The country's conservation policy is being prepared. I hope that this policy will resolve the problem being encountered at present over who controls the conservation areas of Ethiopia-the central government or the newly established regional administration.

The Menagesha State Forest is not only a refuge for

P.albipes, it also harbours large mammals like- leopard, spotted hyena, serval, civet, white-tailed mongoose, vervet monkey, anubis baboon, colobus monkey, rock hyrax, Starek's hare, bushpig, warthog, grey duiker and Menelik's bushbuck. In addition to the above, in the present study 105 species of birds have been recorded at different seasons. This diversity of mammal and bird species and its proximity to the capital city will undoubtedly make the Menagesha State Forest an important attraction both for tourists and students. So, maintaining the biodiversity of this historical site should be the order of the day.

BIBLIOGRAPHY

- Allen, G.M. (1939) A checklist of African Mammals. **Bull. Mus. Comp. Zool. Harv.** 83: 1-763.
- Andersson, M. & Jonasson, S. (1986) Rodent cycles in relation to food resources on an alpine heath. **Oikos**, 46: 93-106.
- Annon. (1991) **Management plan of Menagesha-Suba State Forest Project.** Forest Management Planning Division, Ministry of Agriculture, Addis Ababa.
- Attuquayefio, D.K., Gorman, M.L. & Wolton, R.J. (1986) Home range sizes in the wood mouse **Apodemus sylvaticus**: habitat, sex and seasonal differences. **J. Zool., Lond. (A)** 210: 45-53.
- Baker, C.M. & Meester, J. (1977) Postnatal physical and behavioural development of **Praomys (Mastomys) natalensis** (A. Smith, 1834) **Z. Säugetierk.** 42: 295-306.
- Beer, J.R. (1964) Bait preferences of small mammals. **J. Mammal.** 45: 632-634.
- Belay Tegene (1982) **A study of a soil toposequence in northwestern Alem Gena Woreda.** M.Sc. Thesis, Addis Ababa University.
- Blower, J.G., Cook, L.M. & Bishop, J.A. (1981). **Estimating the size of Animal Populations.** London: Allen & Unwin.
- Bond, W., Ferguson, M. & Forsyth, G. (1980) Small mammals and habitat structure along altitudinal gradients in the southern Cape Mountains. **S. Afr. J. Zool.** 15: 34-43.

- Brambell, R. & Davis, D.H.S. (1941) Reproduction of the multimammate mouse (*Mastomys erythroleucus* Temm.) of Sierra Leone. *Proc. zool. Soc. Lond., Ser. B* 3: 1-11.
- Breitenback, F.V. (1962) National Forestry Development Planning and Priority Study on the example of Ethiopia. *Ethiopian Forestry Review* 3/4: 41-68.
- Breitenback, F.V. & Koukal, J. (1962) Menagesha State Forest: A description of the forest, its management and its future development including the National Park Project. *Ethiopian Forestry Review*, 3/4: 17-34.
- Bronner, G. & Meester, J. (1987) Comparison of methods for estimating rodent numbers. *S. Afr. J. Wildl. Res.* 17: 59-63.
- Caughley, G. (1977) **Analysis of Vertebrate Populations**. Chichester: Wiley.
- Cerqueira, R., Gentile, R., Fernandez, F.A.S. & Danderea, P.S. (1993) A five-year population study of an assemblage of small mammals in southeastern Brazil. *Mammalia* 57(4): 507-517.
- Chapman, B.M., Chapman, R.F. & Robertson, I.A.D. (1959) The growth and breeding of the multimammate rat, *Rattus* (*Mastomys*) *natalensis* (Smith) in Tanganyika Territory. *Proc. zool. Soc. Lond.* 133: 1-9.
- Cheesman, C.L. & Delany, M.J. (1979) The population dynamics of small rodents in a tropical African grassland. *J. Zool., Lond.* 188: 451-475.

- Chidumayo, E.N. (1984) Observations on populations of multimammate mice at Livingstone, Zambia. **Mammalia** 48(3): 363-376.
- Coetzee, C.G. (1965) The breeding season of the multimammate mouse **Praomys (Mastomys) natalensis** (A.Smith) in the Transvaal Highveld. **Zool. Afr.** 1: 29-39.
- Daniel Gamachu (1977) **Aspects of climate and water budget in Ethiopia**. Addis Ababa University Press, Addis Ababa.
- Davis, D.H.S. (1965) Classification problems of African Muridae. **Zool. Afr.** 1: 121-145.
- de Castro, J.D. (1985) Distribution and abundance of small mammals in a gradient of altitude. **Acta Zool. Fennici** 173: 53-56.
- Delany, M.J. (1964) A study of the ecology and breeding of small mammals in Uganda. **Proc. zool. Soc. Lond.**, 142: 347-370.
- Delany, M.J. (1966) Small rodents from the higher altitudes of Mount Moroto, Uganda. **Rev. Zool. Bot. Afr.** 73: 339-344.
- Delany, M.J. (1971) The biology of small rodents in Mayanja Forest, Uganda. **J. Zool., Lond.** 165: 85-129.
- Delany, M.J. (1975) **The rodents of Uganda**. London: British Museum (Nat. Hist.).
- Delany, M.J. (1986) The ecology of small rodents in Africa. **Mammal. Rev.** 16(1): 1-41.
- Delany, M.J. & Happold, D.C.D. (1979) **Ecology of African Mammals**. Longman, London.
- Delany, M.J. & Monro, H (1985) Growth and development of wild and

- captive Nile rats *Arvicanthis niloticus* (Rodentia: Muridae).
Afr. J. Ecol. 23: 121-131.
- Delany, M.J. & Monro, H. (1986) Population dynamics of *Arvicanthis niloticus* (Rodentia: Muridae) in Kenya. **J. Zool., Lond. (A)** 209: 85-103.
- Delany, M.J. & Roberts, C.J. (1978) Seasonal population changes in rodents in the Kenya Rift Valley. **Bull. Carneg. Mus.** 6: 97-108.
- Diamond, A.W. & Hamilton, A.C. (1980) The distribution of forest passerine birds and Quaternary climatic change in tropical Africa. **J. Zool., Lond.** 191: 379-402.
- Dieterlen, F. (1967) Ökologische populationsstudien an Muriden des Kivusee-Gebietes (Congo). **Zool. Jb. (Syst.)** 94: 369-426.
- Dieterlen, F. (1986) Seasonal reproduction and population dynamics in rodents of African lowland rain forest. **Cimbebasia** 8(1): 1-7.
- Dorst, J. (1972) Notes sur quelques rongeurs observés en Éthiopie. **Mammalia** 36: 182-192.
- du Feu, C.R., Hounsom, M.V. & Spence, I. (1983) A single-session mark/recapture method of population estimation. **Ring. Migr.** 4: 211-226.
- Duplantier, J.M., Granjon, L., Bonhomme, F., Catalan, J., Catzeflis, F., Chevret, P., Denys, C., Montgelard, C., and Britton-Davidian, J. (1993) Evolutionary systematics within

the genus **Mastomys** in West Africa: comparison of ecological, biochemical and molecular data. **Mammalia** 57: 628.

Duplantier, J.M., Granjon, L., Mathieu, E. & Bonhomme, F. (1990) Structures genetiques comparees de trois especes de rongeurs africains du genre **Mastomys** au Senegal. **Genetica** 81: 179-192.

Ellerman, J.R. (1941) **The families and genera of living rodents**. London: Trustees, British Museum (Nat. Hist.).

EMA (1988) **National Atlas of Ethiopia**. Ethiopian Mapping Authority, Addis Ababa.

Field, A.C. (1975) Seasonal changes in reproduction, diet and body composition of two equatorial rodents. **E. Afr. Wildl. J.** 13: 221-235.

Fisher, R.A. & Ford, E.B. (1947) The spread of a gene in natural conditions in a colony of the moth **Panaxia dominula** (L.). **Heredity, Lond.** 1:143-174.

Fleming, T.H. (1971) Population ecology of three species of Neotropical rodents. **Misc. Publs. Mus. Zool., Univ. Michigan** 143: 1-77.

Flowerdew, J.R. (1976) Techniques in mammalogy. Chapter 4. Ecological Methods. **Mammal Rev.** 6: 123-159.

Friis, I. (1992) Forests and forest trees of northeast tropical Africa. **Kew Bulletin Additional Series** 15, HMSO.

Gilbert, E.F. (1970) Mount Wachacha: A botanical commentary. **Walia** 2: 3-12.

- Gliwicz, J. (1985) Rodent community of dry African savanna: Population study. **Mammalia** 49: 509-516.
- Gordon, D.H. (1978) Distribution of sibling species of the **Praomys** (**Mastomys**) **natalensis** group in Rhodesia (Mammalia: Rodentia). **J. Zool., Lond.** 186: 397-401.
- Gottelli, D. & Sillero-Zubiri, C. (1992) The Ethiopian wolf-an endangered endemic canid. **Oryx** 26: 205-214.
- Green, C.A., Keogh, H., Gordon, D.H., Pinto, M. & Hartwig, E.K. (1980) The distribution, identification, and naming of the **Mastomys natalensis** species complex in southern Africa (Rodentia: Muridae). **J. Zool., Lond.**, 178: 17-23
- Gurnell, J. (1976) Studies on the effect of bait and sampling intensity on trapping and estimating wood mice, **Apodemus sylvaticus**. **J. Zool., Lond.** 178: 91-105.
- Hanney, P. (1964) The harsh-furred rat in Nyasaland. **J. Mammal.** 45: 345-358.
- Happold, D.C.D. (1974) The small rodents of the forest-savanna-farmland association near Ibadan, Nigeria, with observations on reproduction biology. **Rev. Zool. afr.**, 88: 814-836.
- Happold, D.C.D. (1975) The effects of climate and vegetation on the distribution of small rodents in western Nigeria. **Z. Säugetierk.** 40: 221-242.
- Happold, D.C.D. (1978) Reproduction, growth and development of a West African forest mouse, **Praomys tullbergi** (Thomas). **Mammalia** 42: 73-96.

- Happold, D.C.D. & Happold, M. (1989) Biogeography of montane small mammals in Malawi, Central Africa. *J. Biogeogr.* **16**: 353-367.
- Happold, D.C.D. & Happold, M. (1990) An ecological study of small rodents in the woodland savanna of Liwonde National Park, Malawi. *J. Zool., Lond.* **221**: 219-235.
- Hayne, D.W. (1949) Two methods for estimating population from trapping records. *J. Mammal.* **30**: 399-411.
- Hedberg, I. & Edwards, S. (eds.) (1989) *Flora of Ethiopia 3. Pittosporaceae to Araliaceae*. Addis Ababa, Ethiopia; Uppsala, Sweden.
- Henry, P.W.T. (1973) Notes and maps of the *Eucalyptus* plantations around Addis Ababa and the Menagesha State Forest, Ethiopia. *Miscellaneous Report no. 150*. Land Resources Division, Tolworth, England.
- Hilborn, R., Redfield, J.A. & Krebs, C.J. (1976) On the reliability of enumeration for mark and recapture census of voles. *Can. J. Zool.* **54**: 1019-1024.
- Hillman, J.C. (1993) *Ethiopia: a compendium of wildlife conservation information*. NYZS-The Wildlife Conservation Society & Ethiopian Wildlife Conservation Organization, Addis Ababa.
- Honacki, J.H., Kinman, K.E. & Koeppl, J.W. (eds.) (1982) *Mammal species of the world*. Allen Press, Inc.
- Hubert, B. (1982) Dynamique des populations de deux espèces de

rongeurs du Sénégal, **Mastomys erythroleucus** et **Taterillus gracilis** (Rodentia, Muridae et Gerbillidae). I. Etude démographique. **Mammalia** 46: 137-166.

Hutterer, R. (1981) Zur systematik und verbreitung der Soricidae Äthiopiens (Mammalia; Insectivora). **Bonn. zool. Beitr.**, 31: 217-247.

Hutterer, R. & Yalden, D.W. (1990) Two new species of shrews from a relict forest in the Bale Mountains, Ethiopia. In: **Vertebrates in the Tropics** (ed. by G. Peters & R. Hutterer), pp. 63-72. Museum Alexander Koenig, Bonn.

Ingersol, R.H. (1968) **The ecological stratification of mammals in the eastern Chercher highlands of Harar province, Ethiopia.** Ph.D. Thesis, Oklahoma State University.

Johnston, H.L. & Oliff, W.D. (1954) The oestrous cycle of female **Rattus (Mastomys) natalensis** (Smith) as observed in the laboratory. **Proc. zool. Soc. London**, 124: 605-613.

Jolly, G.M. (1965) Explicit estimates from capture-recapture data with both death and immigration-stochastic model. **Biometrika** 52: 225-247.

Kingdon, J. (1974) **East African Mammals: An Atlas of Evolution in Africa 2B. Hares and Rodents.** Acad. Press, New York.

Largen, M.J. & Rasmussen, J.B. (1993) Catalogue of the snakes of Ethiopia (Reptilia, Serpentes), including identification keys. **Trop. Zool.** 6(2): 313-434.

- Lavrenchenko, L.A., Likhnova, O.P. & Orlov, V.N. (1992) Haemoglobin patterns: A possible implication in systematics of multimammate rats **Mastomys** (Muridae, Rodentia). **Zoologicheskyy Zhurnal** 71(8): 85-93.
- Leirs, H., Stuyck, J., Verhagen, R. & Verheyen, W. (1990) Seasonal variation in growth of **Mastomys natalensis** (Rodentia: Muridae) in Morogoro, Tanzania. **Afr. J. Ecol.** 28: 298-306.
- Leirs, H., Verhagen, R. & Verheyen, W. (1993a) **Mastomys** rats in Tanzania: Taxonomic and geographic considerations. **Mammalia** 57: 635.
- Leirs, H., Verhagen, R. & Verheyen, W. (1993b) Productivity of different generations in a population of **Mastomys natalensis** rats in Tanzania. **Oikos** 68: 53-60.
- Leirs, H., Verhagen, R. & Verheyen, W. (1993c) **Mastomys** seasonal reproduction: tuned by the presence of new vegetation? **Mammalia** 57: 635-636.
- Lyons, N.F., Gordon, D.H. & Green, C.R. (1980) G-banding chromosome analysis of species A of the **Mastomys natalensis** complex (Rodentia: Muridae). **Genetica** 54: 209-212.
- Lyons, N.F., Green, C.R., Gordon, D.H. & Walters, C.R. (1977) G-banding chromosome analysis of **Praomys natalensis** (Smith) (Rodentia: Muridae) from Rhodesia 1. 36 chromosome population. **Heredity** 38: 197-200.
- Matthey, R. (1966) Cytogénétique et taxonomie des rats appartenant

au sous-genres **Mastomys** Thomas (Rodentia-Muridae). **Mammalia** 30: 105-119.

Meester, J. (1960) Early post-natal development of multi-mammate mice **Rattus (Mastomys) natalensis** (Smith). **Ann. Transvaal Mus.** 24: 35-52.

Meester, J. & Hallett, A.F. (1970) Notes on early postnatal development in certain southern African Muridae and Cricetidae. **J. Mammal.** 51: 703-711.

Mesfin Tadesse (1992) A survey of the evergreen forests of Ethiopia. Botany 2000 East and Central Africa. **NAPRECA Monograph 2**: 1-18.

Miller, J.A. & Mohr, P.A. (1966) Age of Wachacha trachyte carbonate volcanic centre. **Bull. Geophysical Observatory (6)**, Addis Ababa, Ethiopia.

Misonne, X. (1971) Part 6: Order Rodentia, pp. 1-39, In: **The Mammals of Africa: An identification manual**. (ed. by J. Meester & H.W. Setzer) Smithsonian Inst. Press, Washington, D.C.

Montgomery, W.I. (1985) Interspecific competition and the comparative ecology of two congeneric species of mice. In: **Case studies in population biology**. (ed. by L.M. Cook), Manchester University Press.

Montgomery, W.I. (1987) The application of capture-mark-recapture methods to the enumeration of small mammal populations. In:

Mammal population studies. (ed. by S.Harris). Oxford Science Publications.

- Müller, V.J.P. (1977) Populationsökologie von **Arvicanthis abyssinicus** in der Grassteppe des Semien Mountains National Park (Äthiopien). **Z. Säugetierk.** 42: 145-172.
- Neal, B.R. (1977) Reproduction of the multimammate rat, **Praomys (Mastomys) natalensis** (Smith), in Uganda. **Z. Säugetierk.** 42: 221-231.
- Neal, B.R. (1986) Reproductive characteristics of African small mammals. **Cimbebasia** 8: 113-127.
- Nowak, R.M. (1991) **Walker's Mammals of the World.** II (5th ed.). The John Hopkins University Press, Baltimore.
- Okia, N.O. (1973) The breeding pattern of the soft-furred rat, **Praomys morio** in an evergreen forest in southern Uganda. **J. Zool., Lond.** 170: 501-504.
- Oliff, W.D. (1953) The mortality, fecundity and intrinsic rate of natural increase of the multimammate mouse, **Rattus (Mastomys) natalensis** (Smith) in the laboratory. **J. Anim. Ecol.** 22: 217-226.
- Orlov, V.N., Bulatova, N.S. & Milishnikov, A.N. (1989) Karyotypes of some mammalian species (Insectivora Rodentia) in Ethiopia. In: **Ecological and faunistic studies in southwestern Ethiopia** (ed. by V.E.Sokolov). Institute of Evolutionary Morphology and Animal Ecology, Moscow.

- Pankhurst, R. (1989) Some notes on deforestation and afforestation in Ethiopia prior to World War I. **Walia** 12: 10-20.
- Petter, F. (1977) Les rats à mamelles multiples d'Afrique occidentale et centrale: **Mastomys erythroleucus** (Temminck, 1853) et **M. huberti** (Wroughton, 1908). **Mammalia** 41: 441-444.
- Pirlot, P.L. (1954) Pourcentages de jeunes et périodes de reproduction chez quelques rongeurs du Congo Belge. **Ann. Mus. Congo, Zool.** 1: 41-46.
- Pohjonen, V. & Pukkala, T. (1992) **Juniperus procera** Hochst. ex Endl. in Ethiopian forestry. **For. Ecol. Manage.** 49: 75-85.
- Qumsiyeh, M.B., King, S.W., Arroyo-Cabrales, J., Aggundey, I.R., Schlitter, D.A., Baker, R.J. & Morrow, K.J. (1990) Chromosomal and protein evolution in morphologically similar species of **Praomys sensu lato** (Rodentia, Muridae). **J. Heredity** 81: 58-65.
- Robbins, C.B. & Straeten, E.V.D. (1989) Comments on the systematics of **Mastomys** Thomas 1915 with the description of a new West African species (Mammalia: Rodentia: Muridae). **Senckenb. biol.** 69: 1-14.
- Rosevear, D.R. (1969) **The rodents of West Africa**. London: Trustees of the Brit. Mus. (Nat. Hist.).
- Rupp, H. (1980) Beiträge zur systematik, verbeitung und ökologie äthiopischer nagetiere: Ergebnisse mehrerer forschungsreisen. **Säugetierkundliche Mitteilungen** 28: 81-123.

- Sebsibe Demissew (1980) **A study of the structure of a montane forest: The Menagesha State Forest.** M.Sc. Thesis, Addis Ababa University.
- Sebsibe Demissew (1988) The floristic composition of the Menagesha State Forest and the need to conserve such forests in Ethiopia. **Mount. Res. & Devpt. 8:** 243-247.
- Sharpe, S.T. & Millar, J.S. (1991) Influence on the variation in initiation of breeding in *Peromyscus maniculatus*. **Can. J. Zool. 69:** 698-705.
- Sheppe, W. (1972) The annual cycle of small mammal populations on a Zambian flood plain. **J. Mammal. 53:** 445-460.
- Sidorowicz, J. (1960) Influence of the weather on capture of micrommalia 1. Rodents (Rodentia). **Acta Theriol. 9:** 139-157.
- Skinner, J.D. & Smithers, R.H.N. (1990) **The mammals of the Southern African subregion.** University of Pretoria, Pretoria.
- Southern, H.N. & Hook, O. (1963) Notes on breeding of small mammals in Uganda and Kenya. **J. Mammal. 44:** 126-129.
- Southwood, T.R.E. (1978) **Ecological methods with particular reference to insect populations.** (2nd edn). Chapman & Hall, London.
- Straeten, E.V.D. & Dieterlen, F. (1983) Description de *Praomys ruppi*, une nouvelle espece de Muridae d'Ethiopie. **Ann. Mus. Roy. Afr. Centr., Sc. Zool. 237:** 121-127.
- Swanepoel, C.M. (1980) Some factors influencing the breeding

- season of *Praomys natalensis*. *S. Afr. J. Zool.* **15**: 95-98.
- Tadesse Worku (1986) **A study report on the protection and development of natural forest** (in Amharic). Ministry of Agriculture, Addis Ababa, Mimeograph.
- Taylor, K.D. & Green, M.G. (1976) The influence of rainfall on diet and reproduction in four African rodent species. *J. Zool., Lond.* **180**: 367-389.
- Wilson, D.E. & Reeder, D.M. (eds). (1993) **Mammal species of the world: A taxonomic and geographic reference**. (2nd ed.). Smithsonian Inst. Press, Washington, D.C.
- Wolton, R.J. (1985) The ranging and nesting behavior of wood mice, *Apodemus sylvaticus* (Rodentia: Muridae), as revealed by radio-tracking. *J. Zool., Lond.* **206**: 203-224.
- Yalden, D.W. (1983) The extent of high ground in Ethiopia compared to the rest of Africa. *Sinet: Ethiop. J. Sci.*, **6**: 35-39.
- Yalden, D.W. (1988a) Small mammals in the Harennna Forest, Bale Mountains National Park. *Sinet: Ethiop. J. Sci.*, **11**: 41-53.
- Yalden, D.W. (1988b) Small mammals of the Bale Mountains, Ethiopia. *Afr. J. Ecol.* **26**: 281-294.
- Yalden, D.W., & Largen, M.J. (1992) The endemic mammals of Ethiopia. *Mammal Rev.* **22**: 115-150.
- Yalden, D.W., Largen, M.J., & Kock, D. (1976) Catalogue of the mammals of Ethiopia. 2. Insectivora and Rodentia. *Monitore Zoologico Italiano (nouva serie) Supplemento*, **8(1)**: 1-118.