

Summer 1995

Demography, Reproduction, Diet and Crop Depredation in Three Species of Rodents in Natural and Irrigated Fields in Nigeria

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DEMOGRAPHY, REPRODUCTION, DIET AND CROP DEPREDACTION
IN THREE SPECIES OF RODENTS IN NATURAL AND
IRRIGATED FIELDS IN NIGERIA

by

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*A Dissertation Submitted to the faculty of
Old Dominion University in Partial Fulfillment
of the Requirements for the Degree of*

**DOCTOR OF PHILOSOPHY
ECOLOGICAL SCIENCES**

OLD DOMINION UNIVERSITY

July, 1995

Approved by:

Dr. Robert K. Rose, Prof. (Director)

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ABSTRACT

DEMOGRAPHY, REPRODUCTION, DIET AND CROP DEPREDAATION IN THREE SPECIES OF RODENTS IN NATURAL AND IRRIGATED FIELDS IN NIGERIA

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Director: Dr. Robert K. Rose, Professor

Rodent populations of *Arvicanthis*, *Mastomys* and *Tatera* were studied during July 1990 to August 1992 in both natural and irrigated savannah fields of northern Nigeria. *Tatera* was entirely absent from the irrigated fields. Irrigation enhanced higher rodent population densities in the magnitude of three to four times over densities in the natural fields. *Arvicanthis* was the most abundant of the three species in both sites. *Tatera* was the least common in the natural site. Adult survival rates in *Arvicanthis* and *Tatera* were significantly higher than *Mastomys*. Survival rates of both adult and young differed between the wet and dry seasons, being lower during the peak rainy months of July-August. Monthly recruitment in the irrigated fields was nearly four-fold higher than that in the natural fields.

In the natural fields all species showed strict seasonal breeding in tune with the rainy months (May - October), with *Arvicanthis* starting at the same time as the onset of the rains but a month or two ahead of *Mastomys* and *Tatera*. In contrast to reproduction in the natural fields, the breeding seasons in *Arvicanthis* and *Mastomys* in the irrigated fields were continuous.

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Stomach contents from necropsized animals of both sexes were processed and used for microscopic analysis to determine patterns of diet selection, and species, seasonal and site differences. Study sites were sampled for their vegetative cover and potential food resources available each season to the rodents. There were no significant differences in species dietary selection between the sexes. Seeds formed an important food group for all species in both sites during the rainy season. *Mastomys* (in both sites) and *Tatera* (in the natural site) maintained almost the same levels of seed intake throughout the year. The amount of seed intake by *Arvicanthis* was enhanced by irrigation. In both sites during the rainy periods, monocots and insects made up the second and third most important food groups by mass of the diet intake of the species. The importance of monocots and insects in the diet diminished, especially to *Arvicanthis* in the natural site during the dry seasons (as more dicots food was consumed). Results of MANOVA tests indicated that species, site, seasons and their interactions had significant effects on the relative quantities of food types selected. There were dramatic differences in apparent seasonal herbage quality, especially in the natural fields.

The damage and yield loss caused by rodents in cereal crops in irrigated savannah fields was investigated. Evidence showed that *Arvicanthis* and *Mastomys* were the culprits responsible for the damage and crop depredation. Random cluster technique and Cut Tiller Count method were used to assess rat-caused damage in cereal crops. In premature rice, damage during 1990 increased steadily from the stage of tillering to the dough stage. The differences in damage levels at the premature growth stages of both crops, being higher at the older stages, were statistically significant. Annual differences in the percentage of damage to mature rice (yield loss), and that in wheat were statistically significant, being higher in the latter. The high level of yield loss in wheat, compared to low and moderate levels in rice (grown for the most part during the rains), was probably a result of the greater depredation rate on the wheat, grown by irrigation during the dry season when other rodent food sources were less abundant.

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By the absence of *Tatera* in the irrigated fields this study provides evidence that the responses of African rodents to irrigation differed among the species. This study also demonstrates the opportunistic tendency of the rodents to exploit new, highly productive habitats as seen in their continuous reproduction, higher population densities and greater depredation of seeds and cereals in the irrigated fields. *Arvicanthis*, *Mastomys* and *Tatera* stand indicted as crop pests in both rainfed and irrigated agriculture.

DEDICATION

To Alhaj Abba Sarina, my late grandfather who first held my hands and led me to school; late Ibrahim Abba, my brother and trusted friend; and Halimat-Sadia, my wife who sacrificed the most for this undertaking.

ACKNOWLEDGEMENTS

The ultimate of helpers and source of all provisions is Allah, the Almighty God. All Praise and gratitude are due to Him.

I am very grateful to the African Dissertation Fellowship Program of the Rockefeller Foundation for their financial support of this study, and to Old Dominion University and Bayero University, Kano, Nigeria for administrative support. My advisor, Dr. Robert K. Rose had sustained the highest level of interest and seriousness of purpose throughout the different stages of this project. He taught me scientific and research proposal writing; the construction of mammal traps and grid surveying among other things. He read this document several times and offered many constructive criticisms. Dr. Rose had also been most helpful, patient and considerate. I thank him very much. I also thank my two other committee members, Dr. Lytton J. Musselman and Dr. Joseph H. Rule for their guidance and support of this research. Dr. Frank P. Day Jr. had also written to my donors in support of this research. Mr. Paul Reynolds and Ms. Alice Souter of the ODU computer services, my colleagues, Rett Weber, Chad Cross, and brothers Amid Oloso and Ibrahim Sarafa have helped me with programing.

My gratitude also goes to the personnel of the Hadejia- Jama'are River Basin Development Authority, Biological Sciences, B.U.K., Kano River Project, and Ministry of Agriculture, Kano, Nigeria for their cooperation. The farmers at Karfi, Kura and Kada-wa villages were very helpful. I am grateful to A. Aliyu, Malam A. Garko, M. N. Nwaiko and M. M. Malam for their assistance with field work. My wife, Halimat-Sadia was helpful with many aspects of this project. I can not thank her enough but she knows that only Allah, the Almighty God rewards in full measure.

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GENERAL INTRODUCTION

This thesis reports the results of the study of three species of rodents in both natural and irrigated savannah fields in northern Nigeria. Different aspects of the field studies are reported separately in the chapters that follow. This section is intended to give general information on the study area of northern Nigeria as well as a brief review of what is known of the biology of the three rodent species.

The aspect of climate, vegetation, and soils of northern Nigeria is not one of the principle elements of the present study, yet in order to appreciate the dynamics of the rodent populations, their breeding patterns and general habits, some background in the geography of the area is necessary. By way of general introduction, therefore, some account of the physical and biological characteristics, and their relationships to that of human activities in the region of the present study, the Kano-closed settled zone (as it is commonly referred to in the geographic literature (Mortimore and Wilson, 1965), is given below.

The physical environment

The area of the present study lies in the northern part of Nigeria within 100 km south of Kano city ($12^{\circ} 03'N$ $8^{\circ} 32'E$, 470 MSL). See Figures 1 and 2 for country map and area location of study sites in Nigeria. The underlying bedrock is of basement complex origin. These are old crystalline rocks formed during the late Precambrian era. The altitude ranges from approximately 430m to 520m above sea level with a generally gentle terrain slope in a northeast direction. Occasionally inselberge can be seen bulging above the almost flat landscape, but these are mostly outside the present study area. The

Figure 1. Nigeria country map and area relative to U.S. map. Redrawn from Metz, H.C. 1991. Nigeria: a country study. Federal Research Division, Library of Congress, USA.

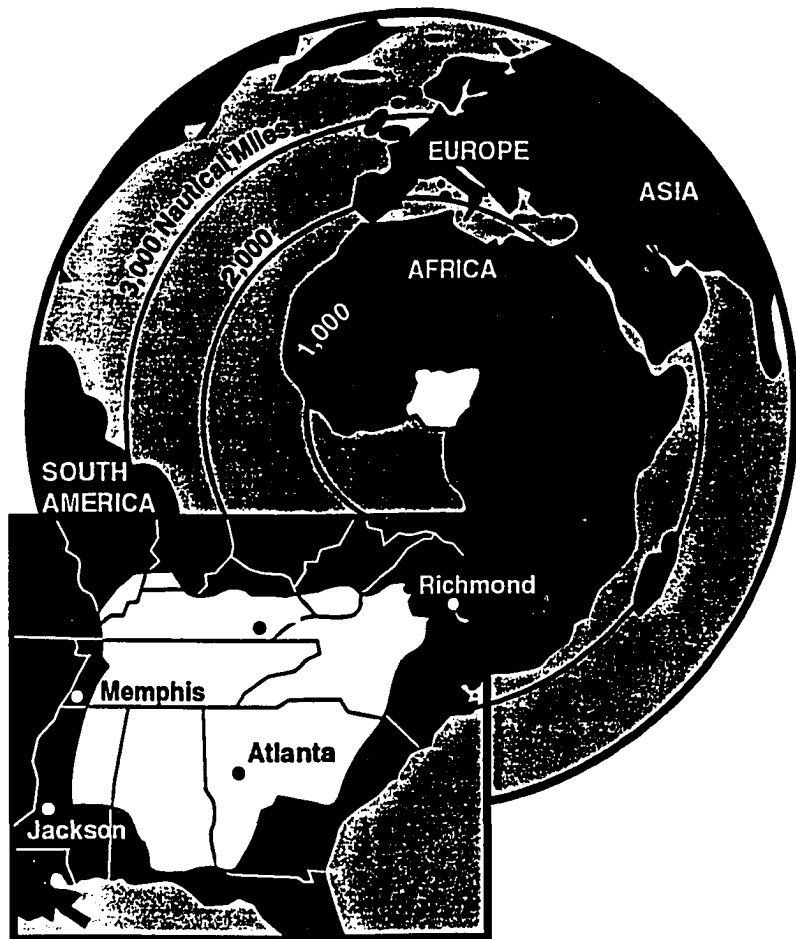
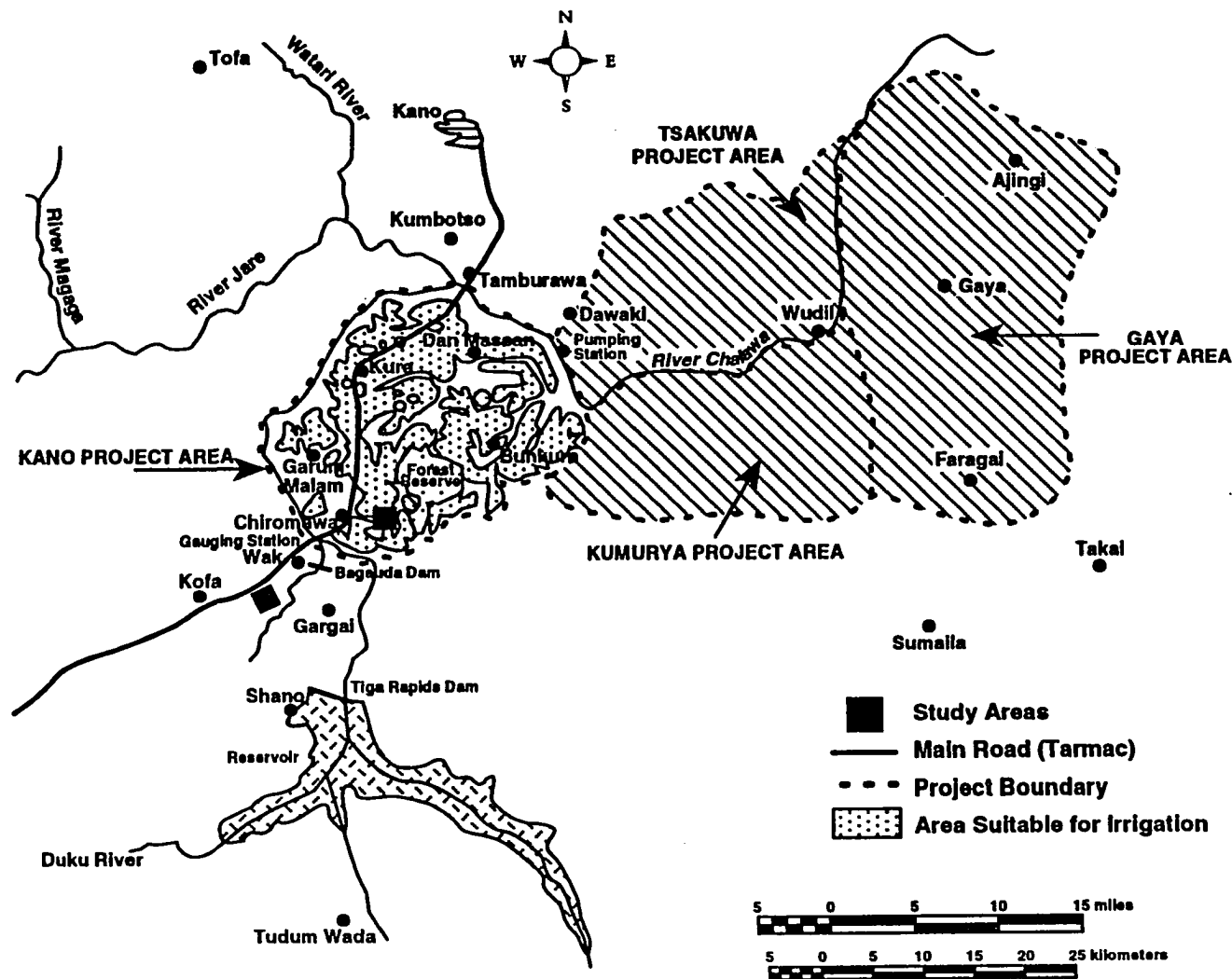


Figure 2. Study sites (in solid squares) in the natural and irrigated areas south of Kano, Nigeria. Notice the Tiga Reservoir Lake south of the study areas. Water from the reservoir is used for the irrigation. Redrawn with modifications from original map. Courtesy of the Data Unit, Hadejia-Jama'are River Basin Development Authority, Nigeria.



main drainage channel for the area is the Kano-Hadejia River, which flows rapidly in its upper reaches of the Jos Plateau and highlands of southern Kano, incising into the plain and exposing the bedrock in places. It runs, in the general, east-northeast direction of the slope, and confluences with the Jama'are River at Gashua. It becomes Yobe River, continues to flow on for several miles, eventually emptying into the Lake Tchad (Figure 3).

Climate

Climatic changes follow the pattern of temporal variations in pressure belts in response to movement of the sun. Beginning in late March, a low pressure zone is created in the north which draws the southwesterly winds (Equatorial Maritime Air Mass) off the Gulf of Guinea. The winds are laden with moisture and their arrival sets the beginning of the rainy season in northern Nigeria from April to May or, sometimes as late as June. In winter, the equatorial maritime winds retreat as the sun shifts southwards. At this time the Northeast Trade Winds (The Tropical Continental Air Masses), dry and cold, blow across over the Sahara Desert to reach the northern part of Nigeria late in November, heralding the beginning of the dry or Harmattan season. The impact of the Harmattan winds, as they dump their load of fine sand and other colloidal particles on the land, decreases from the north to the south of Nigeria. Thus, the year is roughly divided into two halves with summer monsoon rains from May to October, and dry season from November to April. Most of the rains often fall from July to September, and rarely exceeds 900 mm during any typical year. Lower mean monthly temperatures of 10-15° C are seen in December-February during the Harmattan (winter) and during the peak rainy months of July, August and September. Early summer mean monthly temperatures sometimes exceed 32° C. Rainfall and temperature data from the study period are shown in Figure 4.

Figure 3. The inland drainage system of the study area formed by the Kano-Hadejia and Jama'are River Systems and the Lake Tchad Basin. The rivers flow in a northeast direction. Redrawn with modifications from original map. Courtesy of the Data Unit, Hadejia-Jama'are River Basin Development Authority, Nigeria.

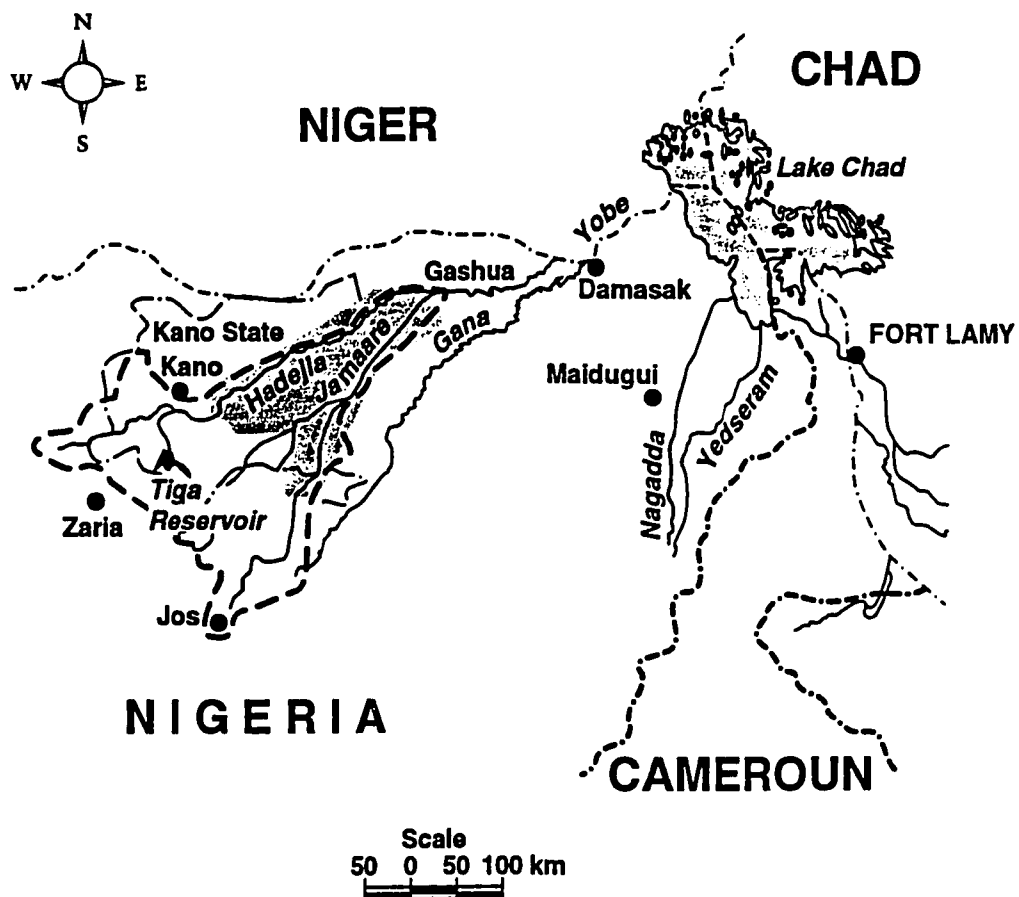
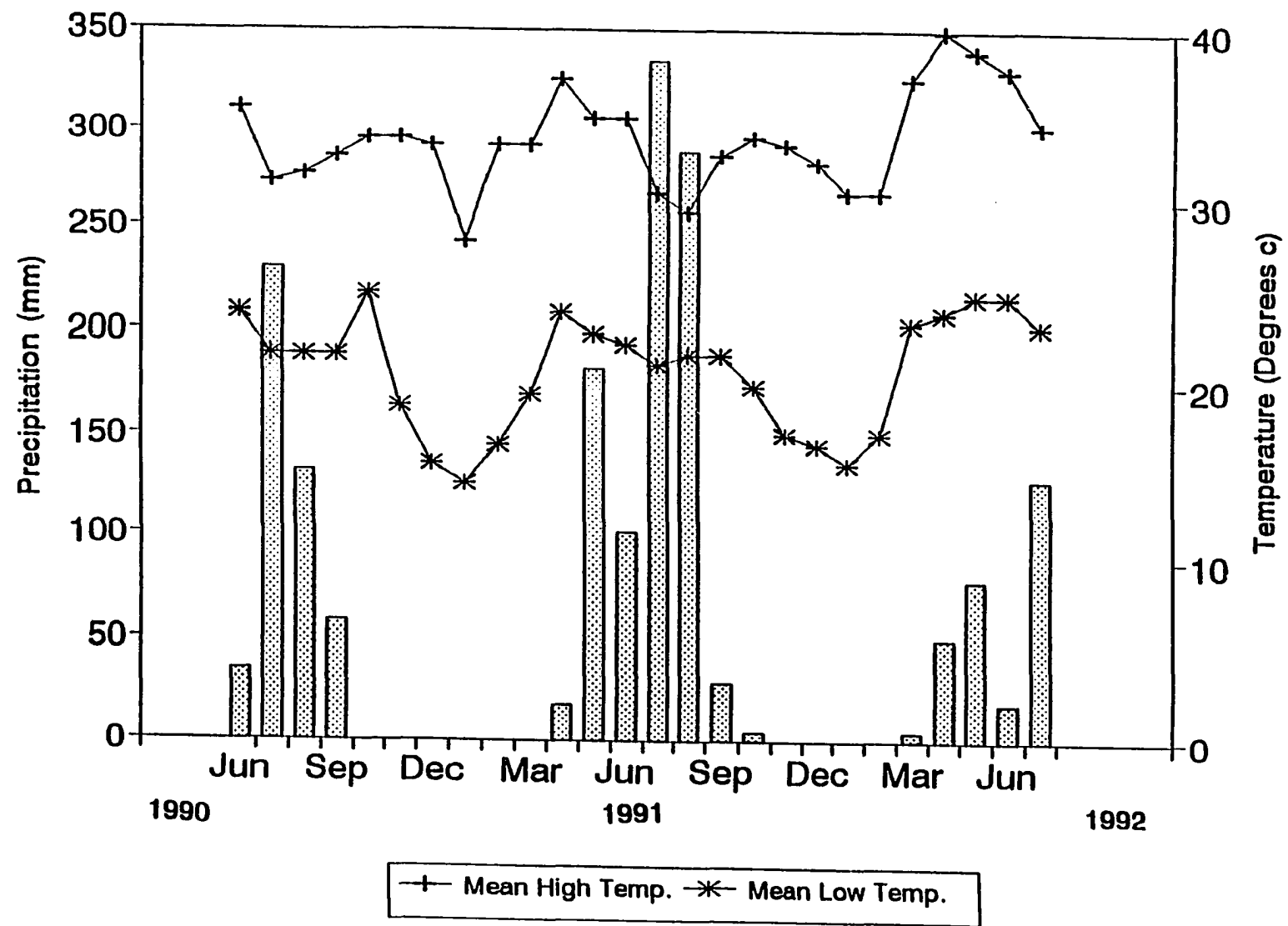


Figure 4. Climatic data of the Kano District, northern Nigeria covering the period of the present study (June, 1990 - July, 1992). Raw data courtesy of the Kadawa Irrigation Research Station. Note the distinct seasonal rainfall pattern.

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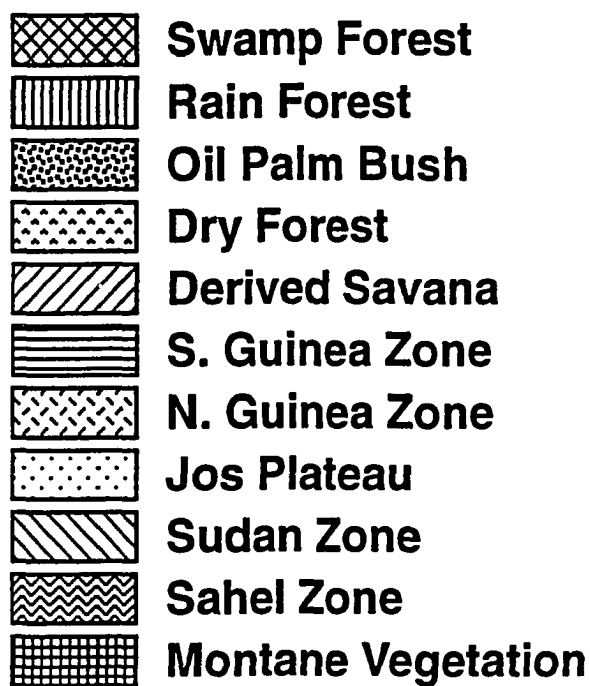
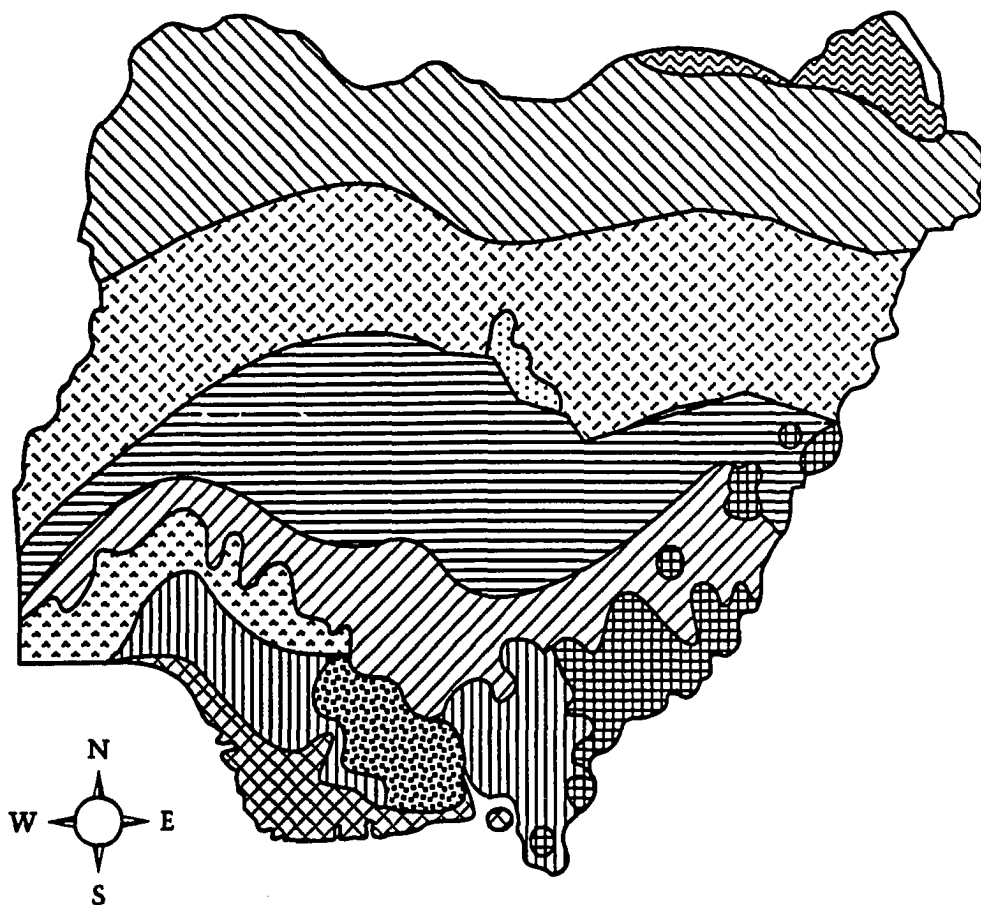
Soils and Vegetation

Soil types are generally derived from quartzite and weathered rock minerals. Other soils in the area developed from sedimentary rock and deposits derived from the desert sands. They include well drained loamy sands and partially drained sandy clay loam in the upland areas. In the lower terraces the loamy types are also well drained but the clay types are relatively poorly drained. As the study area is in the upper catches of the Kano-Hadejia river systems, the rich alluvial soils associated with floodplains are not widespread. Intensive pressure from high density population has led to a decline in fertility of these soils over the centuries of agriculture in the region.

Rainfall is the most important factor in determining the distribution of vegetation in Nigeria. The amount and duration of the rain decrease gradually from a high of 4000 mm per year in the Rainforest areas to as low as 500 mm per year in the extreme north-eastern region of the country. Furthermore, the uneven distribution of the rain is affected by a number of factors. For example, areas of high altitude such as the Jos Plateau, situated further inland from the coast, may receive higher amounts of rain than the surrounding lands. In the gap between the Equatorial Rain Forest Vegetation in the coastal south and the scanty arid vegetation of the Sahel are all gradations of Savannah. In a northbound direction these are the "Derived Savannah," Moist Guinea Savannah, followed by Woodland and Grassland Savannahs. These vegetation belts run approximately parallel with the lines of latitude (Figure 5).

The original vegetation in the region of the present study has been altered through cultivation, grazing and frequent burning over the last 2,000 years. Thus, the so-called Sudan Savannah Woodland (Buchanan and Pugh, 1964; Keay, 1958) is now restricted to patches of forest reserve while much of its vast stretch has changed to degraded savannah in which scrub woodland, low shrubs, or grass scrubland dominate. Common

Figure 5. Vegetation map of Nigeria. Redrawn with modifications from Buchanan and Pugh (1964). Land and people in Nigeria. University of London Press.



tree species included *Parkia biglobosa* Keay, *Sclerokaya birrea* (A. Rich.) Hochst., *Acacia albida* Del, *Vitex doniana* Sweet, *Combretum nigricans* Guill. & Perr., and *Poliostigma thoningi* (Schum.) Milne-Redhead. Shrub vegetation was dominated by *Acacia ataxantha* DC., *Acacia senegal* (L.) Willd., and *Dichrostachys glomerata* (L.) Chiov. Herbs were abundant especially during the rainy season. Commoner species included *Indigofera hirsuta* L., *Tephrosia purpurea* (L.) Pers., *Waltheria indica* L. and *Zornia glochidiata* Reich. ex DC. Vines included *Ipomea aquatica* Forsk, and *Leptodonia hastata* (Pers.) Decne. The grass and sedge communities were predominantly of *Andropogon gayanus* Kunth, *Hypharrhenia* spp. L., *Pennisetum pedicellatum* Trin., *Cynodon dactylon* (L.) Pers, *Eragrostis tenella* (L.) and *Digitaria gayana* (Kunth) Stapf ex Chev.

Before the advent of irrigated agriculture only rain-fed food crops (sorghum, maize, upland rice and cowpeas), and cash crops that include groundnuts (peanuts), beniseeds (sesame) and cotton were grown. Now wheat, maize, tomatoes, and other vegetables are also grown in large quantities during the dry season.

The human population in Nigeria, estimated by the World Bank at over 110 million people in 1990 (88 million is Nigeria's government official figures as at 1991), is the highest in Africa, and one of the highest in the world. With a land surface area of about one million square kilometer, the average density is more than 100 persons per square km. The Kano-closed settled zone has 4-5 times the average national population density. The rate of annual increase is put at 3.3% (Metz, 1991). Such a high and mounting population pressure suggests one obvious thing - - rapid changes in the physical environment, including loss of original vegetation and expanding large scale agricultural projects (as already noted), two factors which create new, favorable conditions for the proliferation of rodent and other vertebrate and invertebrate pests.

Mammalian populations

The Nigerian mammal fauna, with 13 orders, 42 families and 133 genera and 247 species, is very rich and diverse (Happold, 1987). The group of our present interest, the rodents, account for 21.9% of the known species based on Happold (1987) classification which is also adopted here. The rodents are the largest order of Nigerian mammals with nine families, 37 genera and 55 species.

Three species of these rodents, *Arvicanthis niloticus*, *Mastomys natalensis* and *Tatera valida* (Family, Muridae) are of concern to us in the present study. They are among the most widespread and best known taxa on the African continent (Delany, 1986; Green, Keogh, Gordon, Pinto and Hertwig, 1980; Gordon, 1978; Happold, 1987; Hubert, Meylan, Petter, Poulet and Tranier, 1983, Neal, 1982; Rosevear, 1969). The first two have distributions mainly in subsaharan Africa, but the third is also common in the Indian subcontinent (Beg and Ajmal, 1977; Neal, 1982). Their distribution in Nigeria decreases from the northern Savannah to the forests of the south. In the latter region the three rodents are present mainly in the Derived Savannah region and in clearings near human habitations. Body size in adults varies from about 38g in body mass, approximately 100 mm head and body length and 80mm for tail in *M. natalensis*, to 180g or more in body mass, and about 170mm head and body, and 150mm tail lengths in *A. niloticus*. For *T. valida*, the third species in the present study, body size and mass in northern Nigeria are intermediate between those of *M. natalensis* and *A. niloticus* but, elsewhere in Africa it may exceed both *A. niloticus* and *M. natalensis* in length and mass. Indeed, different populations of all three species show considerable physical variations from one African locality to another (Happold, 1987).

The taxonomy of the three species is riddled with confusion and disagreement (Delany & Monro, 1986; Mathey & Petter, 1970; Neal, 1977; Rosevear, 1969; Corbet and Hill, 1980; Honacki, Kinman and Koepl, 1982; Robins and Streaten, 1989; Hubert, Meylan, Petter, Poulet and Tranier, 1983), due to the fact that each constitutes a species complex. See also Delany and Roberts (1986) and Davis (1963). The classification adopted in the present study follows that of Happold (1987). Thus, *M. natalensis* is the group name adopted for all *Mastomys* studied in the present work. Similarly, no subspecies name was considered in the case of either *A. niloticus* or *T. valida*.

Several aspects of the ecology of these species have been documented from many parts of Africa. For example, Delany and Roberts (1978), Delany and Monro (1985a,b, 1986), Ghobrial and Hodieb (1982), Happold (1966), Neal (1981), Poulet and Poupon (1978) and Rabiou and Fisher (1989) studied *Arvicanthis*. The works of Gordon (1978), Hubert *et al.* (1983) and Robins and Streaten (1989) covered *M. natalensis*. Studies on *Tatera*, as earlier noted, have been both in Africa (Cheeseman and Delany, 1979; Delany and Neal, 1969; Happold, 1987; Neal, 1970, 1982) and in Asia (Beg and Ajmal, 1977). Food selection and amounts eaten vary among the species by locality and season of the year (Delany, 1986; Rabiou & Fisher, 1989; Rosevear, 1969; Taylor and Green, 1976). In general, however, all kinds of food items including substantial amounts of cereals and grains are eaten. Reproduction in all species may be seasonal or may extend throughout most of the year depending on local conditions, but in most cases shows some relationship to the months when rain falls (Delany, 1972; Hubert, 1982; Swane-poel, 1980; Taylor and Green, 1976; Rabiou and Fisher, 1989). Mean litter size per adult female varies widely among the species, 4.25 embryos in *Tatera* (Neal 1982), a high mean in *Mastomys* of 11.00 embryos (Sheppe, 1972) or 12.10 embryos (Neal, 1977), and an intermediate number of 5-7 implanted embryos per adult female in *Arvicanthis* (Fisher, 1991). The females of all species have the capacity to produce at least

two litters during any breeding season. Actually, up to five litters may be produced in a year by *A. niloticus* and *M. natalensis* (Rosevear, 1969). The high reproductive capacity of these species and their potential for serious depredation and damage to crops, and their additional role of being zoonotic agents of such diseases as Lassa fever and bubonic plague, especially in the case of *M. natalensis* (Isaacson, 1975; Kingdon, 1974; Leirs, Verhagen, Michiels, Verheyen and Stuyck, 1989; Month, 1975; Pugh and Parker, 1975; Rosevear, 1969), rightly accords them the recognition of being economically important.

The populations of *A. niloticus* fluctuate from high to low between the period following reproduction and that, of nonbreeding or reduced breeding activity (Poulet, 1978; Delany, 1986). The populations are also known to survive at low-density levels and rather suddenly appear in high numbers, sometimes leading to outbreaks and serious damage to crops (Taylor, 1968; Poulet and Poupon, 1978; Poulet, 1982). The population characteristics of *M. natalensis* in the Kenyan highlands has been described as ephemeral (Taylor and Green 1976); the species increases rapidly in relation to ripening cereals. Other workers including Neal (1977), Sheppe (1972) and Telford (1989), have noted similar responses. Perhaps other outbreaks are directly related to causes in changing agricultural practices from small-scale peasant farms, where crops are often mixed, to large-scale farm projects and monoculture irrigation farming over much of sub-saharan Africa and elsewhere in the tropics. These conditions provide for the survival of rodent species that may ravage crops later. On account of such outbreak phenomenon, Happold (1987) predicted high population levels of rodents in the irrigated fields of northern Nigeria. Indeed, this prediction has become true, for the rodents have become increasingly troublesome in recent years, especially in cereal crop fields.

The objectives of the present study were to investigate the ecology of the three rodent species, including their population dynamics, breeding patterns, food selection and crop depredation and damage in the natural (non-irrigated) and irrigated fields at Bagauda-Gwarmai and Kadawa areas near Kano in the north of Nigeria. Additional introductory materials and detailed study objectives are given under appropriate sections of the four chapters that follow.

CHAPTER ONE

POPULATION DYNAMICS

Introduction

The densities of populations of *Arvicanthis* fluctuates from high to low between the period following reproduction and that of nonbreeding or declined breeding season (Poulet, 1978; Delany, 1986). The populations are also known to survive at low density levels and rather suddenly appear in high numbers, sometimes leading to outbreaks and serious crop damage (Taylor, 1968; Poulet and Poupon, 1978; Poulet, 1982). The population characteristics of *Mastomys* in the Kenyan highlands have been described as ephemeral (Taylor & Green 1976) whence the species increases in relation to ripening cereals. Other workers, including Neal (1977), Sheppe (1972) and Telford (1989), have noted similar observations. The high reproductive capacity of these species and their potential for serious depredation and damage to crops, and the additional role of being zoonotic agents of diseases such as Lassa Fever, especially in the case of *Mastomys* and *Tatera* (Isaacson, 1975; Kingdon, 1974; Leirs, Verhagen Michiels, Verheyen and Stuyck 1989; Month, 1975; Pugh and Parker, 1975), rightly accorded them the recognition of being economically important.

This research was aimed at investigating the population dynamics of these three small mammal species in both their natural and irrigated agricultural habitats at Bagauda-Gwarmai and Kadawa villages near Kano, northern Nigeria. The three species are becoming increasingly troublesome and destructive pests of cereal grain crops and in stores in northern Nigeria. Since the completion of irrigation projects in the late 1960s and early 1970s, several thousand hectares of farmlands have been irrigated during the

dry season (i.e., November to March), allowing a second crop each year at these locations. This extended cropping system therefore provides resources to the rodents during the dry period when they do not normally breed (Chapter two). It was our aim also to compare population dynamics between irrigated and non-irrigated sites; and fourthly to test the hypothesis that denser populations are found in the irrigated sites, perhaps because of longer breeding seasons and therefore, higher rates of natural increase.

Materials and Methods

In the irrigated fields the study grids were in grassland-orchard field surrounded on all sides by rice or wheat crop year round. Traps were left in this site for most of the study period (i.e. July 1990 to August 1992) except for one major disruptions (in March-April, 1991) caused by grass slashing and other activities for management purposes. Therefore, capture-recapture data are presented in two parts: July 1990-February 1991 and May 1991-August 1992. Grids could not maintained inside the rice or wheat plots because of flooding caused by irrigation or rain water. The grass-orchard site appeared to serve the role of refugia for rats when the surrounding crop fields were harvested and before the next crop developed to the point of providing sufficient cover for the rats.

In the non-irrigated area at Bagauda-Gwarmai, a site a few kilometers south of Kadawa, once used for agricultural exhibitions and workshops, was selected for establishing a population grid. Work started in July, 1990. In the dry season when surrounding crop fields were harvested, the site would become one of the few undisturbed vegetated places, and undoubtedly served as a refuge also for rats displaced from neighbouring farms. Therefore, rodents in the two major study sites (i.e. the grassland-orchard in the irrigated area and the natural, non-irrigated fields may be considered refuge populations, especially during the crop harvest season, and the late dry season (at the natu-

ral site) when surrounding vegetation become scanty and depleted by grazing livestock. There were still, however, similar though more disturbed habitats in the vicinity of both grids at the irrigated and natural areas. Work at Bagauda was disrupted in early 1991 when suddenly an agricultural activity was initiated on the site after a decade without any disturbances. Massive land clearing of a substantial portion of the area led to the suspension of trapping there. Other sites were trapped but were abandoned because of frequent disturbances and trap loses. Later, following the rains, the site at Bagauda, left for a few months, had made remarkable recovery in terms of vegetation cover sufficient for trapping to resume. Thus, animal population data in respect to the natural site is presented in two parts also. The first, July 1990-February 1991 (running parallel with that in the irrigated fields), and the second from July 1991-July 1992, two months later than in the irrigated fields and terminating a month earlier. Despite this minor differences, the second phase of trapping in the two sites had run parallel for 13 months. Trapping in the non-irrigated crop fields was limited and did not involve establishing permanent grids because of poor catch and heavy losses of traps.

Trapping and Marking

All sampling involved live trapping following the methods of Rose and Gaines (1978). The traps, modified Fitch type (Rose 1973), were placed at 10m intervals in a 10 x 10 grid. Occasional surveillance trapping was also conducted around the grids to monitor the movement of animals in and out of the area. The Fitch trap was found more suitable than the Longworth trap that has a smaller entrance which appeared to exclude Nile rats weighing more than 140g (Fisher and Rabiou, unpublished data). Throughout the study the traps were covered with cardboards to protect the rodents from rain, heat, or cold. The cardboards had to be changed very frequently because they were being eaten by termites or rendered unsuitable by sheltering ants. Trapping lasted six to eight

days every month and sometimes more when the proportion of unmarked to marked animals was so high to warrant continued trapping for additional days.

Animals were noted for their location on the grid, sexed, and marked with numbered ear tags, ear punching, or toe clipping. Occasionally, a combination of two methods was used to mark individual animals, when tags appeared to be coming off. Minimum body weight for mature animals was used to define maturity in all animals of both sexes (*Arvicanthis* 60g, *Mastomys* 38g, and *Tatera* 40g), and animals weighing less were considered young.

Population estimates

Capture-recapture data were analyzed as in the robust design of Pollock (1982) using the fortran program CAPTURE (Otis, Burnham, White and Anderson, 1978; White, Anderson, Burnham and Otis, 1982) to estimate population size based on a probabilistic model which assumes a closed population over the daily (secondary) sampling periods. Thus, population size and other parameter estimates were made from capture histories of six to eight days trapping in each month. CAPTURE has a "diverse quality" in that it includes models that allow the estimation of population size under various assumptions, namely heterogeneity of capture probabilities (model Mh), behavioural response (model Mb) and temporal variations (model Mt) as well as their possible combinations (Nichols, Pollock and Hines, 1984).

For the survival rates of young and adult for each species, estimates were obtained using the program JOLLYAGE (Pollock, Nichols, Brownie and Hines, 1990) based on a modified Jolly-Seber open population model that allows for a specification of two age classes (Pollock, 1981; Stokes, 1984). The survival rate estimator of this model is said to be robust to heterogeneity of capture probability and is not biased by permanent trap

response (Nichols, *et al.*, 1984 and other references cited therein). Estimates with JOLLYAGE methodology are also available in three models namely, A2 (age-specific survival rate, time specific capture probabilities), B2 (constant survival rate and constant capture probabilities) and D2 (constant survival rate and constant capture probabilities per unit time).

Before statistical evaluations, a selection of trapping periods (months) for which estimated population parameters (survivorship, capture probability and population size) were all available was made. This was necessary because the first and last months or last two months estimates of the parameters of a study period are not available with the methodology and algorithm JOLLYAGE. Because of these limitations only 15 months out of a maximum of 24 during which trapping occurred could be used in the analysis. The months were grouped into five seasons: August-October 1990 (wet), November-December 1990 (dry), August-October 1991 (wet), November 1991-April 1992 (dry) and May 1992 (wet). Data distribution was checked for ANOVA conditionalities. Population size estimates were square-root transformed while survivorship rates and capture probabilities were arcsine transformed.

Effects of site (natural versus irrigated) and seasons (rainy versus dry) on population size and survivorship in each species were tested by the General Linear Model (GLM) procedure for ANOVA. The Ryan-Eliot-Gabriel-Welsch Multiple Range test (REGWQ) was used as a test of significant differences of thier population parameter estimates among the species.

Results

Population size estimates by the age-dependent Jolly-Seber method (model A2) was chosen over estimates obtained from the methodology CAPTURE for reasons detailed

below. The closure test in program CAPTURE indicated rejection of the closure hypothesis for most of the secondary sampling periods (daily trappings in a given month) in the present study. And although the data (for all species in both sites) for the majority of the months indicated strong evidence for heterogeneity of capture probabilities, the goodness of fit test did not select the Mh model as the appropriate one. Instead, in nearly all the primary periods (months), the procedure chose the M(tbh) or the M(tb) models.

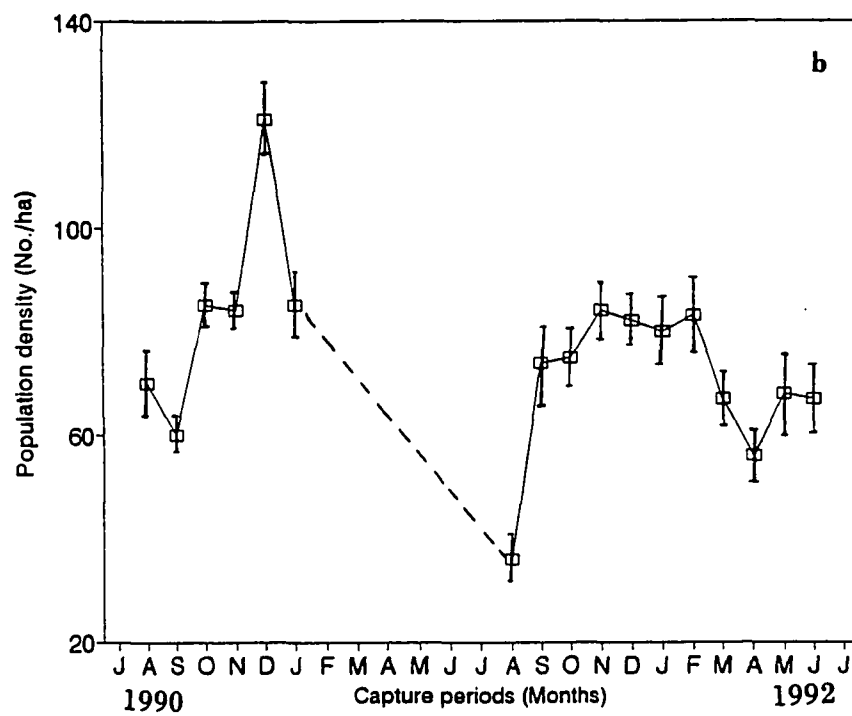
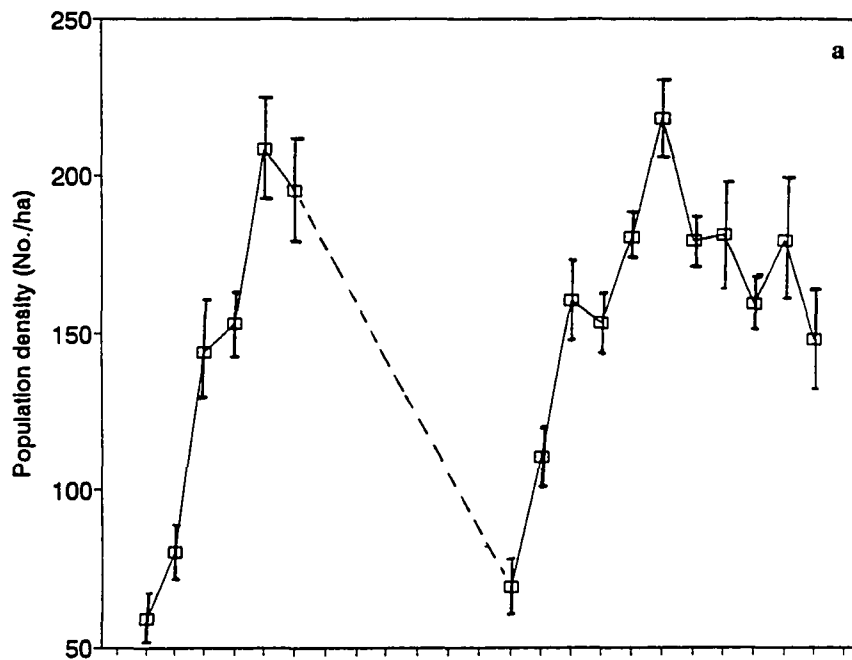
The M(tbh) lacks population estimators while the M(tb) showed wide confidence intervals (and huge standard errors) reflecting unreliability of the population estimates of the model. For example, in one situation where M(tb) model estimates were selected, population size was 664 with standard error of 1025 and approximate 95% confidence intervals of 172 - 8713. Such wide intervals translate into coefficient of variation of over 100%! The resulting problem of lack of closure means the results cannot be presented as valid estimates of the population size. For these reasons and the fact that capture probabilities obtained by JOLLYAGE procedure were high, hence reduced estimate biases, population estimates by the Jolly-Seber method instead of the closed model ones are presented here.

Population density in Natural (non-irrigated) fields:

Arvicanthis.

Estimates of *Arvicanthis* population size in the non-irrigated area (monthly average of 140 animals) shown in Figure 1.1a, was high in general terms but was only about 16% the size of population in the irrigated fields over the same period. Standard error values were less than 24 for each of the month and averaged 7.84. The dynamic trend here was that population estimates were very low in August (59 animals) and September

Figure 1.1(a,b). Population density estimates (no/ha) in *Arvicanthis* (a) *Mastomys* (b) in the natural fields during July 1990 to July 1992. Note the absence of data during March to June 1991 due to disruption in trapping. In addition, population estimates were not computed for the first and last months of each of the two study phases. Standard sampling errors are shown as vertical bars.



1990 (80 animals) during the rainy season (a time when the animals breed also). In October 1990 (end of breeding, Chapter two) there was a surge to 144, and the sizes remained high up to December 1990, early in the dry season (Figure 1.1a).

Mean monthly population size estimate during the remaining months (July 1990 - July 1992) i.e., after March - June disruption. of study was 158 animals with mean standard error of seven (Figure 1.1a), higher than the 140 seen early in the study. In August the population size was only 69 but rose to 110 during the following month. The highest number of 218 animals was in January 1992 two month after breeding has ended (Chapter two). The numbers then declined gently to 148 during June 1992 after the next breeding season had started.

Mastomys.

Estimates of Population size for *Mastomys* were 84 animals on a monthly average, about 30% that in the irrigated fields over the same period (Figure 1.1b). From August through November the size was more or less constant at about 80 per month but rose to 121 in December before falling back to 85 in January. Monthly standard error range (7-35) and monthly mean (9) values were low.

Estimated monthly population size for the last 11 month (July 1991 - July 1992) of study ranged from 36 in August 1991 to 84 animals in November 1991 (Figure 1.1b). From the low of 36 (SE 8) the numbers rose to 74 animals in September and rose again to 84 in November. Density stabilized until March 1992 when it declined to 67 and remained lower than 70 untill the end of the study. Mean approximate 95% confidence intervals were 55-86. An overall dynamic trend showed three parts over the 11 months for which estimates were available: Modest population size during most of the breeding season (August-October 1991), high post-breeding size averaging 82 animals

(November 1991-February 1992), and relatively low size (averaging about 65 animals) in the late dry season to early rains but before the next breeding commenced (March-June 1992). In general, the mean monthly estimated population sizes for *Mastomys* were half those of *Arvicanthis* from the same site and period.

Tatera.

During the early breeding season in August the population size of *Tatera* was estimated at 20 animals only but rose sharply to 56 in September 1990 and increased up to 94 in December 1990 at the end of the breeding season (Figure 1.1c). Standard errors averaged 7.38 per month, and approximate 95% confidence interval ranged from 51 to 80. These estimates were lower than those for *Arvicanthis* by about half but only slightly lower than those of *Mastomys* in the same area over the same time.

Following the March - June 1991 disruption, estimated population size, very low during the rains in August 1991, increased initially to 36 animals in September 1991 and to a maximum of 101 in February 1992, at the end of breeding in the dry season (Figure 1.1c). There was a drop to 84 animals in March 1992 but the size remained stable thereafter. Mean monthly size was 70 (SE 4). Approximate 95% confidence interval was 61-79. These estimates were about the same as those of *Mastomys* (Figure 1.1b).

Population densities in irrigated fields:

Arvicanthis

Estimates of *Arvicanthis* population size (by model A2) were very high for the first six months (8/1990-1/1991) for which estimates were available (Figure 1.2a). Population size ranged from 618 in August 1990 (peak of rainy season) to 1095 in January 1991 (early in the dry season). The increase over these two periods was steady.

Figure 1.1c. Population density estimates in *Tatera* (no/ha.) in the natural fields during July 1990 to July 1992. Note the absence of data due to disruption of trapping during March to June 1991. In addition, population estimates were not computed for the first and last months of each of the two study phases. Standard sampling errors are shown as vertical bars.

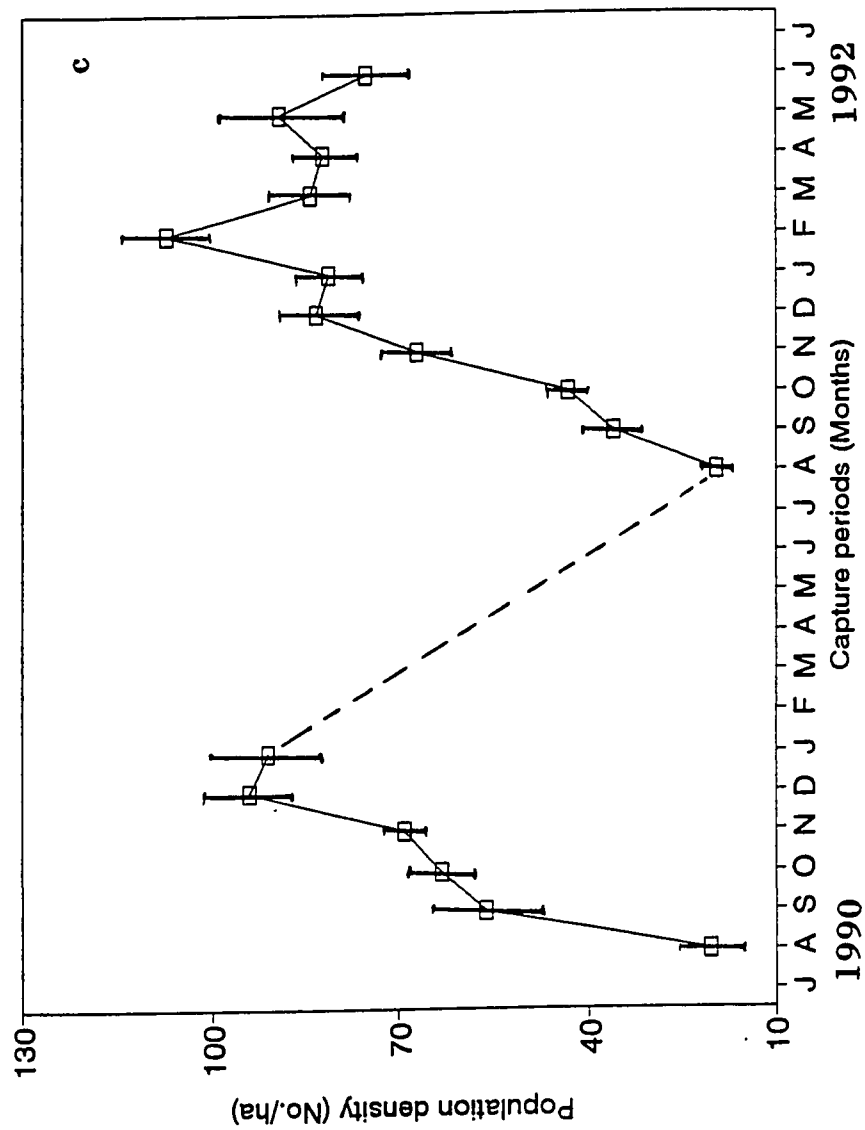
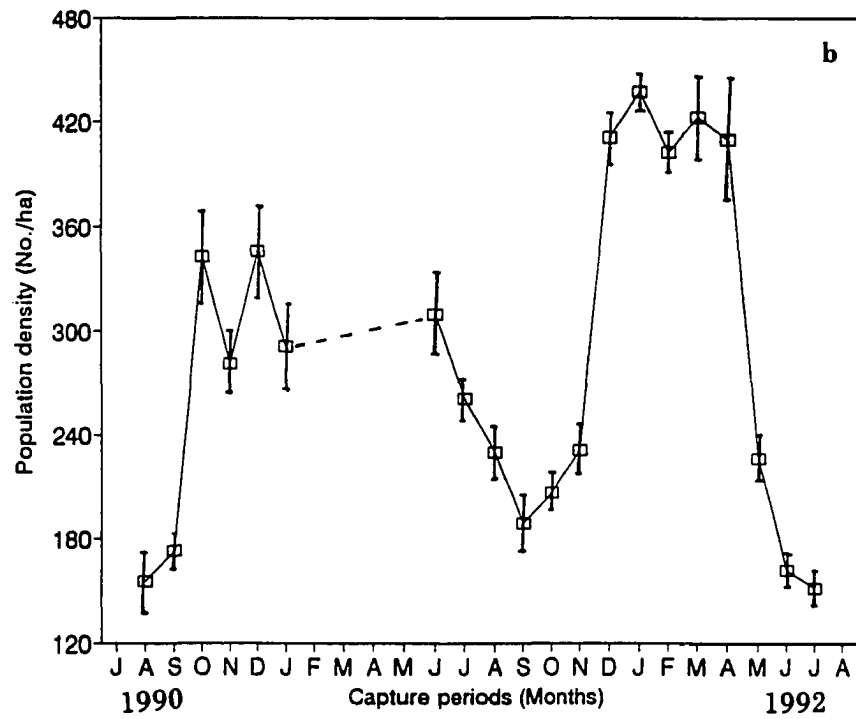
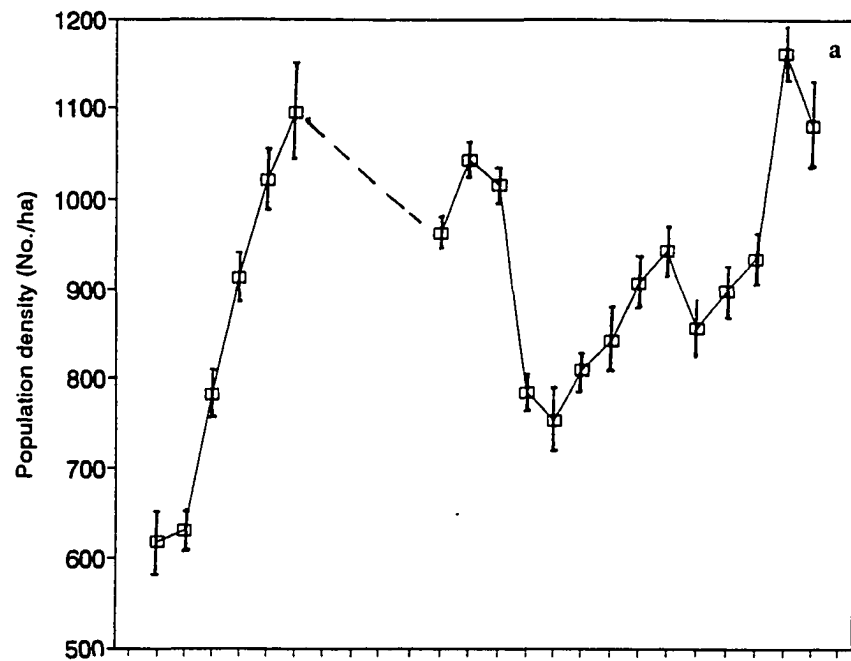


Figure 1.2(a,b). Population density estimates (no/ha) in *Arvicanthis* (a) and *Mastomys* (b) in the irrigated fields during July 1990 to August 1992. Note the absence of data due to disruption of trapping during March to April 1991. In addition, population estimates were not computed for the first and last months of each of the two study phases. Standard sampling errors are shown as vertical bars.



Standard error values were low ranging from 18 in October when the population size was 782 to 53 in January with a population of 1095. Width of approximate 95% confidence intervals were very narrow (mean 811-875) reflecting little over 10% coefficient of variation.

Estimates by models B2 and D2 for which size estimates for the last month of the first phase of study period (i.e. February 1991) were available, indicated a decrease in the population size during that month.

Estimates of population size were higher and more erratic during the remainder of the study after the March - April 1991 disruption (Figure 1.2a). Monthly size ranged from 753 in October 1991 to a high of 1081 in July 1992. Mean monthly size was 928 with standard error of 13. Numbers were noticeably high during June-August 1991 exceeding 900 for each month, then declined to less than 800 in September-October 1991 and remained under 900 until December 1991. In January and February 1992 the size regained its 900 level and remained nearly so until June 1992 when it reached its highest of 1161 (Figure 1.2b). Standard errors were generally low and monthly mean approximate 95% confidence intervals of 902-953, both of which suggest a good precision of estimate.

Monthly estimates of *Mastomys* population densities were high (155-346) during the first six months of study (Figure 1.2b). The average was 265/ha with standard error of 13. Density was relatively low in August and September (155 and 173, respectively) months of peak rainfall, but doubled or more than doubled during the next four months. Mean approximate 95% confidence intervals was 239-293.

Estimates of monthly population density during the next 15 months (May 1991 - August 1992) period were also high, ranging from 151 in July 1992 to 422 in March of

the same year (Figure 1.2b). The estimates in August and September 1991 (rainy period) were similar to those of the same months in 1990. Numbers in November-January 1990 and 1991 were also similar in both years. During June, July and August 1990 numbers were 310, 261 and 230 animals, respectively, a decline during September dropped density below 200. An increase to 437 in January 1992 remained until April (226 animals). The decline continued until the size reached 151 in June, little more than half of the size a year earlier. Mean population size for all months of study was 289 (SE 8). Approximate 95% confidence intervals of the population size was 272-306.

Survival rates, adult capture probability and recruitment of new animals in natural fields:

Arvicantis: 7/1990 - 2/1991.

Adult survival rates in the natural fields during the peak rain period to mid-dry season ranged from 0.66 in July to 0.97 in January 1991 (Table 1.1). On the average this was lower than in the irrigated fields. The same goes for the young where the rates range from 0.39 to 0.87, averaging 0.6 compared to 0.7 in the irrigated fields. The lowest survival rate for the young was 0.39 during the peak rains in July-August. Higher sampling error for the survival rates of young than those of adults indicates less precision of those estimates (probably due to smaller sample sizes). The same finding was in the irrigated fields. Adult capture rates varied, the lowest of being 0.28 in October. Recruitment was highest during September and November, which coincided with the first and second peak of newly reproduced animals (Table 1.1a).

Arvicantis: 7/1991 - 7/1992.

Adult survival was relatively low at 0.6 in July 1990 (Table 1.1b). Survival over the rest of the period averaged higher than 0.8 per month, the lower values being in

Table 1.1. Monthly survival rates, capture probabilities and recruitment of new *Arvicantis* in natural fields during July 1990 - February 1991 (A), and May 1991 - July 1992 (B). Standard errors are given in parentheses. Note: survival estimates for the last two periods are not provided with Jolly-Seber age-dependent Model A2. Similarly, the first period for adult capture rate and the first and last two periods for new animals added are not provided. Asteriks indicate absence of young animals during those periods.

Months	Adult Survival Rate	Young Survival Rate	Adult Capture Probability	New Animals Added
Section A				
Jul 1990	0.667 (0.109)	0.393 (0.179)	-----	-----
Aug	0.930 (0.075)	0.500 (0.188)	0.729 (0.113)	24 (11)
Sep	0.874 (0.103)	0.543 (0.135)	0.617 (0.078)	74 (20)
Oct	0.823 (0.085)	0.867 (0.093)	0.284 (0.058)	35 (18)
Nov	0.973 (0.096)	0.875 (0.119)	0.556 (0.056)	58 (10)
Dec	0.739 (0.099)	0.762 (0.195)	0.406 (0.051)	40 (10)
Jan 1991	-----	-----	0.551 (0.068)	-----
Feb	-----	-----	-----	-----
Section B				
Jul 1991	0.646 (0.088)	0.476 (0.111)	-----	-----
Aug	0.908 (0.071)	0.441 (0.131)	0.770 (0.081)	46 (11)
Sep	0.843 (0.079)	0.658 (0.110)	0.555 (0.070)	67 (9)
Oct	0.869 (0.066)	0.706 (0.091)	0.300 (0.050)	13 (8)
Nov	0.771 (0.054)	0.763 (0.101)	0.716 (0.047)	62 (9)
Dec	0.986 (0.064)	0.861 (0.113)	0.513 (0.047)	40 (9)
Jan 1992	0.747 (0.067)	0.626 (0.170)	0.542 (0.047)	16 (7)
Feb	0.765 (0.088)	0.748 (0.229)	0.528 (0.051)	43 (7)
Mar	0.800 (0.098)	0.791 (0.211)	0.334 (0.049)	14 (7)
Apr	0.759 (0.132)	*	0.551 (0.062)	58 (8)
May	0.897 (0.234)	*	0.259 (0.056)	11 (7)
Jun	-----	-----	0.354 (0.090)	-----
Jul	-----	-----	-----	-----

November 1991, January, February and April 1992 (dry months). Sampling error values were lower than 0.1 excepting in April -May 1992. The survival rates of young animals ranged from 0.4 to 0.8 with the lower rates being during the peak rains (July-September). Note there were no young animals trapped in the population during March-May 1992.

Adult capture rates were lowest in the months of October 1991, March, May and June, 1992, and were between 0.5 to 0.7 for the rest of the study. Recruitment of new animals was high (approximately 50 animals per month) during August, September and November 1991, a period that coincided with the birth of the new young (Chapter two). In February and April 1992 recruitment averaged 50 animals per month - at a time when the species was not breeding in the non-irrigated, natural fields (Table 1.1b).

***Mastomys*: 7/1990 - 2/1991.**

Survival rates were different for adults and young (Table 1.2a). A rate of 0.6 in July was lowest for the adult, and the monthly average for the whole period was 0.74, higher than the mean of 0.56 for the young. For the first three months, July-September the rate was from 0.32 to 0.44 which later rose to more than 0.6. Thus, unlike adults, the monthly survival rates for the young showed some discernible trend, namely, of low rates in the rains and higher rates after the rain. For the first time both rates showed rather high sampling error which exceeded 10 percent coefficient of variation, and in the case of the young even higher (Table 1.2a). Adult monthly capture probabilities, which varied from 0.2 to 0.6, vividly showed lower capture rates in November and December.

Table 1.2. Monthly survival rates, capture probabilities and recruitment of new *Mastomys* in natural fields during July 1990 - February 1991 (A), and May 1991 - July 1992 (B). Standard errors are given in parentheses. Note: survival estimates for the last two periods are not provided with Jolly-Seber age-dependent Model A2. Similarly, the first period for adult capture rate and the first and last two periods for new animals added are not provided. Asteriks indicate absence of young animals during those periods.

Months	Adult Survival Rate	Young Survival Rate	Adult Capture Probability	New Animals Added
Section A				
Jul 1990	0.639 (0.156)	0.329 (0.164)	-----	-----
Aug	0.836 (0.115)	0.342 (0.106)	0.413 (0.142)	13 (14)
Sep	0.733 (0.129)	0.442 (0.185)	0.618 (0.102)	36 (8)
Oct	0.720 (0.124)	0.748 (0.185)	0.433 (0.093)	26 (8)
Nov	0.818 (0.190)	0.656 (0.120)	0.553 (0.092)	39 (9)
Dec	0.728 (0.316)	0.870 (0.275)	0.370 (0.095)	6 (7)
Jan 1991	-----	-----	0.256 (0.011)	-----
Feb	-----	-----	-----	-----
Section B				
Jul 1991	0.810 (0.162)	0.405 (0.196)	-----	-----
Aug	0.809 (0.163)	0.582 (0.148)	0.493 (0.138)	40 (11)
Sep	0.815 (0.134)	0.528 (0.186)	0.362 (0.093)	29 (8)
Oct	0.729 (0.124)	0.714 (0.146)	0.519 (0.092)	27 (7)
Nov	0.626 (0.111)	0.748 (0.193)	0.507 (0.085)	33 (7)
Dec	0.688 (0.126)	0.803 (0.115)	0.549 (0.089)	20 (7)
Jan 1992	0.667 (0.147)	0.741 (0.155)	0.489 (0.092)	26 (7)
Feb	0.618 (0.158)	0.847 (0.187)	0.437 (0.097)	10 (6)
Mar	0.648 (0.201)	*	0.397 (0.011)	12 (5)
Apr	0.708 (0.332)	*	0.418 (0.012)	8 (5)
May	0.900 (0.300)	*	0.176 (0.096)	2 (1)
Jun	-----	-----	0.170 (0.015)	-----
Jul	-----	-----	-----	-----

Mastomys: 7/1991-7/1992.

During this period adult survival rates were very high, 0.8, during the peak rains of July-August 1991. The decline from this rate in September continued through February 1992 at 0.6 (Table 1.2b). In contrast to the adults, the young survivorship showed relatively low rates of 0.4-0.5 during the peak rain (and breeding period too). Although no young *Mastomys* were trapped during March - May 1992.

Adult capture probability was 0.3-0.4 at the earlier in period, then rose to 0.5 from October through December 1991 (Table 1.2b). From then on a trend of more or less continuous decline in capture rates sets in, reaching the lowest value of 0.17 in April and May 1992.

Recruitment figures of new animals into the population showed a general downward trend from 40 animals in August 1991 to a low of 2 animals in May 1992. It is worthy of note, however, that 'birth' estimates based on model B2 and D2 did not show such steady monthly decline over the study period.

Tatera: 7/1990 - 2/1991

Both adult and young survival rates were high with adults ranging from 0.7 in July-August and higher than 0.8 for the remaining period while the young from 0.5 to 0.6 (Table 1.3a). Except for minor inconsistency in December, both adult and young showed increased survivorship from the months of peak rains into the early part of the dry season. Standard error values of survival rates were greater than 15% for both adult and young.

Adult capture rates were low (0.3-0.4) in the beginning and end of this study period but relatively high (0.50 in the middle months of October -November. Recruitment of

Table 1.3. Monthly survival rates, capture probabilities and recruitment of new Tatera in natural, non-irrigated site during July 1990 - February 1991 (A), and May 1991 - August 1992 (B). Standard errors are given in parentheses. Note: survival estimates for the last two periods are not provided with Jolly-Seber age-dependent Model A2. Similarly, the first period for adult capture rate and the first and last two periods for new animals added are not provided. Asteriks indicate absence of young animals during those periods.

Months	Adult Survival Rate	Young Survival Rate	Adult Capture Probability	New Animals Added
Section A				
Jul 1990	0.714 (0.274)	*	-----	-----
Aug	0.793 (0.202)	0.553 (0.216)	0.400 (0.146)	40 (13)
Sep	0.818 (0.131)	0.584 (0.189)	0.308 (0.125)	16 (9)
Oct	0.836 (0.112)	0.666 (0.204)	0.506 (0.101)	16 (9)
Nov	0.947 (0.178)	0.829 (0.242)	0.555 (0.089)	29 (8)
Dec	0.861 (0.274)	0.650 (0.313)	0.354 (0.082)	10 (6)
Jan 1991	-----	-----	0.367 (0.113)	-----
Feb	-----	-----	-----	-----
Section B				
Jul 1991	0.866 (0.151)	*	-----	-----
Aug	0.881 (0.171)	0.546 (0.191)	0.692 (0.177)	18 (9)
Sep	0.843 (0.157)	0.644 (0.184)	0.369 (0.117)	13 (5)
Oct	0.746 (0.129)	0.559 (0.173)	0.586 (0.109)	35 (7)
Nov	0.731 (0.118)	0.754 (0.137)	0.577 (0.102)	33 (6)
Dec	0.726 (0.102)	0.665 (0.165)	0.392 (0.075)	21 (6)
Jan 1992	0.848 (0.139)	0.842 (0.183)	0.707 (0.076)	38 (6)
Feb	0.598 (0.122)	0.693 (0.193)	0.407 (0.078)	20 (5)
Mar	0.630 (0.112)	0.816 (0.160)	0.409 (0.083)	29 (6)
Apr	0.713 (0.130)	*	0.629 (0.087)	30 (7)
May	0.882 (0.263)	*	0.416 (0.091)	3 (5)
Jun	-----	-----	0.341 (0.091)	-----
Jul	-----	-----	-----	-----

new animals was highest during August and November when 40 and 29 animals were added to the population, respectively. Rates in November would most likely represent animals added mostly through reproduction. There were fewer than 20 animals per month in the rest of the other non-breeding months (Table 1.3a).

***Tatera*: 7/1991-7/1992**

There was a slight decline in the survival rates of adult *Tatera* from 0.8 during the peak rains of July-September 1991 to 0.7 during the following three months in the early dry season (Table 1.3b). In January 1992 the rate rose again to 0.8, then fell to 0.6 in March 1992. The young showed a reverse trend of survivorship compared to the adults with low rates (0.5) during the rains (August-October 1991) and an increase to an average of approximately 0.7 during the dry season (November 1991 - March 1992). Sampling errors of about 15% for survival rate of both adult and young were high (Table 1.3b). Absence of young *Tatera* in July 1991 and April and May 1992 prevented survival rates computation for them.

No trend was discernible for the probability of adult capture which varied from 0.3 to 0.7. The lowest rates were in the months of September and December 1991 and June 1992 (Table 1.3b). Recruitment of new animals was low during August - September 1991 (13-18 animals per month) but higher in October and November 1991 (late in the breeding season: 20-30 animals per month) but declined sharply to 3 animals in May 1992 at the onset of rains.

Survival rates, adult capture probability and recruitment of new animals in the irrigated fields:

Arvicantis: 7/1990 - 2/1992.

Survival rates for both young and adults were high throughout the period with that of young being generally lower than adults. For adults, survival rates changed from 0.8 to 0.9 and for the young from 0.5 to 0.8 (Table 1.4) over the period July 1990 to February 1991 which corresponded with the period of peak rains to dry season. Adult capture probability (the probability that an animal can be captured at least once during a trapping occasion) declined from 0.5 to 0.4 over the same period. Such high capture probability indicates good precision of the survival estimates.

Rates of birth or rather number of new animals added to the population (since the animals are not distinguished between reproductive recruits and new immigrants) also showed no discernable trend.

Arvicantis: 5/1991 - 8/1992.

Parameter estimates are given in section B of Table 1.4. Adult monthly survival rates remained nearly 100 percent from May to July 1991 until the peak rainy month of August when the rate dropped to 0.7 (Table 1.4b). This rose to 0.8 from September 1991 through June 1992, with drop of about 20% in December 1991 and April 1992. Survival rate for the young averaged about 0.5 during the rains of 1991 but for most months was at approximately 0.7 (Table 1.4b). There appeared to be high sampling errors for survivorship of the young during August to November 1991 and March to April 1992. As in section A of Table 1.1, adults recapture probabilities were high, varying from 0.4 to 0.6 with the lowest being towards the end of the rain (October to November and at the peak dry season from February to April (Table 1.4).

Table 1.4. Monthly survival rates, capture probabilities and recruitment of new *Arvicantis* in irrigated site during July 1990 - February 1991 (A), and May 1991 - August 1992 (B). Standard errors are given in parentheses. Note: survival estimates for the last two periods are not provided with Jolly-Seber age-dependent Model A2. Similarly, the first period for adult capture rate and the first and last two periods for new animals added are not provided.

Months	Adult Survival Rate	Young Survival Rate	Adult Capture Probability	New Animals Added
Section A				
Jul 1990	0.888 (0.032)	0.584 (0.053)	-----	-----
Aug	0.796 (0.025)	0.614 (0.046)	0.567 (0.328)	139 (26)
Sep	0.955 (0.021)	0.781 (0.032)	0.526 (0.024)	178 (15)
Oct	0.913 (0.023)	0.800 (0.036)	0.577 (0.020)	199 (11)
Nov	0.951 (0.030)	0.849 (0.051)	0.554 (0.019)	152 (10)
Dec	0.905 (0.056)	0.836 (0.139)	0.412 (0.019)	114 (7)
Jan 1991	-----	-----	0.422 (0.024)	-----
Feb	-----	-----	-----	-----
Section B				
May 1991	0.985 (0.012)	0.746 (0.029)	-----	-----
Jun	0.980 (0.015)	0.683 (0.040)	0.698 (0.020)	99 (8)
Jul	0.985 (0.026)	0.575 (0.098)	0.558 (0.017)	12 (5)
Aug	0.731 (0.259)	0.608 (0.156)	0.499 (0.019)	41 (12)
Sep	0.830 (0.030)	0.448 (0.204)	0.619 (0.021)	101 (22)
Oct	0.835 (0.035)	0.678 (0.202)	0.483 (0.023)	179 (23)
Nov	0.842 (0.036)	0.755 (0.107)	0.438 (0.024)	159 (31)
Dec	0.649 (0.028)	0.784 (0.079)	0.538 (0.026)	359 (33)
Jan 1992	0.835 (0.027)	0.773 (0.077)	0.582 (0.025)	185 (24)
Feb	0.846 (0.030)	0.885 (0.063)	0.476 (0.022)	58 (18)
Mar	0.965 (0.045)	0.751 (0.208)	0.448 (0.021)	70 (27)
Apr	0.652 (0.032)	0.704 (0.056)	0.342 (0.021)	349 (25)
May	0.957 (0.031)	0.825 (0.041)	0.564 (0.022)	266 (16)
Jun	0.844 (0.044)	0.718 (0.070)	0.506 (0.021)	108 (10)
Jul	-----	-----	0.476 (0.026)	-----
Aug	-----	-----	-----	-----

There were few additions during the peak rain in July (12 animals), and August 1991 (41 animals), somewhat more in the dry season months of February (58) and March (70) 1992, but other months had approximately 100 or more new animals. Over 300 estimated new recruits were in December 1991 and April 1992, when high number of *Arvicanthis* were seen roaming in the fields.

***Mastomys*: 7/1990-2/1991.**

Estimates of Survivorship for both young and adults (Table 1.5) were lower than in *Arvicanthis*. Adult survival rates in the first three months averaged 0.8 which declined to 0.6 in December 1991. As already noted, survivorship rates for the last two months were not computed with this model. The rates for the young, unlike those of adults, showed low values (0.4) during the initial three months and gradual increases thereafter. Standard error values for the survivorship were much higher than for adult values, perhaps indicating poorer precision of the estimates.

Excepting the month of September 1990 when adult capture probability was 0.7, the probability averaged about 0.45 over much of the study period. The recruitment rate was erratic early in the study, going from 41 in August 1990 to over 100 in September, then 31, 147, and 74 for each of the subsequent three months of the year.

***Mastomys*: 5/1991 - 8/1992.**

The first three months of this period showed high survival rates of 0.8 or higher. Then a sharp decline to 0.5 followed from August through October 1991, a period of heavy rains (Table 1.5b). There was a surge in survival rates during November 1991 and another decline during April to June 1992. The rates for the young were generally

Table 1.5. Monthly survival rates, capture probabilities and recruitment of new *Mastomys* in irrigated site during July 1990 - February 1991 (A), and May 1991 - August 1992 (B). Standard errors are given in parentheses. Note: survival estimates for the last two periods are not provided with Jolly-Seber age-dependent Model A2. Similarly, the first period for adult capture rate and the first and last two periods for new animals added are not provided.

Months	Adult Survival Rate	Young Survival Rate	Adult Capture Probability	New Animals Added
Section A				
Jul 1990	0.888 (0.103)	0.470 (0.111)	-----	-----
Aug	0.846 (0.062)	0.499 (0.094)	0.446 (0.090)	41 (7)
Sep	0.868 (0.078)	0.495 (0.179)	0.703 (0.571)	192 (31)
Oct	0.715 (0.069)	0.699 (0.131)	0.403 (0.052)	36 (2)
Nov	0.725 (0.079)	0.820 (0.115)	0.505 (0.051)	147 (23)
Dec	0.628 (0.081)	0.871 (0.147)	0.425 (0.049)	74 (13)
Jan 1991	-----	-----	0.515 (0.062)	-----
Feb	-----	-----	-----	-----
Section B				
May 1991	0.889 (0.057)	0.647 (0.072)	-----	-----
Jun	0.846 (0.045)	0.665 (0.092)	0.558 (0.052)	31 (2)
Jul	0.818 (0.078)	0.408 (0.174)	0.678 (0.041)	15 (2)
Aug	0.556 (0.079)	0.360 (0.313)	0.508 (0.054)	62 (7)
Sep	0.617 (0.076)	0.456 (0.076)	0.371 (0.057)	90 (10)
Oct	0.657 (0.051)	0.565 (0.099)	0.550 (0.055)	94 (13)
Nov	0.942 (0.060)	0.852 (0.070)	0.688 (0.047)	194 (40)
Dec	0.683 (0.052)	0.727 (0.102)	0.498 (0.039)	156 (46)
Jan 1992	0.608 (0.043)	0.770 (0.070)	0.523 (0.040)	136 (28)
Feb	0.905 (0.083)	0.779 (0.187)	0.631 (0.038)	57 (15)
Mar	0.721 (0.101)	0.615 (0.187)	0.357 (0.039)	106 (26)
Apr	0.478 (0.068)	0.617 (0.180)	0.300 (0.043)	30 (4)
May	0.460 (0.054)	0.589 (0.144)	0.496 (0.057)	58 (17)
Jun	0.558 (0.074)	0.592 (0.164)	0.833 (0.056)	60 (13)
Jul	-----	-----	0.625 (0.081)	-----
Aug	-----	-----	-----	-----

lower than those of adults (Table 1.5b). The values decreased from 0.6 in May 1991 to 0.3-0.4 in the rainy months of July-September 1991. Again standard error values for survivorship of the young were higher than those for adults.

Adult capture probabilities averaged 0.55 in June-July 1991, then showed a decline to 0.37 in September 1991 before regaining the 0.5 level in October 1991-February 1992.. There was another decline to 0.3 level followed during the next two months.

Addition of new animals to the population was low during June (31) and July (15) 1991. In August 1991 the number was 62 and was 194 by November 1991. Higher monthly recruitment values (August 1991, 62 and 194 in November 1991) were seen until February (57) before rising again to 106 animals in March 1992.

Age-specific variation in survival and capture probabilities: Natural fields

The tests for age-specific variation (adult versus young) in survival and capture probabilities for *Arvicanthis* data narrowly rejected the hypothesis that adult and young survival and capture probabilities are the same (7/1990-2/1991: chi-square=14.54, df=7, p=0.042; 7/1991-7/1992: chi-square=18.73, df=9, p=0.027). Thus, we concluded on the need for the age dependent model. However, the data from two study periods (Table 1.6) showed a poor fit to the model. Neither of other models (D2 and B2) was selected over model A2.

In respect to *Mastomys* capture data during both study periods (i.e, 7/1990-2/1991

Table 1.6. Results of hypotheses tests regarding age-specific (adult and young) variation in Arvicanthis, Mastomys and Tatera survival rates and capture probabilities in natural fields, and goodness of fit test to age-dependent (model A2) Jolly-Seber model (Pollock et al., 1990).

Species	Study periods	Adult and young survival and capture rates			Goodness of fit tests		
		Total Chi-square	df	P	Overall Chi-square	df	P
<u>Arvicanthis</u>	7/1990 - 2/1991	14.54	7	0.042	39.49	22	0.01
	5/1991 - 8/1992	14.73	9	0.027	160.52	46	<0.001
<u>Mastomys</u>	7/1990 - 2/1991	8.12	6	0.229	19.49	14	0.14
	7/1991 - 8/1992	7.10	8	0.525	76.64	34	<0.001
<u>Tatera</u>	7/1990 - 2/1991	3.19	5	0.671	26.56	14	0.03
	7/1991 - 8/1992	4.90	8	0.768	102.98	36	<0.001

and 7/1991-7/1992), the age-specific variation tests failed to reject the hypothesis of equal survival and capture probabilities for adult and young, though the goodness of fit tests selected the model for the data for the first period (7/1990-2/1991). The goodness of fit to model tests selected B2 over A2 for the second study period (7/1991- 7/1992)

The same test results were found for to *Tatera* population data i.e., the tests failed to reject the hypothesis of equal survival and capture probabilities for adults and young (Table 1.6). And in the case of the first study period (7/1990-2/1991), the goodness of fit to model tests selected model B2 (constant survival rate, time-specific capture probabilities). For the second study period (7/1991-7/1992) neither model B2 or D2 (constant survival rate and constant capture probabilities per unit time) was selected over the A2 model.

Age-specific variation in survival and capture probabilities: Irrigated fields

Summary of tests of hypotheses of equal survivorship and capture probabilities showed that adult and young survival and capture probabilities were not the same for *Arvicanthis* and *Mastomys* in the irrigated areas (Table 1.7) During the period July 1990 to February 1992, the results showed a chi-square value of 86.62, $df=7$, $p<0.001$, indicating a strong evidence for the age-dependent effect. However, the overall goodness of fit test indicated a rejection, though half of the individual tests showed evidence that the data did fit the model. For the 16-months period (May 1991-August 1992), hypothesis tests for adult and young survival and capture rates and goodness of fit test were similar to the first 8 months study, i.e., evidence for the age dependent model (chi-square=208.31, $df=15$, $p<0.001$), but a rejection by the goodness of fit test to the model A2 (chi-square=1220.52, $df=65$, $p<0.001$).

Table 1.7. Results of hypotheses tests regarding age-specific (adult and young) variation in *Arvicanthis* and *Mastomys* survival rates and capture probabilities in irrigated fields, and goodness of fit test to age-dependent (model A2) Jolly-Seber open model (Pollock et al, 1990).

Species	Study periods	Adult and young survival and capture rates			Goodness of fit tests		
		Total Chi-square	df	P	Overall Chi-square	df	P
<u>Arvicanthis</u>	7/1990 - 2/1991	86.62	7	<0.001	303.10	27	<0.001
	5/1991 - 8/1992	208.31	15	<0.001	1220.52	65	<0.001
<u>Mastomys</u>	7/1990 - 2/1991	24.98	7	<0.001	81.61	26	<0.001
	7/1991 - 8/1992	27.38	14	0.017	576.22	61	<0.001

Results of hypotheses tests regarding age differences in survival and capture rates in *Mastomys* showed evidence for the age-dependent effect (Table 1.7), more so in the first period of study i.e. 7/1990 -2/1991 (chi-square=24.98, df=7, $p<0.001$) than in the second- 5/1991- 8/1992 (chi-square=27.38, df=14, $p=0.017$). This was a similar result to that of *Arvicanthis* from the same area (Table 1.7).

Statistical evaluations

Population sizes differed among the species ($F=202.95$, $df=2$, $P<0.001$) and there were also significant effects of species x site interaction ($F=243.28$, $df=1$, $P<0.001$). Adult survival rates differed among the three species ($F=12.66$, $df=2$, $p<0.001$) with mean survival rate in adult *Arvicanthis* (0.84) not differing from that of adult *Tatera* (0.74) but each of the two differing significantly (REGWQ test, $p<0.05$) from 0.71 for *Mastomys*. The survival rates of young did not differ among the species ($F=2.50$, $df=2$, $p=0.092$). There were no site effects in either adult or young survival rate of the three species. There were however, seasonal differences ($F=14.51$, $df=4$, $p<0.001$) with significantly higher (REGWQ tests, $p<0.05$) young survival rates (0.74-0.79) at the end of the rains (also the end of peak breeding season in both sites) than during the rains (0.56-0.60).

Rates of recruitment among the species differed ($F=4.88$, $df=2$, $p=0.011$) with that of *Arvicanthis* (105/month) being the highest, followed by *Mastomys* (mean of 60 per month) and *Tatera* (23 per month). Overall monthly recruitment was also different between the two sites ($F=40.45$, $df=1$, $p<0.001$), being higher in the irrigated fields (137 animals) compared to 28 for the natural fields (REGWQ test, $p<0.05$).

Arvicanthis

The mean survival rates of adult *Arvicanthis* mean survival rate did not differ between sites ($F=0.11$, $df=1$, $P=0.740$) or the seasons ($F=1.15$, $df=4$, $P=0.236$) nor their interactions ($F=0.43$, $df=4$, $P=0.788$). The young, however, did show significant differences in survival rates between the seasons ($F=4.43$, $df=4$, $P=0.01$), with lower survivorship rates during the wet (peak breeding) seasons than in the dry seasons (REGWQ-test, $P<0.05$). Seasonal changes and seasons x site interaction had no effect on their survival. Recruitment of new animals significantly differed between the sites ($F=19.66$, $df=1$, $P<0.001$), being higher (REGWQ-test, $P<0.05$) in the irrigated fields (monthly mean=169) compared to 40 animals per month in the natural fields.

Population sizes differed between the sites ($F=619.59$, $df=1$, $P<0.001$), the monthly mean of 846 *Arvicanthis* in the irrigated fields being significantly higher (REGWQ test, $P<0.05$) than the mean of 148 in the natural fields. Seasonal effect on population size was also significant ($F=6.68$, $df=4$, $P<0.01$). The highest population levels were always after the breeding seasons.

Mastomys

Mastomys, unlike *Arvicanthis*, responded to the differences between the sites in survivorship rates of adults ($F=10.58$, $df=1$, $P<0.01$). There was no seasonal effect ($F=1.02$, $df=4$, $P=0.42$) but there was an interaction effect of site x season ($F=4.92$, $df=4$, $P<0.01$). The survivorship rates of young differed between the seasons ($F=8.23$, $df=4$, $P<0.001$) only, no site effects. Additions of new animals differed between the seasons ($F=13.60$, $df=1$, $P=0.0015$) but not between the sites or site x season interaction effects. This 'birth' rate, which has been noted to include both reproductive recruits and immigrants, was always higher in the irrigated fields (98 animals

per month) than 21 animals per month in the natural fields (REGWQ test, $P < 0.05$). Seasonal effect on population size was significant ($F = 4.67$, $df = 4$, $P < 0.01$).

Tatera

Being absent from the irrigated fields, *Tatera* population estimates could only be tested for seasonal effects within the natural fields. Adult and young survival rates differed marginally between the seasons ($F = 3.87$, $df = 4$, $P = 0.037$; $F = 4.86$, $df = 4$, $P = 0.021$, respectively). Seasonal changes had no effect on rate of recruitment of new animals into the population. However, the sizes of the populations differed significantly among the seasons ($F = 7.41$, $df = 4$, $P < 0.01$), always higher in the early part of the dry season after the species had stopped breeding and the surrounding fields had been harvested.

Discussion

Rejection of the closure hypothesis for most of our capture-recapture data by the closure test in algorithm CAPTURE, coupled with large standard errors (and wide approximate 95% confidence intervals) for estimated population sizes showed a breakdown of the closure assumption. It was not surprising that the closure test failed given the nature of the habitats we trapped. The grids in the irrigated fields were surrounded by crop fields that were irrigated and harvested at varying times throughout the year. This meant that while some plots were drained others were flooded, and when other plots had standing crops still others were being harvested. Thus, even within a short span of a week of trapping, animals should be expected to move in and out of the grids on a habitat which served as a sort of refuge. Indeed, some tagged animals were caught in surveillance traps 300m outside the grid area.

A similar situation probably prevailed in the natural fields. In the rainy season when crop fields became dense with vegetation, the rodents probably dispersed outside the refuge, and in the dry months there was influx of migrants as they return for refuge again in the relatively less disturbed grid area. There was evidence of this influx in the frequency distribution of our data.

The rejection of the closure hypothesis has probably led to the selection of model M(tbh) which had no estimates. Otis *et al.* (1978) note that the test can result in false rejection in some situations such as behavioral response. There was evidence for this type of response during most of our studies. White *et al* (1982) suggest eliminating data from the secondary trapping days in excess of five days and re-analyzing the rest of the data. However, a trial using this approach did not prove helpful.

Thus, we were unable to obtain valid and presentable estimates of population size using the methodology CAPTURE. We noticed evidence of behavioural response during most of the study period as well as strong evidence of heterogeneity in individual capture probabilities. These observations pre-empted the consideration of the Lincoln-Peterson index as an alternative to CAPTURE since they are exceptional conditions to its guarantee of low biases and low standard errors (Menkens and Anderson, 1988). Despite the failure of CAPTURE to provide useful estimates of population size due to the poor performance of its model selection procedure, (also noted by Menkens and Anderson, 1988), the package nonetheless served a useful purpose as a screening technique for evidence of behavioural response and for individual heterogeneity in capture probabilities as noted earlier.

We observed a surge in an already high *Arvicanthis* population levels in the irrigated fields during January-March and May-July from 700-800 animals in previous months to 1000 animals per ha and over. Although breeding in irrigated fields was con-

tinuous (Chapter two), the numerous reproductive recruits in April-May and October-December periods which soon became trappable, thus raising the estimated population levels. By contrast July-August population levels were relatively lower.

Mastomys in irrigated fields had overall smaller population size (mean 289 animals/month), about 30% that of *Arvicanthis*. *Mastomys* also showed smaller population sizes in July-August but high levels in the following months, over 400 in January and March-April or nearly double the monthly average. It follows that despite continuous breeding in the irrigated fields (Chapter two), there were marked periods (December-January, March-June) of higher population levels hence significant seasonal effects on population size. Interestingly, neither of the two periods of population peaks coincided with rains.

It is clear from these trends that population levels were relatively low during peak rains, in July-September perhaps due to excessive water that may have destroyed nesting sites and limit movement and foraging. In general, our data showed decreased population sizes around July-September for both *Arvicanthis* and *Mastomys* (Figure 1.2). For rodent management (control), this would be the time for treatments (trapping and poisoning). In October-January, fields became drained, and rice and other crops as well weed seeds in surrounding fields became mature (Chapter three) thereby improving general habitat conditions.

The population dynamics in the natural fields also indicated low numbers in August-September (peak rains) for both *Arvicanthis* and *Mastomys*. For example, *Arvicanthis* population size in August 1990 was only 59 per ha but doubled in December the same year. *Arvicanthis* population levels, although in its peak breeding activity in July-September (Chapter two), had barely recovered from the low levels at the end of the previous dry season, and the was beginning to show signs of increase when the heavy

rains probably caused increased adult and young mortality. Moreover, since many newly born individuals were being added to the population it is conceivable that a good proportion of them were too young to venture out or were untrappable due to small size at that time.

Tatera's population size in the natural fields was similarly small during the heavy rains in August-September (20-56 animals) but this was less likely a result of mortality but rather due to late and slow breeding (Chapter two). Highest population levels of approximately 100 animals or more were observed at the end of the breeding in December-January, two months after the rains had stopped (Figure 1.1c).

Survival rates in young of all species generally were lower than those of adults. The rates for both adults and young also were lower during the heavy rains of July-September in both sites, perhaps for the same reasons that population sizes were small during that period (i.e. poorly drained conditions which probably limited foraging and successful nesting). The young of all species showed increased survival rates beyond the breeding season. Survivorship presumably increased as animals live longer and mature. Lower rates of survival have been observed also at the end of dry season for adult *Arvicanthis*. This was probably related to food shortages to this species whose diet was known to fluctuate greatly with seasonal changes (Chapter three).

In the irrigated fields we observed reduced survival rates in adult *Mastomys* not only during July-August heavy rains but also in April and June. This may reflect a life history strategy of rapid population turnover and loss of large proportion of the adult population. For example, in November 1991 to January 1992, the survival rate of young *Mastomys* increased from a previous low of 0.4 (during the heavy rains) to exceed even that of the adults. This is additional evidence for high adult mortality after the breeding season. In respect to both adult and young survival rates in natural fields, we

observed high sampling error coupled with somewhat low adult capture probability. This made for poor precision in estimation compared to the data in the irrigated fields. This may be the result of a smaller population size in the natural fields.

Comparisons of adult survivorship rates among the three species showed that although *Arvicanthis* (with a mean rate of 0.84) did not differ from *Tatera* (0.74), both were significantly higher than in *Mastomys* (0.71). This supports our earlier claim that *Mastomys* employs an annual type of life history strategy where a good proportion of the adults die soon after breeding. In the earlier stages of development the three species did not differ significantly in their survival.

Arvicanthis had higher recruitment rates than either *Mastomys* or *Tatera*. This is rather surprising since the reproductive capacity of *Mastomys* was higher than that of *Arvicanthis* (Chapter two) but given the combinatory poor performance of *Mastomys* in irrigated fields and the loss of a large proportion of adult population after breeding, led to a lower density than *Arvicanthis*. We speculate here on the basis of trapping outcome near homes and other domestic habitats that the lower recruitment rate (and to a small extent, lower population size) in *Mastomys* was partly due to its greater dispersal rates into those habitats. In respect to *Tatera*, it was simply a late and slow breeder (Chapter two; Neal, 1982).

We saw that overall recruitment of all animals in the irrigated fields (where there were only two species) was nearly four times (same as population size differences) that in the natural fields, where three species co-exist. Again, this was not surprising since breeding in the irrigated fields was continuous in a generally more productive and protective habitat by virtue of food supply and vegetation cover. On a species level, both *Arvicanthis* and *Mastomys* had greater population sizes in the irrigated fields than in the natural fields for the same reason given above. Seasonal changes affected survival rates

of the young but not the adults, though its interaction with site factors did have a significant effect of the survival rate of adult *Mastomys*.

Neither adult or young *Tatera* showed decreased survival rates during the heavy July-August rains perhaps because breeding was just beginning, hence there were fewer or no litters to suffer any substantial losses. Being a slow breeder in response to the onset of the rainy season, *Tatera* did not show any significant seasonal difference in the rate of recruitment of new animals. In other words, the monthly addition of reproductive recruits and immigrants combined during the breeding season did not exceed that of immigrants entering the population during the non-breeding season.

Variable density estimates have been reported for *Arvicanthis* from various habitats and regions. Muller (1976), working in Ethiopian highlands recorded 65-250 animals/ha. This is similar to the range of the population size in the natural fields though the onset of *Arvicanthis* breeding in Ethiopia is after the rains rather than before, as in the present study. In rodent outbreak situation in rice fields at Fete-Ole, Senegal, Poulet and Poupon (1978) and Poulet (1982) estimate *Arvicanthis* population density at 638/ha and 100/ha in surrounding savannah. They attribute the high densities to the heavy rains of 1974, to which the species responded favorably. The Fete-Ole situation was a rather brief phenomenon because the population became extinct after only four years. The amount of rainfall in Kano, Nigeria is about three times higher than at Fete-Ole, and by comparison the *Arvicanthis* population in savannah habitat better established (and not merely a temporary phenomenon caused by heavy rains), by comparison. The high population levels in the irrigated fields in the present study, by accounts of undocumented reports, have existed for at least six years before the present study commenced (i.e., for longer periods than at Fete-Ole). Despite these differences the population data in the two regions are comparable and both demonstrate the opportunistic characteristics of *Arvicanthis* in rapidly exploiting productive new habitats.

Arvicanthis data from Kenya, East Africa by Delany and Monro (1986) offer another basis for comparison. They record low recruitment rates in June-July (during the breeding time) and low survivorship of 43% for individuals younger than 15 days, which improved to 90% at age 3-4 months. These are consistent with our findings in the present study, and we especially note the striking similarity in lowest survivorship during mid to late wet season. We have made repeated references in the preceding pages to low adult and young survivorship during the peak rainy months of July-August, in agreement with Delany and Monro (1986).

Like *Arvicanthis*, population size in *Mastomys* varies from one locality to another. Hubert and Adam (1983) record densities greater than 90 /ha at peaks during 1976 in Senegal. Though a comparatively drier area than Kano region, the population density was similar to that in the natural field in Kano. In an interesting work, Telford (1989) described *Mastomys* as an annual species, supporting our evidence for loss of large proportion of adults after the breeding seasons.

Data on survival rate for a related species (*T. leucogaster*) to the one in the present study showed a 53% pre-weaning survival, and 66% and higher survival for juveniles and adults (Chidumayo, 1980). We recorded similar results for both young and adult survival rates. In general, and consistent with our results, population size of *Tatera* is often small.

The present study demonstrates that both *Arvicanthis* and *Mastomys* can respond to irrigation by increased population size over their densities in natural fields, by up to the magnitude of four and three times, a respectively. We have also seen that the irrigated habitat supports rodent population densities nearly four times that of the natural fields, despite having only two of the three species. Among the three species *Arvicanthis*, always had the highest population density in both sites regardless of seasonal changes.

This, we have already noted, is in spite of its lower turnover than *Mastomys* (Chapter two). The explanation for this finding was in higher adult survival rates for *Arvicanthis*. The rates for young *Arvicanthis* also were marginally higher than those for *Mastomys*. Our data for both the natural and irrigated sites have demonstrated a link of the the peak rainy periods of July- September with decrease in the survival rates of both adult and young. We suggest that excessive moisture may have caused over-saturation and flooding in the fields, thus inhibiting nesting and foraging activities.

In addition to higher populations in the irrigated fields, our data also showed overall higher recruitment of new individuals throughout the seasons. Recruitment rate among the species differed in both sites, highest in *Arvicanthis* followed by *Mastomys* and *Tatera* (only in the natural fields) in that order.

CHAPTER TWO

PATTERNS OF REPRODUCTION

Introduction

Although the study of reproduction was a principal focus of rodent investigations in Africa in the 1960s and 1970s (Delany, 1972), the subject remains one of interest to many workers, in part because rodents constitute the largest mammalian group in the region (Happold, 1987; Rosevear, 1969), often attack crops and stored grains (Delany, 1986; Taylor, 1968) or are vectors of diseases (Monath, 1975; Pugh and Parker, 1975; Rosevear, 1969). In subsahara Africa, *Arvicanthis niloticus*, the Nile rat, *Mastomys natalensis*, the multimammate rat, and *Tatera valida*, the Savannah gerbil, are such economic pests (Delany, 1986; Funmilayo and Akande, 1977; Happold, 1987; Neal, 1977; Taylor, 1968).

These three species along with several others often show pronounced seasonality in their reproductive activity, i.e. associated with rainy months (Cheeseman and Delany, 1979; Chidumayo, 1984; Delany, 1986; Hubert, 1982; Leirs, Verheyen, Michiels, Verhagen and Stuyck, 1989; Moro and Hubert, 1983; Neal, 1982; Sheppe, 1972; Taylor and Green, 1976). The exceptions to this rule (Delany, 1986) can be interesting and puzzling. For example, *T. valida* breeds only during the rains, whereas the related species, *T. nigricauda*, breeds throughout the year in Kenya (Neal, 1982). In general, all three species in the present study show great geographic and temporal variability in the timing and length of breeding seasons. The influence of moisture through rainfall, flood, or irrigation in regulating, either directly or indirectly, the reproductive activity of African rodents is probably not in question (Delany, 1964; Rabiou and Fisher, 1989; Taylor and Green, 1976). Moisture is needed for successful reproduction. However, its influ-

ence, or that of any other environmental factor for that matter, in determining the onset of reproductive rhythm in any species remains elusive (Leirs *et al.*, 1989 Neal, 1977; Swanepoel, 1980).

A primary objective of our study was to examine the timing and duration of breeding (breeding seasons) of the three species of rodents from their natural habitats, and to compare to populations of the same species from a site where reservoirs provide irrigation water to farm fields (and marginal land) during the dry season. A secondary objective was to test the null hypothesis of no significant difference in breeding intensity (proportions breeding) in natural and irrigated habitats.

Materials and Methods.

Monthly rodent samples for necropsy (Table 2.1) were collected, using modified Fitch live traps (Rose, 1973). We considered these traps more suitable than Longworth traps, which exclude animals heavier than 140g (Fisher and Rabiou, unpublished data). Sorghum seeds, as bait, were placed at the entrance of each trap and inside its nest chamber. Traps were set at multiple trapping plots to reduce the effect of spatial bias. Thus, the irrigation site (as used hereafter) is actually a composite of six trapping plots, and the natural, non-irrigated site is a composite of seven trapping plots. Preliminary study revealed that minimum body weights for both fertile males and pregnant females were 60g for *Arvicanthis*, 38g for *Mastomys*, and 42g for *Tatera*. Because nothing can be learned about reproduction in, e.g., 20g juveniles, only adult-sized animals above these minimum weights were included in these analyses.

Necropsy methods follow Rose and Gaines (1978). Standard measurements of body, reproductive organs, and counts of embryos and placental scars were taken. In males, the weights, lengths and widths of testes and seminal vesicles were recorded; condition

Table 2.1. Number of mature (adult-size) animals from natural (non-irrigated) and irrigated sites necropsied for the assessment of breeding conditions. Sampling periods indicated by months were from July, 1990 to June, 1992. Rainy Season was from May to October; Dry Season was from November to April. Note the absence of Tatera from the irrigated sites. In the analyses, monthly samples are pooled by season.

NON-IRRIGATED SITES.

	Seasons	<u>R A I N</u>				<u>D R Y</u>						<u>R A I N</u>						<u>D R Y</u>						<u>R A I N</u>			
	Months	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J		
Species	Sex																										Total
<u>Arvicanthis</u>	Male	8	8	8	8	10	11	8	9	10	9	11	11	11	8	8	8	10	7	9	7	8	9	10	8	214	
	Female	9	7	8	11	9	8	10	8	10	11	10	10	11	6	10	8	8	2	9	9	9	9	10	10	212	
<u>Mastomys</u>	Male	6	8	6	6	5	6	9	7	4	8	7	7	8	7	7	6	6	6	7	7	2	7	6	7	155	
	Female	7	6	7	6	8	8	9	8	9	8	8	8	9	7	5	5	7	8	6	8	6	7	8	7	175	
<u>Tatera</u>	Male	5	5	6	8	7	6	10	8	8	6	7	10	8	7	7	8	6	8	8	7	7	7	7	6	172	
	Female	6	6	4	5	8	9	8	8	8	10	6	8	6	9	8	5	7	9	8	7	6	8	7	8	174	

IRRIGATED SITES.

<u>Arvicanthis</u>	Male	9	10	13	12	12	9	13	9	8	7	10	13	8	7	7	9	9	10	11	11	9	11	10	11	238
	Female	10	11	11	13	11	8	11	13	9	7	8	9	9	8	9	8	8	9	11	10	11	9	8	7	228
<u>Mastomys</u>	Male	6	5	7	6	4	5	6	7	8	8	8	9	9	7	8	8	5	5	6	7	9	7	7	8	165
	Female	8	8	4	6	6	7	8	4	10	7	4	8	8	9	10	8	7	7	7	4	7	8	7	6	168

of epididymis (convoluted only in breeding males) and male fertility were determined by the presence of active sperm cells assayed in each month from a smear of cauda epididymis placed in 0.8% saline solution under a microscope. Pregnancy was the criterion for breeding, but lactation tissue and placental scars presented evidence for recent or past breeding in parous females.

The influence of body weight was eliminated by the use of ANCOVA (only the *P* values are given here) to determine the effects of site and seasons and their interactions on the reproduction of the species. Adjusted mean values of reproductive parameters of the same species in the two sites were compared using multiple comparison *t*-tests.

Results

All three species were notable seasonal breeders in the natural habitats. Under irrigation, *Arvicanthis* and *Mastomys* bred continuously (with some differences) whereas *Tatera* disappeared.

Male *Arvicanthis*:

No fertile male *Arvicanthis* was seen in the natural grassfields (Figure 2.1a) during December through March (dry periods), but as the rains increased, so did the proportions of fertile males. By comparison, more than 50% of the mature animals were fertile in *every* month in the irrigated site (Figure 2.1b), with the lowest percentages of about 60% fertile males in the dry season during December 1991. Results of ANCOVA tests revealed significant ($P < 0.001$) site and seasons effects on male reproductive parameters. There were significant differences (*t*-test, $P < 0.001$) in mean values of reproductive parameters between sites during the dry seasons (Table 2.2) and between seasons within each site. Note the statistical tests in Table 2.2 compare adjusted mean values between the two sites. Mean values of these parameters showed similar patterns to those

Figure 2.1(a,b). Percent fertile adult-sized male *Arvicanthis* in natural (A) and irrigated (B) fields near Kano, northern Nigeria. Wet and Dry refer to wet and dry seasons, which roughly correspond to May-October and November-April periods, respectively.

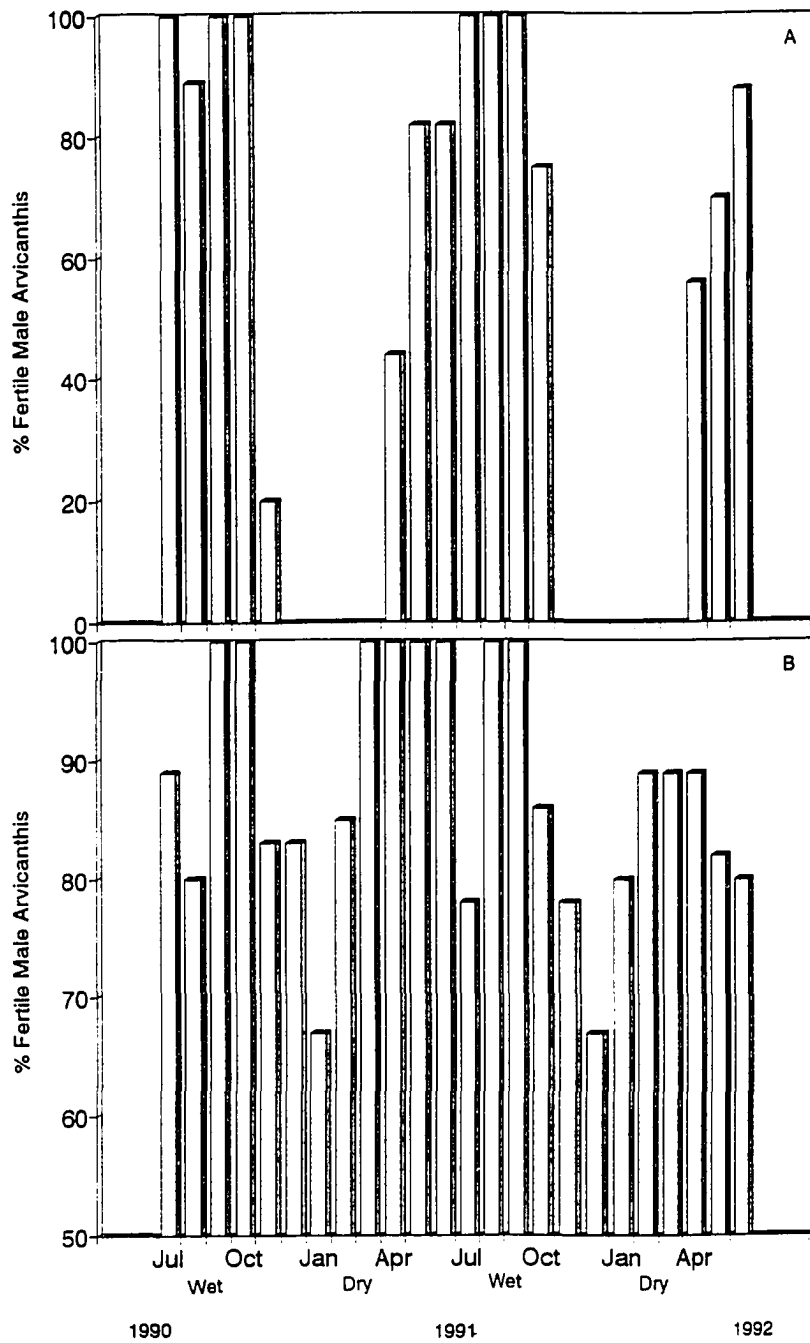


Table 2.2. Mean values (means adjusted for body mass in ANCOVA test) of reproductive parameters in mature male *Arvicanthus* in irrigated and non-irrigated sites by seasons, and statistical results for the hypothesis H_0 : mean (irrigated) = mean (non-irrigated). NS = No significant difference; (i.e. $P > 0.05$); *** = Significant difference at $P < 0.001$. Standard error values of means are given in parentheses. TL = Testes Length (mm); TW = Paired Testes Weight (mg); SVL = Seminal Vesicle Length (mm); SVW = Paired Seminal Vesicle Weight (mg).

Seasons	N (Irrg.)	Reproductive Parameters	Mean (Irrg.)	N (Non-irrg)	Mean (Non-irrg.)	Statistical Results
Wet Jul.'90 - Oct.'90	44	TL	19.62 (0.41)	32	19.31 (0.45)	NS
		TW	2540.65 (75.02)		2440.12 (85.26)	NS
		SVL	17.95 (0.59)		18.70 (0.67)	NS
		SVW	951.89 (60.69)		869.94 (68.97)	NS
Dry Nov.'90 - Apr.'91	58	TL	14.01 (0.30)	57	9.05 (0.32)	***
		TW	1204.86 (460.14)		502.58 (48.52)	***
		SVL	9.34 (0.43)		3.23 (0.46)	***
		SVW	458.23 (27.03)		83.35 (28.42)	***
Wet May.'91 - Oct.'91	54	TL	19.14 (0.34)	57	18.42 (0.38)	NS
		TW	2277.44 (97.87)		2091.19 (95.20)	NS
		SVL	15.62 (0.66)		15.70 (0.64)	NS
		SVW	696.95 (51.75)		703.54 (50.34)	NS
Dry Nov.91 - Apr.'92	61	TL	14.58 (0.36)	50	8.83 (0.39)	***
		TW	1202.14 (52.93)		439.95 (56.53)	***
		SVL	11.57 (0.46)		3.40 (0.49)	***
		SVW	406.12 (25.17)		60.01 (26.88)	***
Wet May.92 - Jun.'92	21	TL	17.23 (0.72)	18	16.83 (0.78)	NS
		TW	1880.70 (169.35)		1868.61 (182.93)	NS
		SVL	13.96 (0.92)		13.15 (0.99)	NS
		SVW	626.68 (78.40)		568.75 (84.68)	NS

of the histograms in Figure 2.1, namely of relatively modest regression of organs in the males from the irrigated fields, but drastic regression in the non-irrigated fields. Thus, irrigation enhanced reproduction in male *Arvicanthis* during the wet seasons (in which irrigation may also be occasionally employed during short spells of drought) but even more so during the dry seasons.

Female *Arvicanthis*:

Breeding activity in the non-irrigated site (Figure 2.2a) was strictly seasonal, being associated with the rains (same as the males), but with the first pregnancy recorded a month after the appearance of the first scrotal male. In the irrigated fields nearly 50% or more of the females were pregnant throughout most of the year (Figure 2.2b), excepting the month of August of 1991 when the fields were virtually flooded with rain water. There were significant ($P < 0.001$) site effects and seasonal effects (within the non-irrigated site only) on mean values of reproductive parameters. Thus, all reproductive parameters of females, excepting placental scars, showed significant (t -test, $P < 0.001$) differences between the two sites during the dry seasons (Table 2.3) and similar differences between seasons in the non-irrigated fields. There were, however, no significant seasonal differences in either the mean embryo numbers (range 4.73 - 5.58) or other reproductive parameters within the irrigated site. It follows then, in contrast to the conditions in *Arvicanthis* males, that irrigation enhanced female breeding only during the dry seasons.

Male *Mastomys*:

The proportions of male *Mastomys* in both natural and irrigated sites (Figure 2.3) indicate a pattern of reproductive activity strikingly similar to that of male *Arvicanthis* but breeding started *after* the onset of rainfall. Breeding activity during the dry season

Figure 2.2(a,b). Percent adult-sized female *Arvicantis* in reproductive condition in natural (A) and irrigated (B) fields near Kano, northern Nigeria. Wet and Dry refer to seasons, which roughly correspond to May-October and November- April, respectively.

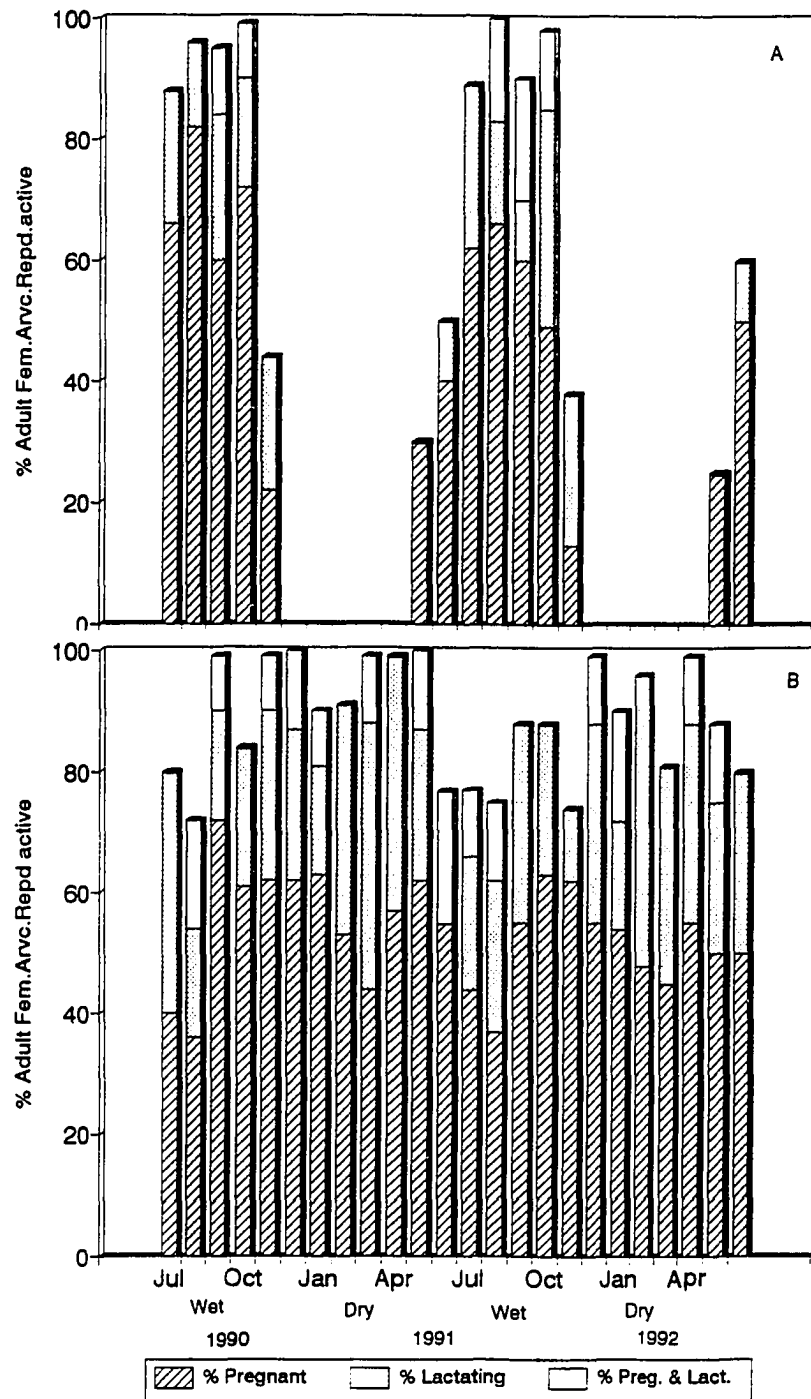
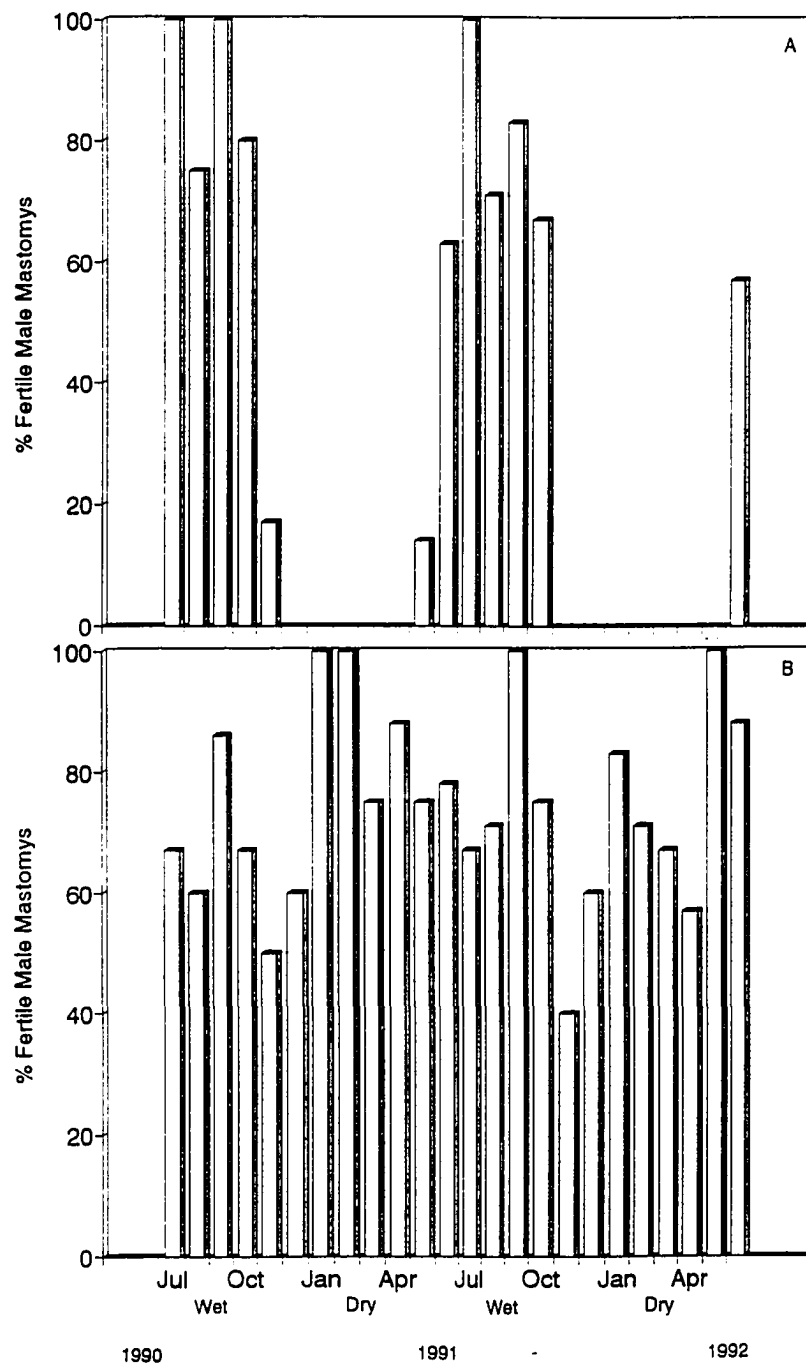


Table 2.3. Mean values (means adjusted for body mass in ANCOVA test) of reproductive parameters in mature female *Arvicanthus* in irrigated and non-irrigated sites by seasons, and statistical results for the hypothesis H_0 : mean (irrigated) = mean (non-irrigated). NS = No significant difference (i.e. $P > 0.05$); *** = Significant Difference at $P > 0.001$. Standard error values of means are given in parentheses. EMN = Embryo Number; EW = Embryo Weight (mg); PLS = Number Placental Scars; EML = Embryo Length (mm); UDM = Uterine Diameter (mm).

Seasons	N (Irrg.)	Reproductive Parameters	Mean (Irrg.)	N (Non-irrg.)	Mean (Non-irrg.)	Statistical Results
Wet Jul.'90 - Oct.'90	45	EMN	5.31 (0.57)	35	5.47 (0.64)	NS
		EMW	6261.18 (1384.72)		6985.90 (1558.14)	NS
		PLS	5.81 (0.55)		6.27 (0.62)	NS
		Eml	9.45 (1.49)		9.95 (1.68)	NS
		UDM	6.58 (0.66)		6.73 (0.75)	NS
Dry Nov.'90 - Apr.'91	59	EMN	4.80 (0.42)	56	0.41 (0.04)	***
		EMW	5128.44 (721.93)		869.34 (700.45)	***
		PLS	5.83 (0.57)		6.78 (0.55)	NS
		EML	9.30 (0.96)		1.17 (0.93)	***
		UDM	6.44 (0.53)		2.64 (0.51)	***
Wet May.'91 - Oct.'91	51	EMN	5.58 (0.69)	55	4.94 (0.66)	NS
		EMN	5582.13 (1041.65)		5189.91 (1000.14)	NS
		PLS	7.25 (0.50)		6.09 (0.48)	NS
		EML	9.01 (1.37)		9.34 (1.32)	NS
		UDM	6.61 (0.64)		6.24 (0.61)	NS
Dry Nov.91 - Apr.'92	58	EMN	5.26 (0.56)	46	0.09 (0.60)	***
		EMW	4538.05 (591.08)		467.35 (635.47)	***
		PLS	5.54 (0.58)		6.13 (0.63)	NS
		EML	8.98 (10.01)		0.50 (0.09)	***
		UDM	5.96 (0.46)		2.32 (0.50)	***
Wet May.92 - Jun.'92	15	EMN	4.73 (1.08)	20	3.92 (1.00)	NS
		EMW	2493.06 (691.01)		1917.89 (637.04)	NS
		PLS	5.58 (1.00)		6.42 (0.93)	NS
		EML	8.58 (1.77)		5.13 (1.63)	NS
		UDM	5.97 (0.86)		4.06 (0.79)	NS

Figure 2.3(a,b). Percent fertile adult-sized male *Mastomys* in natural (A) and irrigated (B) fields near Kano, northern Nigeria. Wet and Dry refer to wet and dry seasons, which roughly correspond to May-October and November- April periods, respectively.



in the non-irrigated fields (Figure 2.3a) was only apparent during the rains, but continued in the irrigated fields (though at reduced rates) immediately after the rains. Statistical analyses showed significant site and seasonal effects on all male reproductive parameters ($P < 0.001$), and the mean values of the reproductive parameters were significantly higher (t -test, $P < 0.001$) in the irrigated sites in all seasons except the wet season of 1990 (Table 2.4), suggesting that irrigation enhanced reproduction in male *Mastomys* too (as in male *Arvicanthis*) even during the rains.

Female *Mastomys*:

Breeding in the non-irrigated site was strictly seasonal during the rainy months, but the length of breeding was shorter by up to two months than in female *Arvicanthis* (Figure 2.4a). Although female *Mastomys* had year-round breeding in the irrigated fields, the overall monthly rates were lower (Figure 2.4b) than in female *Arvicanthis*. In the natural fields during the rains, and throughout the year in the irrigated fields, embryo numbers averaged more than eight per fertile female (Table 2.5). There were significant ($P < 0.001$) site and seasonal (in natural fields only) effects on these mean embryo numbers and on other reproductive features. Thus, seasonal differences in reproductive parameters within the irrigated fields were not significant, as in female *Arvicanthis*. In the dry season, female *Mastomys* (as with the males) in the irrigated fields maintained the size of reproductive organs and similar embryo counts as during the rains (Table 2.5), supporting the pattern seen for pregnancy (Figure 2.4).

Male *Tatera*:

Tatera responded by its complete disappearance from the irrigated site, hence only the percentages of fertile males for the non-irrigated site are given (Figure 2.5). In July, August and September of 1990, all adult *Tatera* males were fertile but by November

Table 2.4. Mean values (means adjusted for body mass in ANCOVA tests) of reproductive parameters in mature male *Mastomys* in irrigated and non-irrigated sites by seasons, and statistical results for the hypothesis H_0 : mean (irrigated) = mean (non-irrigated). NS = No significant difference; (i.e. $P > 0.05$); * = significant difference at $P < 0.01$; *** = Significant difference at $P < 0.001$. Standard error values of means are given in parentheses. TL = Testes Length (mm); TW = Paired Testes Weight (mg); SVL = Seminal Vesicles Length (mm); SVW = Paired Seminal Vesicles Weight (mg).

Seasons	N (Irrig.)	Reproductive Parameters	Mean (Irrig.)	N Non-irrig.)	Mean (Non-irrig.)	Statistical Results
Wet Jul.'90 - Oct.'90	24	TL	13.73 (0.53)	26	14.01 (0.52)	NS
		TW	1308.47 (63.28)		1103.06 (62.00)	NS
		SVL	12.79 (0.71)		12.71 (0.69)	NS
		SVW	509.56 (48.46)		444.25 (47.48)	NS
Dry Nov.'90 - Apr.'91	38	TL	13.83 (0.45)	39	9.13 (0.42)	***
		TW	1059.08 (45.51)		441.85 (42.29)	***
		SVL	11.31 (0.54)		3.79 (0.50)	***
		SVW	401.13 (28.46)		103.79 (26.45)	**
Wet May.'91 - Oct.'91	49	TL	14.92 (0.44)	52	13.49 (0.49)	**
		TW	1377.48 (66.90)		1053.07 (74.36)	**
		SVL	14.24 (0.65)		10.67 (0.73)	***
		SVW	515.35 (35.97)		366.69 (39.98)	**
Dry Nov.91 - Apr.'92	39	TL	12.81 (0.33)	43	7.36 (0.34)	***
		TW	829.52 (45.51)		262.85 (46.12)	***
		SVL	9.65 (0.51)		2.08 (0.52)	***
		SVW	283.05 (22.03)		7.09 (0.32)	***
Wet May.92 - Jun.'92	15	TL	14.83 (0.75)	13	10.65 (0.80)	***
		TW	1299.48 (115.03)		924.82 (123.81)	**
		SVL	12.35 (1.09)		7.66 (1.17)	**
		SVW	525.05 (64.38)		206.46 (69.30)	**

Figure 2.4(a,b). Percent adult-sized female *Mastomys* in reproductive condition in natural (A) and irrigated (B) fields near Kano, northern Nigeria. Wet and Dry refer to wet and dry seasons, which roughly correspond to May-October and November- April periods, respectively.

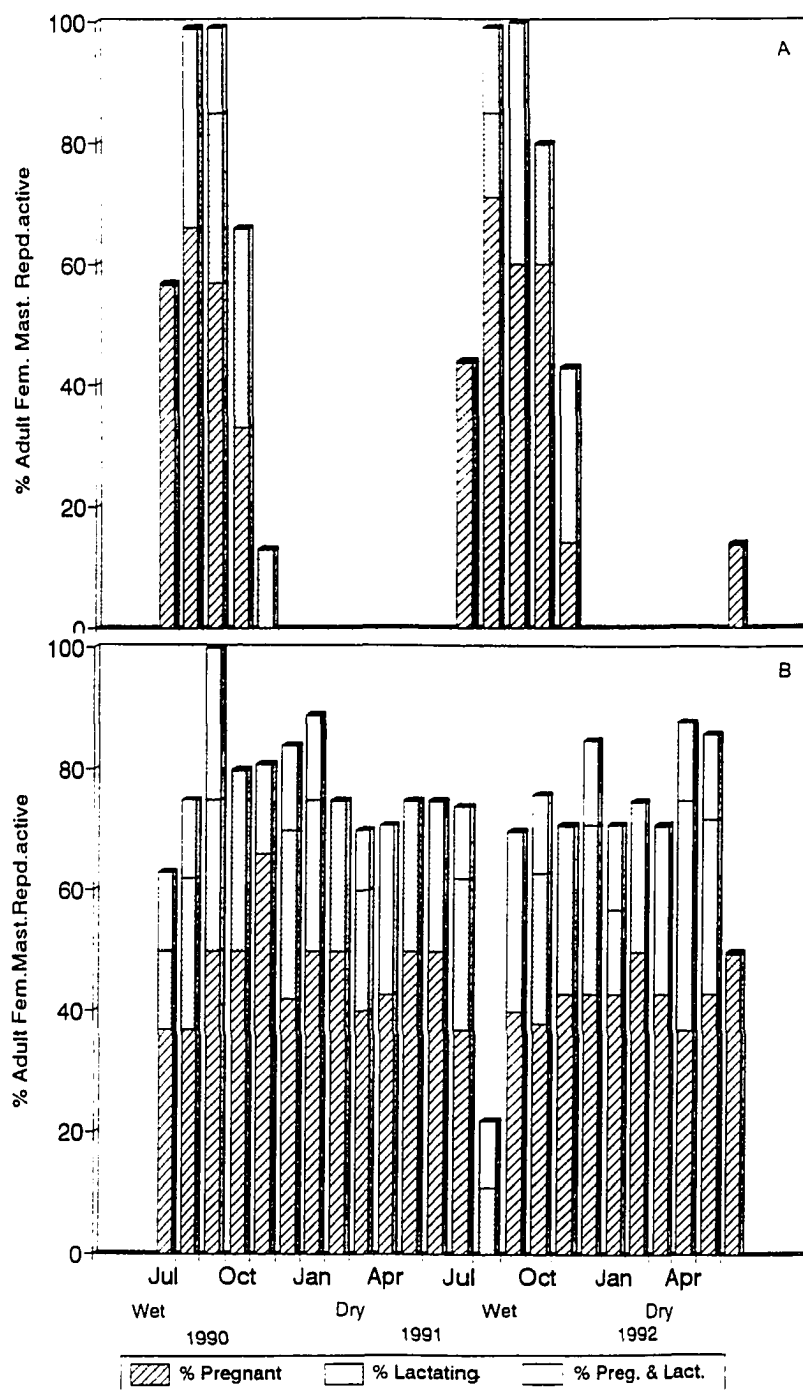
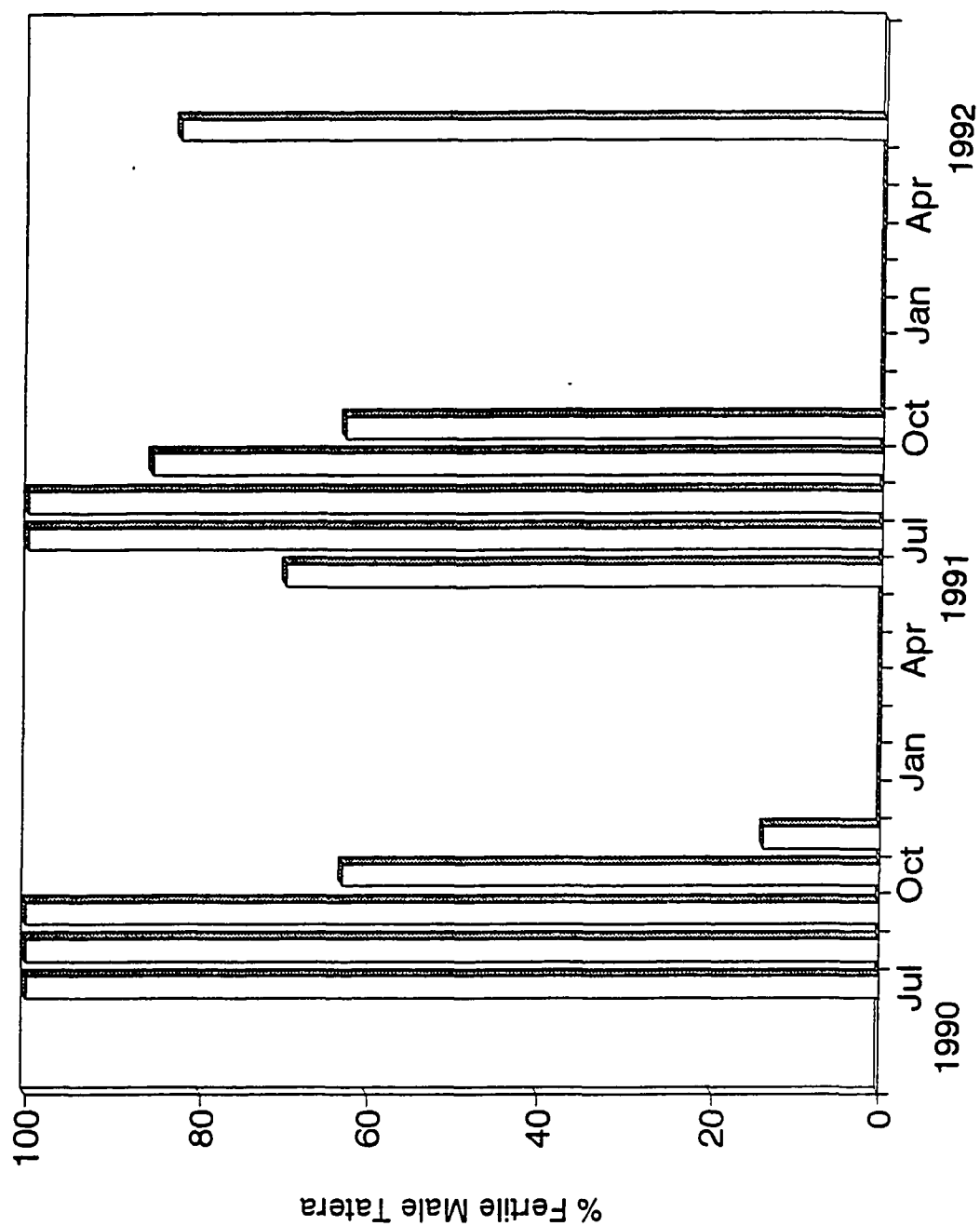


Table 2.5. Mean values (means adjusted for body mass in ANCOVA tests) of reproductive parameters in mature female *Mastomys* in irrigated and non-irrigated sites by seasons, and statistical results for the hypothesis H_0 : mean (irrigated) = mean (non-irrigated). NS = No significant difference (i.e. $P > 0.05$); *** = Significant difference at $P < 0.001$; ** = significant at $P < 0.01$; * = significant at $P < 0.05$. Standard error values of means are given in parentheses. EMN = Embryo Number; EMW = Embryo Weight (mg); PLS = Number Placental Scars; EML = Embryo Length (mm); UDM = Uterine Diameter (mm).

Seasons	N (Irrig.)	Reproductive Parameters	Mean (Irrig.)	N (Non-irrig.)	Mean (Non-irrig.)	Statistical Results
Wet Jul.'90 - Oct.'90	26	EMN EMW PLS EML UDM	8.91 (1.02) 4692.82 (911.72) 10.94 (1.17) 8.50 (1.17) 5.54 (0.58)	26	8.75 (1.06) 4467.36 (948.98) 8.47 (1.22) 8.66 (1.23) 5.41 (0.61)	NS NS NS NS NS
Dry Nov.'90 - Apr.'91	42	EMN EMW PLS EML UDM	8.48 (0.58) 4295.40 (426.76) 9.59 (0.91) 8.22 (0.70) 5.88 (0.38)	40	0.01 (0.01) 271.62 (387.87) 8.24 (0.83) 0.01 (0.01) 1.89 (0.35)	*** *** NS *** ***
Wet May.'91 - Oct.'91	47	EMN EMW PLS EML UDM	8.61 (0.98) 4701.69 (680.40) 9.56 (1.06) 8.10 (1.11) 5.66 (0.55)	42	8.00 (0.99) 3955.58 (688.78) 8.80 (1.07) 8.54 (1.13) 4.87 (0.53)	NS NS NS NS NS
Dry Nov.91 - Apr.'92	40	EMN EMW PLS EML UDM	8.46 (0.49) 3964.87 (457.28) 8.15 (0.77) 8.01 (0.57) 5.78 (0.33)	42	0.19 (0.45) 404.25 (428.12) 8.21 (0.72) 0.30 (0.53) 1.89 (0.30)	*** *** * *** ***
Wet May.92 - Jun.'92	13	EMN EMW PLS EML UDM	8.48 (1.42) 4507.29 (670.95) 7.98 (1.45) 7.81 (1.15) 5.96 (0.70)	15	1.37 (1.32) 198.34 (623.95) 9.94 (1.34) 0.69 (1.07) 2.02 (0.65)	** *** NS *** ***

Figure 2.5. Percent fertile adult-sized male *Tatera* in natural fields near Kano, northern Nigeria. Wet and Dry refer to wet and dry seasons, which roughly correspond to May-October and November- April periods, respectively.



fewer than 20% were fertile. In 1991, male *Tatera* had fewer months of reproductive activity than males of either *Arvicanthis* or *Mastomys*. Results of ANCOVA showed significant ($P < 0.001$) seasonal effects on the size of reproductive organs, such as testes and seminal vesicles. It is not surprising, given the virtual absence of breeding in the dry season, that the sizes of reproductive organs (testes and seminal vesicles) were significantly higher during the rains (t -test, $P < 0.001$).

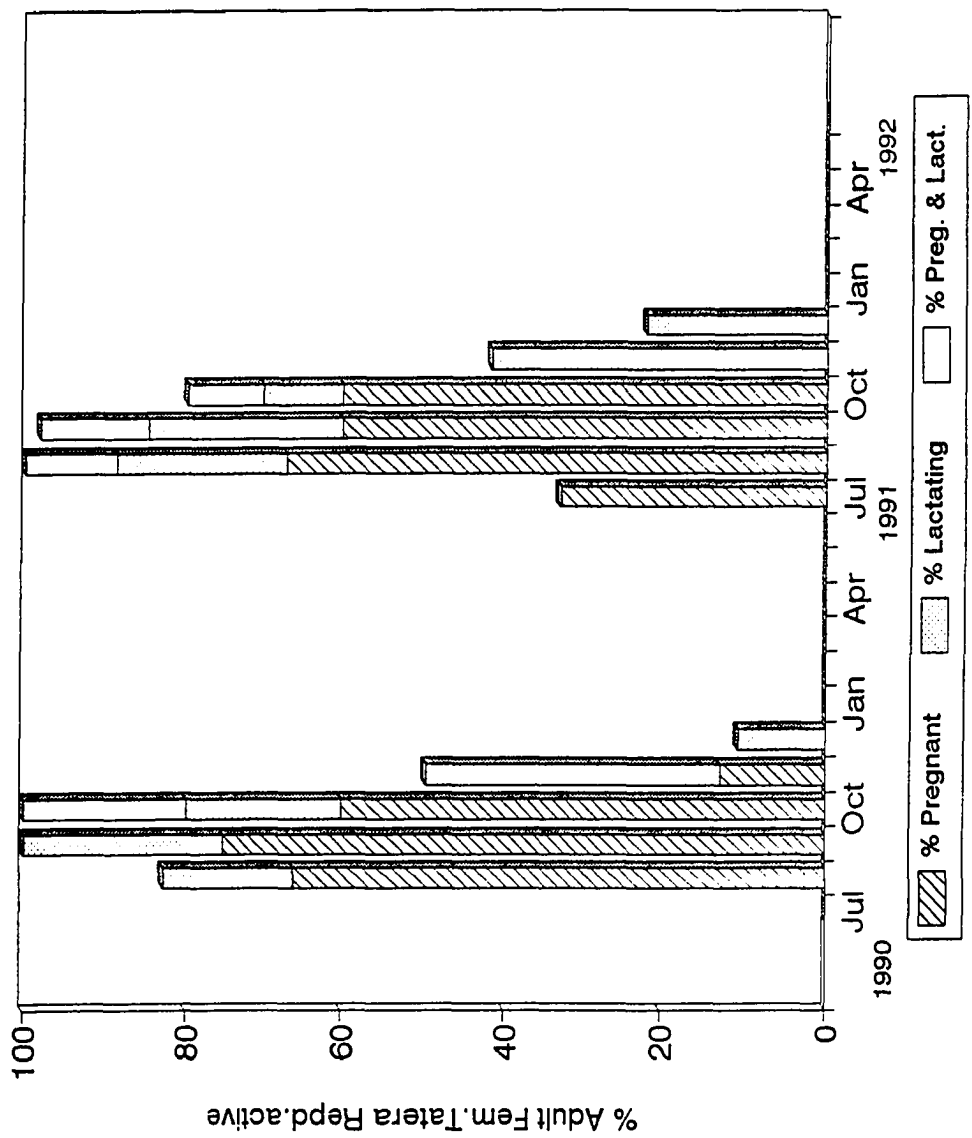
Female *Tatera*:

Female *Tatera* in the non-irrigated site started breeding (Figure 2.6) well after both *Arvicanthis* and *Mastomys*, but lactation extended into the early part of the dry seasons in December, beyond those of *Arvicanthis* and *Mastomys*, and two months after the rains had stopped. Results showed significant seasonal effects on mean litter size ($P < 0.001$). The mean value of 3.45 embryos during the rainy season of 1990 was significantly higher (t -test, $P < 0.001$) than 0.12 embryos per female recorded during the dry season of November, 1990 - April, 1991. Values for the next year (3.32 and 0.11 embryos) likewise were significantly (t -test, $P < 0.001$) different. Breeding had not started in the early part of 1992 rainy season when sampling was terminated.

Discussion

Although strictly wet season breeders in natural fields, differences in the onset and end of breeding seasons were noted among the three species. Breeding in *Arvicanthis* most closely bracketed the rainy season, whereas *Tatera* started later and its lactation continued one or two months into the dry season. *Mastomys* lies between these two species in the timing of its breeding season. Thus, despite sharing their peaks of breeding season during the rainy months, the breeding seasons of the three species overlap somewhat. Stated another way, the species seemed to respond differently to the onset of rains, or to the factors derived therefrom.

Figure 2.6. Percent adult-sized female *Tatera* in reproductive condition in natural fields near Kano, northern Nigeria. Wet and dry refer to seasons, which roughly correspond to May - October and November - April, respectively.



When crop fields and their margins are irrigated in the dry season, green vegetation is present that is not available to small mammals elsewhere. The three rodents responded differently to irrigation. *Tatera* disappeared; not even one animal was trapped from irrigated fields over the course of this study. This was a surprising response. The other two species responded to irrigation by extending their breeding throughout the year, about doubling the number of months of breeding for each. Male *Mastomys* and *Arvicanthis* responded more favorably in that breeding was enhanced by irrigation even in the rainy seasons (Table 2.4). Females of the two species showed no significantly different responses (no enhancement) between the two sites during the rainy seasons. Although breeding in *Arvicanthis* and *Mastomys* continued throughout the year in the irrigated fields, there were no significant seasonal differences in litter sizes in either of the two species. Our study does not, therefore, support Delany's (1986) suggestion that where *Arvicanthis* breeds aseasonally its litter size is smallest.

The seasonal pattern of breeding in *Arvicanthis* in the natural grassfields was consistent with a previous study from a nearby area in northern Nigeria (Rabiu and Fisher, 1989). In Kenya, *Arvicanthis* starts breeding either a month after the rains (Delany and Monro, 1986) or two to three months after the rains (Taylor and Green, 1976) rather than before or at the onset of the rains as in northern Nigeria. A similarity shared between the present study and that of the Kenyan region, however, is that of greater breeding intensity during the peak rains (Delany and Monro 1986, Delany and Roberts, 1978). *Arvicanthis* breeds throughout the year in Gezira, the Sudan (Ghobrial and Hodieb, 1982; Happold, 1966) and in Uganda (Delany and Neal, 1969) but at higher rates during the rainy months. The Gezira region is a famous irrigation project, and the Ugandan study area has a short dry season; hence, breeding in both areas is continuous, as in the irrigated fields of northern Nigeria. Thus, moisture appears to be a key factor whether in seasonal or aseasonal breeding in *Arvicanthis*.

In northern Nigeria, *Mastomys* has the same breeding strategy as *Arvicanthis* (breeding continuously in the irrigated fields but only during the rains in the natural grassfields). Elsewhere in tropical Africa both seasonal and continuous breeding in *Mastomys* have been reported. For example, seasonal breeding is known in Tanzania (Leirs *et al.*, 1989 Telford, 1989), in the Kafue River Flats of Zambia (Sheppe, 1972), and in Senegal (Hubert, 1982; Moro and Hubert, 1983). In contrast, studies from parts of southern Africa, e.g., Coetzee (1965) and Smithers (1971) report *Mastomys* to be breeding throughout the year. In Uganda, the species exhibits two breeding seasons, which according to Neal (1977) may conform to the bimodal pattern of rainfall in the area. Delany (1974, 1986) also indicates the existence of flexibility in the reproductive season of *Mastomys*. In one of the most interesting studies, Swanepoel (1980) reports that breeding in *Mastomys* is confined to the summer months in the natural grassland areas but occurs in winter in the adjacent wheat fields, a very similar observation to that of the present study.

According to Happold (1987), the Savannah Gerbil (*Tatera*) in Nigeria shows greater preference for drier Savannah than for the derived humid Savannahs. Still, it came as a surprise in our study that *Tatera* was entirely absent from irrigated areas, probably because they were subjected to occasional flooding. The green vegetation and the moist soil throughout most of the year did not seem adaptive to it. A related species, *T. robusta*, in eastern Africa, similarly avoids areas that are subject to flooding (Delany, 1986, and references therein). The restricted seasonal breeding pattern in *Tatera* has also been observed in Uganda (Delany and Neal, 1969; Neal, 1982). The litter size (3.25 embryos per mature female) recorded in the present study is smaller but in the same range as the 4.25 reported in Neal (1982).

From the foregoing account, we conclude that breeding in the three species in the natural Savannah fields of northern Nigeria was seasonal, but was continuous for *Arvicanthis* and *Mastomys* in the irrigated fields, from which *Tatera* was completely absent. While this study and others reviewed herein provide additional support to the hypothesis that the application of water, and consequently improved food supply, does help to extend the breeding season of African rodents, the general conclusion drawn here is of a variable response to irrigation by these species.

CHAPTER THREE

DIET SELECTION

Introduction

In the grassland and agricultural fields of Savannah northern Nigeria three species of small mammals, namely *Arvicanthis niloticus*, *Mastomys natalensis* and *Tatera valida*, are commonly found together, often with one or more other species of rodents, where they may feed on local crops and cause some damage (Happold, 1987). The three species are among the most widespread in West Africa (Rosevear, 1969) and in the savannah north of Nigeria, though *Arvicanthis* may be localized in distribution to crop fields and moist areas. In general, the distribution of the species within Nigeria decreases from the savannahs of the north to the forests of the south. In the south, they are restricted to areas close to human habitation in the "derived savannah" (Happold, 1987). Despite this commonness, little information on their food habits and feeding ecology from these areas is known. Ecological notes in Rosevear (1969) and Happold (1987) are mostly generalized; the latter refers to some unpublished data on the food selection of *Tatera valida* in Nigeria from areas north of latitude 10° N. Recently, Rabiou and Fisher (1989) documented the diet of *Arvicanthis* from northern Nigeria. With these exceptions most dietary studies in the same or related taxa have been in other parts of Africa, e.g. Swanepoel (1980) in Southern Africa; Hubbert, Guillion and Adam (1981) in Senegal, and Field (1975) and Taylor & Green (1976) in Eastern Africa.

Most recent studies and two older ones on techniques of dietary analysis, notably Hansson (1971), Neal (1984), Rabiou and Fisher (1989), Williams (1959), Perrin (1980) and Bar, Abramsky & Gutterman (1984), have used some form of microscopic method of food particle examination. Still other studies, such as Swanepoel (1980), have

relied on visual assessment of the composition of gut content. Generally, food items consumed by the species vary with seasonal and local availability, and include insects and other animal material, grain and weed seeds, and monocot and dicot vegetative plant materials. This is true for all three species in the present study, as demonstrated by several workers, including Swanepoel (1980), Taylor and Green (1976), Neal (1984) and Rabiou and Fisher (1989). However, a large potential of diet overlap exists among rodent species (Neal, 1984). Indeed, as noted earlier, part of the economic importance of some species, particularly *Arvicanthis* and *Mastomys*, relates to their depredation of and damage to food crops (Taylor, 1968; Taylor and Green, 1976; Poulet and Poupon, 1978).

The rationale for the present study lies in the importance of food in assessing the role of these animals in natural and cultivated ecosystems and its importance on such ecological factors as breeding and population dynamics (Chapters one and two). In fact, much of the research involving seasonal changes of small mammal diet in Africa has been on the influence and regulatory role of diet in reproduction (Gautun, 1975; Delany and Monro, 1986; Delany, 1986; Swanepoel, 1980; Gobriel and Hodieb, 1982; Leirs, Verheyen, Michiels, Verhagen and Stuyck, 1989; Neal, 1977, 1982, 1984; and Sheppe, 1972). The objectives in the present study were to make a quantitative analysis of food items consumed by three species of rodents, namely the Nile rat, *A. niloticus*, the Multimammate rat, *M. natalensis* and Savannah gerbil, *T. valida* with a view to establishing their pest status in the natural grasslands and irrigated fields of northern Nigeria. Our two-year study was designed to cover two rainy and two dry periods, thus making it possible to compare seasonal changes in species and dietary selection. This paper also documents the habitat conditions and potential food available during different seasons in both the natural and irrigated sites.

Materials and Methods

Analysis of Stomach Contents.

Animals of the three species were collected live using baited modified Fitch traps (Rose, 1973) placed near burrow entrances and across runways in both irrigated and non-irrigated sites. Traps were left in the field for two to three days or until the desired sample size for the month was obtained. Animals were necropsized and stomach contents were prepared for quantitative volume estimates according to the methods described by Gebczynska and Myrcha (1966) and Hansson (1970, 1971). Bait material (mixed seeds), usually confined to the cardiac end, was easily removed. The contents were washed in warm water, dried and weighed. After the material was thoroughly homogenized, it was diluted with water (0.04ml water/mg sample). A small portion of the homogenate for each animal was then added to a slide, spread evenly and covered with a 10x24 mm cover slip.

From these slides the percent of one ocular area (at 100x magnification) covered by individual food items was estimated using a 10x10 squares ocular grid. Fifteen fields were examined for each slide. Food items were identified and recorded as dicot vegetative materials; monocot vegetative materials; seeds, cereals and starch; and insects and animal Materials. For smoother reading these food groups are hereafter simply referred to as dicots, monocots, seeds and insects, respectively. A fifth category of unidentifiable material (usually no more than 5% by mass of the total food fragments) was noted and it included all those items that could not be identified with certainty. No further consideration was given to this category of stomach fragments. Considering the surface area occupied by all food items to be 100%, the percent of each food type in a stomach was estimated by assuming that its proportion in the visual field of the microscope corresponds

to its weight proportion (Gebczynska and Myrcha, 1966; Hansson, 1970). For experimental tests and discussions on the validity of this assumption, see Hansson (1970).

Identification of food particles was achieved by comparison with "Reference Slides" made earlier of potential food items from the study sites, using methods described in Williams (1959) and Hansson (1970). Vegetative plant materials were softened by warm water or lactic acid, and the epidermal layers stripped or scrapped off, and other parts of the plant were sliced or minced. These were then washed and stained with 1% haemotaxylol solution. Weed and crop seeds as well as insect parts were minced to the same texture as those of the stomach contents. Finally, the materials were mounted on microscopic slides and ultimately used for comparison with, and identification of, the fragments taken from rodent stomachs. Because examination of at least 10 ocular areas on each sample (Gebczynska and Myrcha, 1966; Hansson, 1970) is required, we based our estimates on 15 ocular areas in the present study.

For a determination of the mean percent food composition of the series of stomachs (e.g., for each species in a given season) the diet estimation formula described in Delany and Monro (1986) was used:

$$*a = (I_a) / T \cdot 100$$

where $*a$ = mean contribution of food 'a' to the diet in a particular month, I = percent of the contribution of food 'a' to the identifiable fraction of that sample, Σ = sum of all the contributions of 'a' in the samples, and $T = \Sigma (I_a)$ for all food types in that series. Data thus obtained were pooled on monthly bases and transformed using arcsin square root prior to statistical evaluations. The mean percent consumption of food groups of each species was examined by Chi-square tests to detect any food selection differences between the sexes. A three-factor Multivariate Analysis of Variance (MANOVA)

was used to test the effect of species, seasons, sites and their interactions on mean food groups consumed in both irrigated and natural grass fields. Following the MANOVA, a Canonical Discriminant Analysis was used to identify those food groups that contributed significantly to the differences among species, sites, seasons and their interactions.

Habitat Evaluation.

A modified Point Quadrant Method (Goodall, 1957) was used to evaluate plant cover in the habitats and to determine the potential vegetative food available each season to the rodents. The Point Quadrant is a non-dimensional quadrant represented by a small point. The sampling equipment consisted of ten pins arranged 10 cm apart on a 1-m long aluminium frame that keeps the pins in a straight position and perpendicular to the ground surface. There are some recent modifications to this basic version discussed in Baker and Thomas (1983), and Taha, Fisher and Ries (1983). The method is one of high utility and has been widely used in the analysis of pasture and grassland vegetation to measure the effect of grazing and for other similar purposes. The sampler was moved randomly in the study sites until 100 samples (per ha plot) were taken. The procedure was carried out quarterly (February, May, August and November) in both the irrigated and non-irrigated sites. These periods corresponded to the mid dry season, early rainy season, mid rainy season, and early dry season periods, respectively. Plant cover was equal to the fraction of the total pins, expressed in percentage, that touched any part of the plant as the frame was lowered to the ground:

$$C = f/T \cdot 100$$

where C=percent cover of plant species x; f=number of pins that made contact with plant x in all samples taken in a given sampling period; and T=total number of pins in all samples taken during a given period. Mean percent annual cover for each plant was subsequently computed from values of four sampling periods.

The effect of seasonal changes on plant species composition was tested by a one-way ANOVA, and the differences in values compared using Ryan-Einot-Gabriel-Welsch Multiple Range Test (REGWQ). Qualitative changes in the vegetative matter, such as desiccation of the grasses and the availability of seeds either on the plants or on the ground, were examined only visually. Since data on the nutritive values (such as dry matter content, caloric value and crude protein content) of fodder resources in northern Nigeria abound in the literature (e.g. Luning, 1963; Miller and Rains, 1963; Miller, Rains and Thorpe, 1964; Raay and Leeuw, 1974), no attempt was made to estimate these variables in the present study.

Results.

More than 90% of the contents of each stomach was identified. Differences in dietary selection of food groups (dicots, monocots, seeds, and insects) were not significant between the sexes in rodent species in both irrigated and natural grass fields. The closest to a marginally significant result was that of *Arvicanthis* in the intake of monocots during the 1990 rainy season in the irrigated site (Chi-Square = 88.02; $P = 0.072$). Thus, dietary data of males and females were pooled for subsequent analyses.

Seasonal dietary selection of *Arvicanthis* in both irrigated and non-irrigated fields is shown in Table 3.1. In the non-irrigated fields during the rainy season of July 1990 to October 1990, monocots (46.50%) and seeds (26.50%) predominated in the diet. Insects (20.50%) were also important part of the diet. In the following dry season, dicots (45.33%) assumed greater importance than Monocots (28.83%) and seeds (18.16%), even though they remained important also. A similar trend of alternation between monocots (in the wet season) and dicots (in the dry season) as the most important food group in the natural fields was observed during the remaining seasons (Table 3.1). The differences in the proportions of insects in the diet between the wet seasons (19.00% to

Table 3.1. Seasonal Mean Percent Diet Selection assayed microscopically in both sexes of *Arvicanthis* in natural, grassfield refuge (Non-irrigated) at Bagauda-Gwarmai area and in irrigated crop and grass-orchard fields at Kadawa, near Kano, Nigeria. Figures in parentheses are for Mean Percent Standard Error. Values do not add up to 100% because a small percentage of the stomach contents could not be identified.

Seasons	Number of Stomachs Examined		% Dicot. Vegetative Material		% Monocot. Vegetative Material		% Seeds, Cereals & Starch		% Insects & Animal Material	
	Natural Irrig.		Natural Irrig.		Natural Irrig.		Natural Irrig.		Natural Irrig.	
Wet Jul.'90 - Oct.'90	73	90	2.50 (0.28)	6.50 (0.86)	46.50 (1.93)	25.10 (4.20)	26.50 (1.55)	47.12 (7.35)	20.50 (1.04)	19.10 (4.52)
Dry Nov.'90 - Apr.'91	141	141	45.33 (9.50)	10.66 (2.02)	28.83 (4.90)	35.66 (4.96)	18.16 (4.33)	40.33 (3.17)	4.50 (1.68)	9.66 (0.55)
Wet May.'91 - Oct.'91	129	121	3.10 (1.50)	8.33 (2.01)	45.50 (0.71)	25.50 (2.80)	27.16 (1.97)	44.83 (4.48)	20.66 (1.28)	17.33 (1.85)
Dry Nov.91 - Apr.'92	112	133	27.66 (9.80)	10.66 (1.81)	29.16 (5.76)	32.66 (5.28)	32.33 (3.37)	42.33 (4.43)	5.835 (1.07)	10.16 (1.01)
Wet May.92 - Jun.'92	39	43	18.50 (2.31)	10.50 (1.81)	45.00 (8.00)	31.10 (4.50)	13.50 (0.50)	37.50 (4.50)	19.00 (1.00)	16.50 (2.50)

20.66%) and dry seasons (4.50% to 5.83%) for the natural fields were very large. In the irrigated fields, however, the seeds rather than monocot or dicot vegetative materials was the most important diet group throughout the study period. Values ranged from 37.50% (in the wet season of 1992) to 47.12% (in the wet season of 1990). Thus, seasonal differences in seeds consumption within the irrigated site were not as profound as in the natural fields. Monocots, the second most important diet for *Arvicanthis* in the irrigated fields, ranged from 25% to 35% of the total food intake with the greater amounts consumed during the dry seasons. Consumption of dicot vegetation in the irrigated fields was generally lower than 10% during most seasons. Insects generally constituted no more than 20% of the diet even during the rains but the amounts were as twice as that of the natural fields during the dry seasons. (Table 3.1).

Mastomys had different patterns of food consumption from that of *Arvicanthis* in both natural and irrigated fields (Table 3.2). For example, consumption of seeds was always higher, accounting for nearly 50% of the total food intake by mass, in the natural, non-irrigated site regardless of the season. Although there were seasonal fluctuations in consumption of insects, from 9.33% in the dry season of November, 1991 - April, 1992 to 26.50% in the wet season of 1990, these amounts were higher than those of *Arvicanthis*. Consumption of dicot vegetative matter in the natural fields was sharply different between the dry and wet seasons (as was the case with *Arvicanthis*). For example, dicots constituted only 7.50% of the diet during the rains of 1990, and the value in the following dry season was 28.66% (Table 3.2). In the irrigated fields, seeds remained the most important diet group throughout all seasons, even exceeding 50% of the total foods consumed during the wet seasons of 1991 and 1992 (Table 3.2). There were hardly any seasonal differences in the proportions consumed. Insect foods ranked second in importance (12.50% to 26.75% of the total diet), with the greatest difference between the wet and dry seasons of 1990/1991. Monocot and dicot vegetative materials

Table 3.2. Seasonal Mean Percent Diet Selection assayed microscopically in both sexes of *Mastomys* in natural, grassfield (Non-irrigated) refuge at Bagauda-Gwarmai area and in irrigated crop and grass-orchard fields near Kano, Nigeria. Figures in parentheses are for Mean Percent Standard Error. Values do not to 100 percent because a small percentage of the contents of many stomachs could not be identified.

Seasons	Number of Stomachs Examined		% Dicot. Vegetative Material		% Monocot. Vegetative Material		% Seeds, Cereals & Starch		% Insects & Animal Material	
	Natural	Irrig.	Natural	Irrig.	Natural	Irrig.	Natural	Irrig.	Natural	Irrig.
Wet Jul.'90 - Oct.'90	46	54	7.50 (1.65)	6.50 (1.04)	17.50 (3.12)	15.50 (2.62)	44.50 (5.42)	46.25 (6.14)	26.50 (4.94)	26.75 (5.12)
Dry Nov.'90 - Apr.'91	105	89	28.50 (6.25)	10.66 (1.49)	11.50 (1.54)	16.83 (1.90)	45.50 (6.05)	51.66 (2.74)	9.66 (1.33)	14.00 (1.75)
Wet May.'91 - Oct.'91	89	102	8.33 (1.11)	9.20 (1.09)	19.83 (1.24)	17.83 (1.57)	48.16 (3.75)	47.16 (3.78)	19.33 (3.64)	19.50 (3.30)
Dry Nov.'91 - Apr.'92	88	91	28.66 (4.21)	8.66 (1.47)	12.11 (1.31)	19.16 (2.52)	47.50 (4.97)	49.23 (2.12)	9.33 (0.66)	15.66 (1.96)
Wet May.'92 - Jun.'92	28	31	14.00 (2.00)	11.50 (4.50)	18.50 (7.50)	16.50 (2.50)	49.50 (9.41)	55.00 (7.00)	16.07 (8.00)	12.50 (5.50)

came third and fourth, respectively with little seasonal differences. Unlike *Arvicanthis*, no class of food was seriously and consistently enhanced by irrigation in *Mastomys* (Table 3.2)

Food selection in *Tatera* in the natural, non-irrigated fields was very similar to that of *Mastomys* in the same area, i.e. means of 47% to 50% of the diet being seeds (Table 3.3). As with *Arvicanthis* and *Mastomys*, more insects were consumed during the rains (18% to 25% of the diet) than in the dry seasons (11% to 15% of the diet). Slightly more vegetative materials were consumed during the dry seasons than in wet seasons.

The monthly (and seasonal) changes in the diets of the three species over the entire study period are illustrated in Figures 3.1, 3.2 and 3.3. It is apparent that both monocots and dicots are far more important in the diet of *Arvicanthis* in the natural, non-irrigated fields (Figure 3.1a) than in the irrigated fields (Figure 3.1b). In general, the seasonal changes in intake of all kinds of food groups were less pronounced in the irrigated fields than they were in the natural grass fields. The same seasonal effects apply to *Mastomys*, except for the fact that its diet was less enhanced by irrigation (Figure 3.2). *Tatera* was the greater consumer of seeds and insects, and showed the least seasonal fluctuations in terms of mean percent mass of these foods consumed (Figure 3.3).

Results of MANOVA (Table 3.4) indicated that the food groups eaten were significantly affected by the nature of site, i.e., whether irrigated or not (Wilks' Lambda=0.66; $F=11.70$; $P<0.001$), whether it was rainy or dry season (Wilks' Lambda=0.41; $F=5.82$; $P<0.001$), and by the rodent species concerned (Wilks' Lambda=0.26; $F=21.91$ $p<0.001$). There were also significant effects of site and species interaction (Wilks' Lambda=0.78; $F=6.38$; $p<0.001$) and season and rodent species interaction (Wilks' Lambda=0.61; $F=1.47$; $p<0.05$), and site and season interactions (Wilks' Lambda=0.63; $F=2.83$; $P<0.001$) on the type of food eaten.

Table 3.3. Seasonal Mean Percent Diet Selection assayed microscopically in both sexes of *Tatera* in natural, grassfield refuge at Bagauda-Gwarmai area near Kano, Nigeria. Figures in parentheses are for Mean Percent Standard Error. Note that *Tatera* was absent from irrigated crop and grass-orchard fields. Values do not add to 100 percent because a small percentage of the contents of many stomachs could not be identified.

Seasons	Number of Stomachs Examined	% Dicot. Vegetative Material	% Monocot. Vegetative Material	% Seeds, Cereals & Starch	% Insects & Animal Material
Wet (Rain) Jul.'90 - Oct.'90	54	5.25 (0.75)	16.75 (1.25)	52.33 (2.16)	24.50 (2.59)
Dry Nov.'90 - Apr.'91	29	16.50 (1.64)	19.16 (1.10)	47.83 (1.70)	14.90 (0.89)
Wet (Rain) May.'91 - Oct.'91	92	9.83 (3.70)	19.50 (1.11)	49.33 (1.33)	18.33 (1.80)
Dry Nov.'91 - Apr.'92	89	17.50 (2.72)	17.16 (1.16)	47.50 (2.34)	15.16 (0.90)
Wet (Rain) May.'92 - Jun.'92	29	18.50 (3.50)	19.50 (2.50)	47.86 (2.93)	11.65 (2.30)

Fig. 3.1. Diet of *Arvicanthis* determined from microscopic analysis of stomach contents in both natural (A) and irrigated (B) areas near Kano, northern Nigeria. Study period was July 1990 to June 1992.

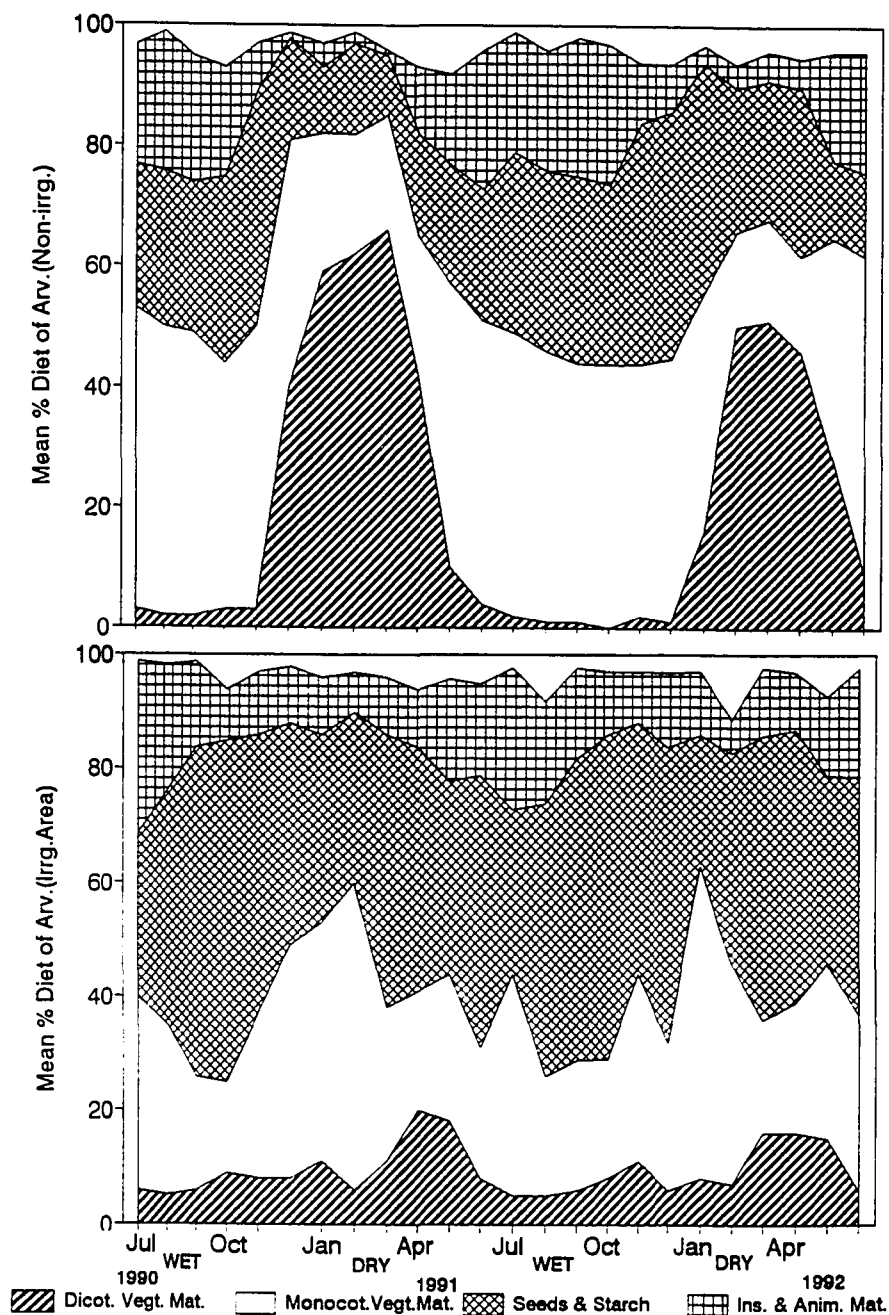


Fig. 3.2. Diet of *Mastomys* determined from microscopic analysis of stomach contents in both natural (A) and irrigated (B) areas near Kano, northern Nigeria. Study period was July 1990 to June 1992.

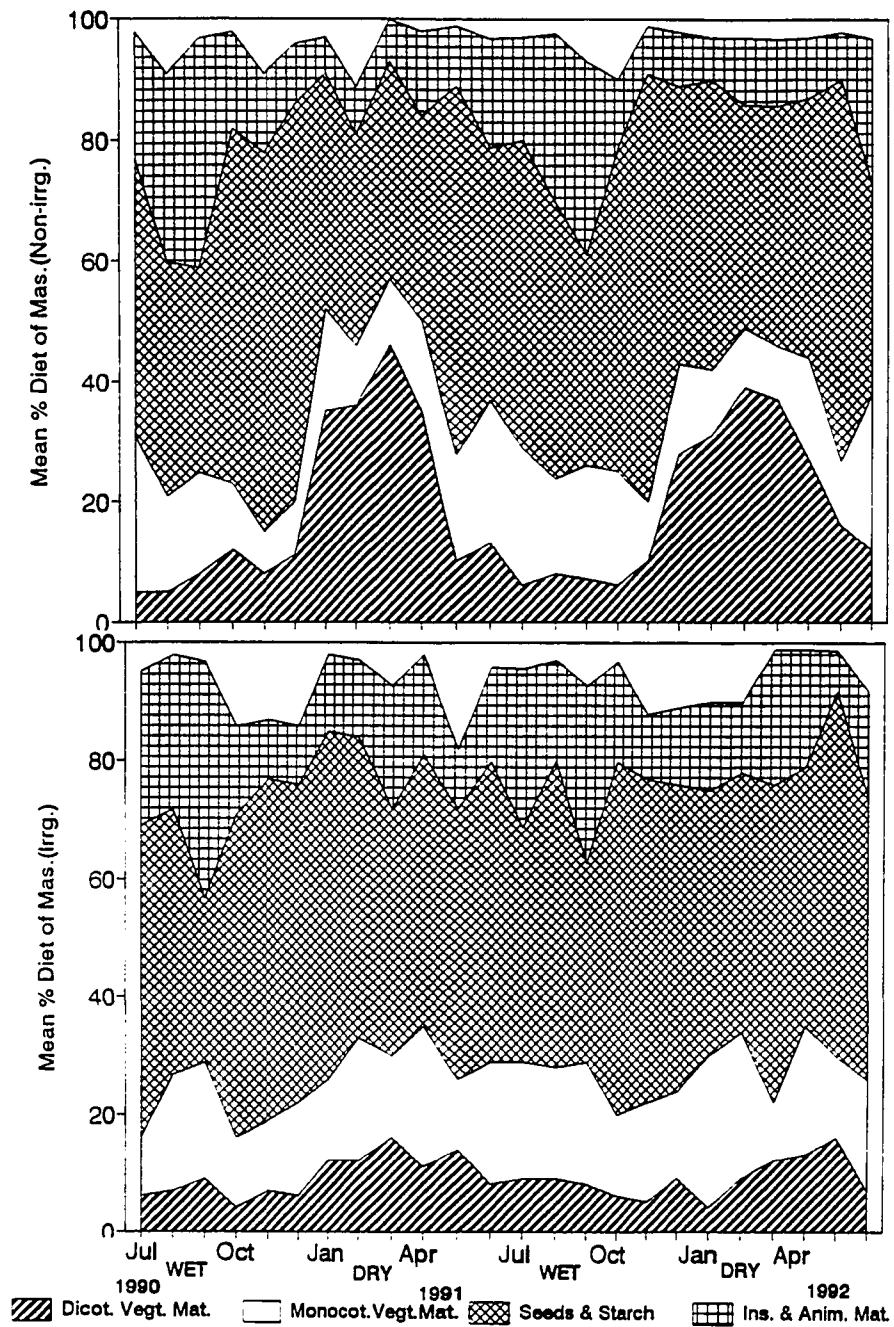


Fig. 3.3. Diet of *Tatera* determined from microscopic analysis of stomach contents in natural areas near Kano, northern Nigeria. Study period was July 1990 to June 1992.

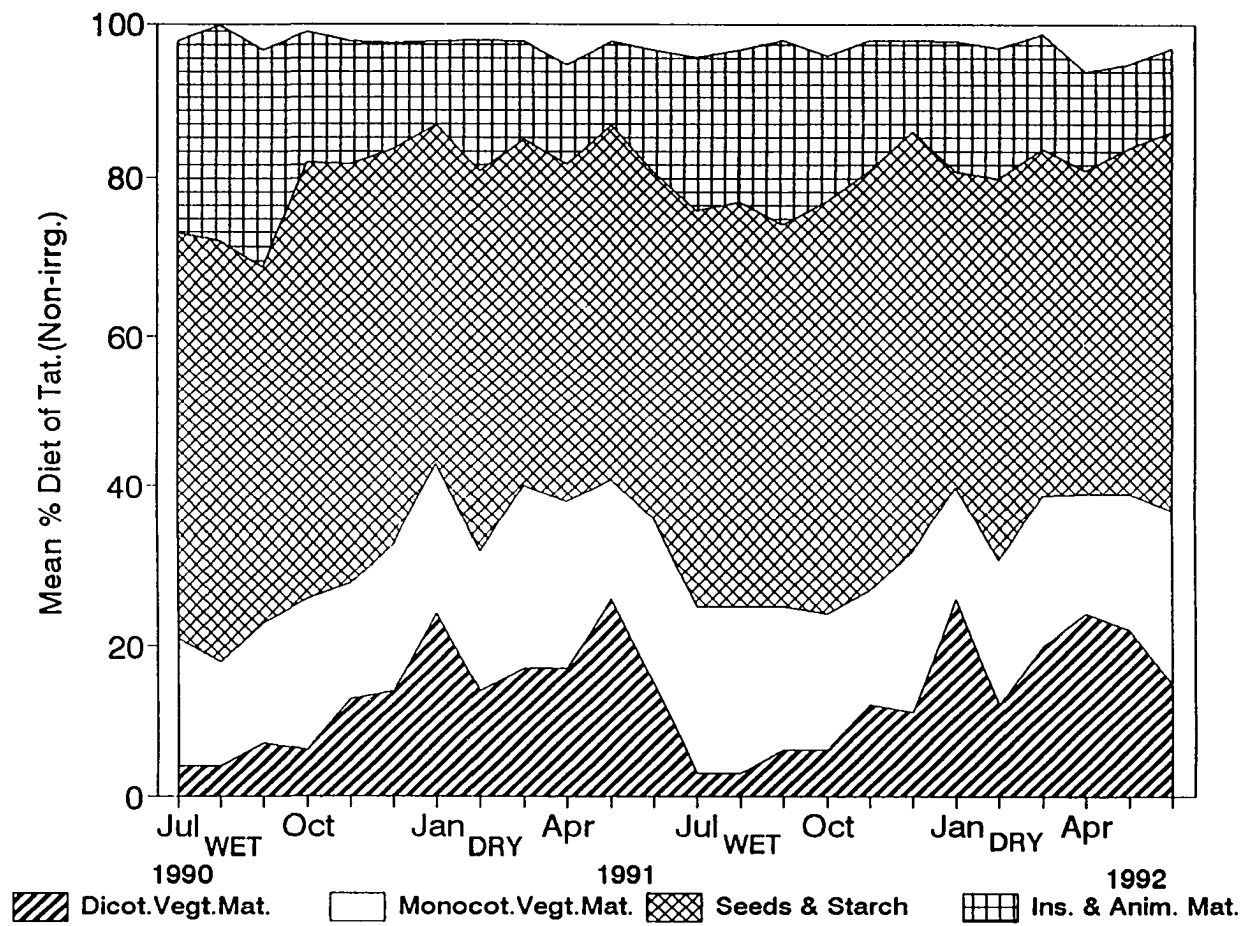


Table 3.4. Results of a three-factor MANOVA testing the effects of sites (Irrigated and Natural grassfields), species (*Arvicanthis*, *Mastomys*, and *Tatera*) and seasons (Wet and Dry) and their interactions on the consumption of four groups of food materials (1.Dicot and 2.Monocot Vegetative Plant Materias, 3.Seeds, Starch and Cereals, and 4.Insects and Animal Materials).

Source	Hypothesis df	Error df	F value	Wilks' Lambda	P
Sites	4	92	11.70	0.6626	< 0.001
Species	8	184	21.91	0.2622	< 0.001
Seasons	16	281.70	5.82	0.4177	< 0.001
Sites*Species	4	92	6.38	0.7825	< 0.001
Species*Seasons	32	340.87	1.47	0.6190	< 0.05
Sites*Seasons	16	281.70	2.83	0.6335	< 0.001
Sites*Species*Seasons	16	281.70	0.79	0.8742	0.694

However, the effect of the interaction of site, rodent species and seasons was not statistically significant (Wilks' Lambda: 0.79; $F=0.8742$; $p=0.69$).

Canonical Discriminant Analysis indicated that the significant differences in types of foods consumed as detected by MANOVA (Table 3.5) corresponded to the relative availability of the foods between sites, seasons, and preference of the animal species (Table 3.5). With respect to site, dicot and monocot vegetative materials had high positive correlations, whereas both seeds and insects had negative correlation with the vegetative materials (see Table 3.5). The proportion of insects consumed made no significant contribution to the effect of site (Coeff=-0.03; Corr=-0.12; $F=0.70$; $P=0.40$). Monocots made the highest contribution to the significant differences caused by the effect of rodent species, and had high positive correlation with other food categories eaten (Coeff=1.5263; Corr=0.76; $F=72.35$; $P<0.001$). The insects diet group was marginally significant in its contribution to species effect on types of foods consumed (Coeff=-0.5767; Corr=-0.15; $F=3.05$; $P=0.05$). Both dicots (Coeff=0.9803; Corr=0.5275; $F=8.93$; $P<0.001$), and insects (Coeff=-1.1101; Corr=-0.8516; $F=22.68$; $P<0.001$) contributed highly, though in an opposite way, to the significant seasonal effect detected by MANOVA. Thus, when dicots were consumed in large quantities in the natural grass fields during the dry season, insects were in short supply, and conversely in the rainy season when monocots and insects became available, less of dicots were eaten.

The effects of site and species interaction on type of food consumed indicated no significant contribution from dicots and insects (Table 3.5). Seeds, with negative coefficient and correlation values (Coeff=-2.5052; Corr=-0.7695; $F=15.63$; $P<0.001$), made the most contribution to the significant effect of site and species interaction. On the effect of the interaction of species and seasons, the contributions of dicots

Table 3.5. Standardized Discriminant Canonical Coefficients (Coeff.), Within Canonical Correlations (Corr.), F-values (F), and Significant Levels (P) for Mean Percent rodent species diet groups detected by MANOVA. There were no significant Sites*Species*Seasons interaction and its results have been omitted from this tabulation.

Sites				
Food Type	Coeff.	Corr.	F value	p
Dicot Vegetative Material	1.7103	0.3445	17.47	< 0.001
Monocot Vegetative Material	1.7285	0.6001	5.74	< 0.05
Starch, Seeds & Cereals	0.2017	-0.7570	27.71	< 0.001
Insects & Animal Material	-0.0300	-0.1207	0.70	0.403
Species				
Dicot Vegetative Material	0.4893	0.0801	1.79	< 0.05
Monocot Vegetative Material	1.5263	0.7668	72.35	< 0.01
Starch, Seeds & Cereals	-0.4453	-0.5824	42.47	< 0.001
Insects & Animal Material	-0.5767	-0.1579	3.05	0.05
Seasons				
Dicot Vegetative Material	0.9803	0.5275	8.93	< 0.001
Monocot Vegetative Material	0.8123	0.0432	0.50	0.73
Starch, Seeds & Cereals	0.1320	-0.0655	0.35	0.84
Insects & Animal Material	-1.1101	-0.8516	22.68	< 0.001
Sites*Species Interaction				
Dicot Vegetative Material	-1.6250	0.0864	0.20	0.65
Monocot Vegetative Material	-0.5570	0.6231	10.25	< 0.01
Starch, Seeds & Cereals	-2.5052	-0.7695	15.63	< 0.001
Insects & Animal Material	-1.1995	0.0907	0.22	0.64
Species*Seasons Interaction				
Dicot Vegetative Material	1.5035	0.7370	2.64	< 0.05
Monocot Vegetative Material	0.4926	-0.4892	1.44	0.17
Starch, Seeds & Cereals	0.6986	0.0567	1.36	0.22
Insects & Animal Material	-0.6024	-0.7783	2.67	< 0.05
Sites*Seasons Interaction				
Dicot Vegetative Material	-1.4549	-0.8754	9.48	< 0.001
Monocot Vegetative Material	0.1859	0.8041	7.90	< 0.001
Starch, Seeds & Cereals	-0.6378	0.0271	0.84	0.54
Insects & Animal Material	0.0261	0.4283	2.46	0.05

(Coeff=1.5035; Corr=0.7370; $F=2.64$ $P<0.05$) and insects (Coeff=0.6024; Corr=0.7783; $F=2.67$; $P<0.05$) were the most important, just as were the contributions of dicots and monocots under the effect of sites and seasons interactions. As already seen from MANOVA tests, the interactive effect of site, species and seasons on food selection was not significant, thus making redundant the need for any further Discriminant Analysis test.

Habitat Assessment

In all, 86 plant species were recorded in both irrigated and non-irrigated sites. In the irrigated fields, results showed that nearly 80% of the total mean annual vegetation cover was dominated by 15 plant species, nearly half (40%) of which were members of the Family Gramineae in terms of both number and mean percent cover (Table 3.6a). The other species, including annual and perennial dicot plants, constituted the second half of the vegetative cover. About 60 other less important species, not listed here, made up the remaining 20% vegetative cover. Compared to the irrigated fields, grasses in the non-irrigated fields were even more important in their mean annual proportion (64.18%) of the total vegetation cover (Table 3.6b). Results of ANOVA showed no significant site or seasonal effects on the amount of vegetation cover, but the species effect was significant (ANOVA: $F=3.87$, $P<0.001$); hence we saw few (mostly grass) species

Discussion

In the natural grass fields monocot vegetative materials were consistently the dominant diet of *Arvicantis* during the rains. Seeds and insects followed in the that order, with each group constituting more than 20% of the total diet by mass. With the exception of the wet season of 1992, very small amounts of dicots were consumed during the rains. The seasonal importance of the two vegetative diet groups was somewhat reversed

Table 3.6a. Selected plant species constituting the highest annual Mean Percent Vegetative Cover in the irrigated fields at Kadawa, near Kano, northern Nigeria. The single asterisks (*) refer to those seasons in which species' Mean Percent vegetative cover were significantly higher (Bonferroni (Dunn) test, $P < 0.05$) than in other seasons. A D.=Annual Dicot; P S.=Perennial Shrub; P M.=Perennial Monocot; P T.=Perennial Trailer; A/P M.= Annual/Perennial Monocot; A/P D.= Annual/Perennial Dicot.

Plant Species	Form & Habit	Annual % Vegetative Cover	S e a s o n s			
			Mid-Dry	Early Rain	Mid-Rain	Early Dry
<u>Papilionaceae</u>						
<u>Alysicarpus vaginalis</u> **	A D	2.10	*	*		
<u>Graminae</u>						
<u>Cynodon dactylon</u> **	A M	7.43		*	*	*
<u>Eragrostis ciliaris</u> **	A M	3.37	*			
<u>Eragrostis spp</u>	A M	2.82				*
<u>Eragrostis tremula</u>	A M	4.75	*			
<u>Hyparrhenia rufa</u> **	A/P M	8.98	*	*		*
<u>Hyparrhenia violescens</u>	A M	29.96		*	*	*
<u>Oryza barthii</u>	P M	9.34	*		*	*
<u>Mimisceae</u>						
<u>Dichrostachys nutans</u> **	P S	2.31	*		*	
<u>Malvaceae</u>						
<u>Hibiscus cannabinus</u> **	A D	2.95		*	*	
<u>Convolvulaceae</u>						
<u>Ipomea eriocarpa</u>	P T	14.71		*	*	
<u>Cruciferae</u>						
<u>Lepidium sativum</u>	A D	2.26				*
<u>Asclepiadaceae</u>						
<u>Leptadenia hastata</u>	P T	2.34				*
<u>Periplocaceae</u>						
<u>Raphionacme brownii</u>	A/P D	4.23			*	
<u>Typhaceae</u>						
<u>Typha australis</u>	A/P D	3.50			*	

** Materials identified in certain stomachs.

Table 3.6b. Selected plant species constituting the highest annual Mean Percent Vegetative Cover in the natural grassland fields at Bagauda-Gwarmai area near Kano, northern Nigeria. The single asteriks (*) refer to those seasons in which species' Mean Percent vegetative cover were significantly higher (Bonferroni (Dunn) test, $P < 0.05$) than in other seasons. A D.=Annual Dicot; P S.=Perennial Shrub; P M.=Perennial Monocot; P T.=Perennial Trailer; A/P M.= Annual/Perennial Monocot; A/P D.=Annual/Perennial Dicot.

Plant Species	Form & Habit	Annual % Vegetative Cover	Seasons			
			Mid-Dry	Early Rain	Mid-Rain	Early Dry
Compositaeae						
<u>Ambrosia maritima</u>	A D	4.80	*			*
Gramineae						
<u>Aristida adscensionis</u>	A M	11.87	*			*
<u>Chloris breviseta</u> **	A M	13.65	*			*
<u>Dactyloctenium aegypticum</u>	A M	4.76		*	*	
<u>Penicum subalbidum</u> **	A M	10.13	*	*		
<u>Hyparrhenia rufa</u> **	A/P D	18.29		*	*	
<u>Sorghum arundinacium</u>	**A M	2.95			*	*
<u>Eragrostis spp</u>	A M	2.53		*	*	
Caesalpiniaceae						
<u>Cassia absus</u>	P S	2.41		*	*	
<u>Polio stigma reticulatum</u>	P S	2.04			*	*
Papilionaceae						
<u>Crotolaria obvata</u> **	P S	2.57			*	*
Cyperaceae						
<u>Cyperus rotundus</u> **	A M	2.62			*	*
Malvaceae						
<u>Hibiscus cannabinus</u>	A/p D	2.69		*	*	

** Material identified in some stomachs.

during the dry seasons, i.e., consumption of larger amounts of dicots, and lesser though still substantial amounts of monocots. Amounts of seeds eaten in the dry seasons also declined below that of the wet season levels (although high during the early post-harvest dry season). However, the dry season of 1991 was an exception, for seeds made up the most important diet group (over 30%). Consumption of insects declined sharply during the dry seasons.

In the irrigated fields, seeds were clearly the dominant food materials preferred by *Arvicanthis* year-round, constituting more than 40% of total foods eaten in most seasons. Monocots ranked second in order of dietary importance, with larger amounts being eaten during the rains, contrary to the situation in the non-irrigated fields. Amounts of insects eaten during the rains were about the same as in the non irrigated site, but the decline was not as sharp during the dry seasons.

These seasonal fluctuations in food selection in *Arvicanthis* in the natural fields indicated a readiness to switch diet depending on seasonal availability. On the other hand, consumption of consistently high amounts of seeds throughout the year in the irrigated fields showed an opportunistic tendency, and thus potential as pests in cultivated crops. Another interesting feature of the dietary selection was that of eating even larger amounts of monocots in the dry seasons than in the wet seasons, perhaps making up for what was missing in lesser amounts of insects. Thus, the diet of *Arvicanthis* was enhanced by irrigation in terms of selection of seeds, monocots, and to a lesser extent, insects.

In the natural fields *Mastomys* rated higher than *Arvicanthis* in respect to seed volume intake, with a mean of nearly 50% of its food made of seed materials. More insects were eaten during the rains as was the case with *Arvicanthis*, since they were abundant. Vegetative materials were not as important as in *Arvicanthis*, even though substantial

quantities of dicots were eaten during the dry seasons. The lower significance of vegetative foods in this species may be due to its apparently greater preference and perhaps search effort for seeds than *Arvicanthis*. In the irrigated fields *Mastomys* consumed slightly more seeds (by about 2% to 3%) throughout the year than it did in the natural grass fields. Thus, the present study showed less enhancement by irrigation in the diet of *Mastomys* than for *Arvicanthis*.

The diet of *Tatera* in the natural site (it was not present in the irrigated site) showed high preference for seeds with little seasonal fluctuation in amounts eaten, similar to that of *Mastomys*. Amounts of insects eaten, though showing decline during the dry seasons, were generally larger than in either *Arvicanthis* or *Mastomys*. Dicots eaten were slightly more selected during the dry seasons, than in the wet seasons. Seasonal differences were less pronounced in the selection of monocots. In general, the importance of vegetative foods to *Tatera* was lower than in *Arvicanthis* and more or less the same with *Mastomys*.

The diets of *Arvicanthis* in northern Nigeria as reported in Rabiou and Fisher (1989), from very similar sites within the same ecoclimatic zone as the natural sites in the present study, showed a similar pattern of seasonal fluctuation in terms of the major food groups consumed. However, the seeds were not as important in their contribution to the overall diet, and the proportions of insects (27.7% and 31.7% during the rains of 1984 and 1985, respectively) were greater than the 20.50% and 20.66% recorded in the present study during the rains of 1990 and 1991, respectively (Table 3.1). This might be attributed to the smaller number of stomachs examined in the former study since there were no apparent differences in the supply of insects, at least from a subjective assessment, between the 1984 and 1985 rainy periods and those of 1990 and 1991.

Thus, in northern Nigeria, seeds predominated in the diet of *Arvicanthis* in the later part of the rains, and dicot vegetative material during the late dry seasons. In that region, a good supply of monocots was limited to the wet season in the natural fields. During this period the only source of fresh monocots was from perennial grasses, such as *Andropogon gayanus*, which was not an important plant species in terms of vegetative cover, but probably was a source of moist food and perhaps of water too. It was not surprising, therefore, that large amounts of dicots were consumed in the dry seasons. Rabiou and Fisher (1989) observe that the importance of seeds and monocots on the diet of *Arvicanthis* was less than that in East Africa. In the light of findings in the present study, that observation still holds as true.

In Kenya, the diet of *Arvicanthis* was mainly of monocots during the late dry seasons (rather than dicots as in natural fields of northern Nigeria), and seeds in the later part of the rains up to the early part of the dry season (Delany and Monro, 1986). Taylor and Green (1976) also note a similar pattern of seasonal changes in diet selection by *Arvicanthis* from the East African region. Thus, dicots, as noted in Rabiou and Fisher (1989), were more important in the diet of *Arvicanthis* in the dry seasons in northern Nigeria than in East Africa.

Mastomys ate larger amounts of seeds throughout the year in both the natural (non-irrigated) and irrigated fields than *Arvicanthis* did. But *Tatera* was the greatest consumer of seeds and insects among the three rodent species in the natural grassfields. These findings are consistent with results from other parts of the continent. From southern Africa, Swanepoel (1980) reports that seeds were important constituents in the diet of *Mastomys*, present in all stomachs examined and forming the major dietary component in 93% of those stomachs. Abramsky (1983) and Bar, Abramsky and Gutterman (1984) note the efficiency of gerbilline rodents in active search and utilization of seeds includ-

ing those buried below the ground. Happold (1987) also refers to the savannah gerbil in Nigeria as granivorous. In the present study, the high proportions of seeds eaten by both *Mastomys* and *Tatera* in the natural fields during the late dry seasons (when they were in relatively short supply) may have come from seed banks in the soil and nearby farm stores and granaries. Another explanation may be that *Mastomys* manages to continue to find seeds by ranging widely over open ground during the dry seasons when the seeds become less common (Taylor and Green, 1976), and in *Tatera* perhaps through both active seed searching and feeding from reserves hoarded when supplies were better.

Given the differences in the dietary selection in the three species, it was not surprising that the results MANOVA showed significant effects of species, sites and seasons as well as their interactions on rodent dietary consumption. Results in the present study revealed that *Arvicanthis* in the natural grass fields was more flexible in its seasonal dietary selection, easily switching to a diet of dicots when seeds and monocots became less abundant. Both *Mastomys* and *Tatera* were able to sustain a relatively higher level of seed intake during the dry season by, as noted above, ranging widely and by active search. There is the additional possibility that *Tatera* may hoard large quantities of seeds in its burrows, and is thus able to sustain large seed intake throughout the year. Our data from the irrigated fields demonstrate the opportunistic tendency of both *Arvicanthis* and *Mastomys* by exploiting the large supply of seeds (and cereals) that were abundant year-round. It is a reasonable conclusion, therefore, that all three species considered here stand indicted as crop pests in both irrigated and natural, rain-fed fields. When comparing the intake of seeds, *Mastomys* and *Tatera* seem to be worse potential pests than *Arvicanthis*. However, the lower population levels of *Tatera* and *Mastomys* (Chapter one) and the inability of *Tatera* to invade the irrigated fields (the irrigation scheme has been established in northern Nigeria for more than two decades now) put them at no higher pest status than *Arvicanthis*.

The significance of diet, especially the role of seed and insect foods and perhaps some vegetative grass material, in rodent reproduction has been extensively discussed in the literature (Delany and Monro, 1986; Gautun, 1975; Rabiou and Fisher, 1989; Swanepoel, 1980). It is, however, outside the scope of this paper to delve in depth on that subject. Suffice it to say that reproduction in *Arvicanthis* and *Mastomys* was continuous in the irrigated fields of northern Nigeria but was discontinuous, or seasonal in the natural, non irrigated fields (Chapter two), a fact which might have some bearing on the food conditions in the two sites. Delany and Monro (1986) report that vegetation was an important source of cover and food to rodents. Indeed, we have observed loss of populations or drastic declines when the grasses in our demographic study grids were slashed for routine management purposes (Chapter two). The present study also provides ample evidence of the role of vegetation in food supply. Vegetative materials and seeds of certain plants (*Eragrostis ciliaris*, *Hypharrhenia rufa*, *Penicum* spp, *Crotalaria obvata* and a species of *Amaranthaceae*) were identified in some stomachs. The importance of vegetation for food supply and protection (cover) to rodents, recognized by Delany (1986), Delany and Monro (1986) and Neal (1984) and several other workers, cannot be overstressed.

The vegetation dynamics in the present study did not show any significant seasonal differences in the amount of annual vegetation cover in either the irrigated or natural grass fields. However, as noted earlier, there were significant seasonal changes in the contributions of individual and group plant species to the total cover. It also appeared that despite the absence of significant seasonal differences in vegetation cover in the two study sites, there were dramatic seasonal changes in vegetation quality, especially in the non-irrigated site. Raay and Leeuw (1974) estimate that the crude protein in upland savannah herbage (i.e., drained, non-irrigated fields) in northern Nigeria drops from a high of 12% - 14% during the early rains to low of 2% - 3% in the dry season. But this

decline varies from one plant species to another. By contrast, the herbage in the Fadama areas (low-level lands that are subject to flooding, here considered the equivalent of the irrigated fields) may always include young shoots containing up to 20% crude protein (Raay and Leeuw, 1974). It is tempting to suggest that these important differences in the nutritive quality of the vegetations between irrigated and non-irrigated fields in terms of protein contents and of estrogen levels, a stimulant to breeding known to be present in green grass (Miller and Rains, 1963), might explain part of the differences in continuous and seasonal breeding patterns of rodents inhabiting those fields (Chapter two).

CHAPTER FOUR

CROP DAMAGE AND YIELD LOSS

Introduction

Rodent depredation and damage to food crops is probably as old as agriculture, although the data on the magnitude of food losses are limited (Jackson, 1977; Bernand, 1977). Where the data exist, documentation and reliability often are in question (Jotwani and Beri, 1971). Rodent damage to food crops in many Third World countries, excepting some states of the Southeast Asia, not only is unmeasured but the rodent species involved are either not mentioned or are incorrectly identified (Barnard, 1977; Personal observation). Until recently, there has also been a shortage of practical and reliable methods of estimating rodent damage in the African agricultural fields (Fieldler, 1988; Jackson, 1977). A reliable quantitative assessment of crop losses is vital for management research programs, for evaluation of control measures and for consideration of alternatives (Rennison and Buckle, 1988).

Most food crop types and tree crops are attacked by rodents (Funmilayo and Akande, 1977; Williams, 1973, 1974; Taylor, 1968), but according to Jackson (1977), the best documented and probably the most important is the damage to rice, with the heaviest losses suffered in the countries of Southeast Asia. Damage and losses ranging from 5 to 100 percent are reported from the Philippines (Lavoie, Swink and Sumangil, 1970) and 10 to 100 percent from Thailand (Shuyler and Ratanaworabhan, 1970). Damage to cereal crops may occur at all stages of the development of the crop, including the tillering stage (the stage when new shoots are sprouting), but usually is more severe during the reproductive (dough and booting stages) and maturation stages. Sometimes the damage is concentrated along field edges and in weedy and unclean plots (Taylor, 1972; personal observation.) or in the center of plots rather than at the edges.

Damage to rice and other crops in Africa, as in the Southeast Asia, also varies widely also (Bernard, 1976). During the 1962 rodent outbreak in parts of East Africa, crop yield losses of more than 50% were incurred in about 5% of the total acreage of wheat and maize, and more than 20% of the total acreage of both wheat and maize had from 0 to 50% damage (Taylor, 1968). In Southwestern Nigeria, pre- and post-harvest damage to rice is estimated at 40% per annum (Funmilayo and Akande, 1977). In that study, as in the present one, *Arvicanthis niloticus*, *Mastomys natalensis* and *Tatera kempi* (*T. valida*) are among the culprits causing damage to crops.

Rodent populations causing damage often occur at low levels, then suddenly flare up (Taylor, 1972). It has been argued that these irruptions, in fact, are man's creation, and are due to the innovation of "super optimal" or highly productive environments such as large-scale agricultural and irrigation projects that provide the conditions for the survival of rodent species that may later ravage crop fields. Changes in the agricultural practice that include massive land clearance, for example, the one in the Philippines in the 1950s, provide new, hitherto unavailable food supply, and probably a new habitat, one without the range of natural enemies for the rats. This view has also been advanced by Bernard (1977). However, Taylor and Green (1976), citing evidence from their own experience, point out that factors other than food may also be involved in rodent outbreaks. In the same line of argument, Happold (1987) predicts high population levels for rodents in the irrigated fields in northern Nigeria. In many cases, populations of rodent pest species are ephemeral (Poulet and Poupon, 1978) and hence are r-strategists (Taylor and Green, 1976; Delany, 1986). Phenomenal outbreaks have been reported for many species at different places, notably involving *Rattus sp.* in the Philippines in the 1950s and in Indonesia in the 1960s (Taylor, 1972), *A. niloticus* in eastern Africa (Taylor, 1968), and *Meriones shawi* in Morocco, Tunisia and Algeria (Bernard, 1977). When outbreaks occur, numbers can reach very high densities. For example, in

the Philippines, *Rattus* numbers climbed from 20 to 200/ha at low densities to a high of perhaps 10,000/ha during outbreaks (Jackson, 1977). Damage levels naturally also rise, sometimes resulting in the "eatouts" where farmers experience total crop loss.

Other rodent outbreaks were observed when heavy rains ended a period of drought. For instance, Taylor (1968) suggests that the 1962 rodent outbreak in Kenya was correlated with abundant weed and crop seeds as well as sufficient vegetation cover caused by the heavy rains in the previous year. Similarly, the outbreak in Senegal in 1975, with high densities of 600 animals / ha in crop fields, followed the unusually heavy rains of 1974 (Poulet and Poupon, 1978). Other rodent outbreaks tend to coincide with food abundance also, such as in Brazil with the maturation of bamboo every 30 years or so, in Ceylon with flowering of *Strobilanthes*, and in New Zealand with periodic seed crops of the indigenous southern beech (Taylor, 1968 and references therein).

In Nigeria and other parts of West Africa, the ecology and involvement in damage to crops by some of the important rodent pests, namely *Arvicanthis*, *Mastomys* and *Tatera*, have not been as well studied as in East Africa (Happold, 1987; Delany, 1986). Although *Tatera* has been reported to cause some damage by feeding on food crops (Funmilayo and Akande, 1977; Happold, 1987), its status as a pest has not been as well documented as that of *Arvicanthis* or *Mastomys*. This may be related to the low breeding rate in *Tatera* (Neal, 1982), and by implication, the low level of natural increases in the populations or, as suggested by Neal (1984), because of effective natural population regulation mechanisms which usually prevents their damage from being severe.

Since the development of large-scale irrigation facilities in the northern parts of Nigeria in the late 1960s and early 1970s, rodent species have become increasingly troublesome. The present research was aimed at: 1. assessing the damage done to rice and wheat crops by *Arvicanthis* and *Mastomys* at different stages of crop development in

irrigated crop fields. 2. estimating the crop losses to these damages and 3. comparing the magnitude of damage done in rice fields with that in wheat fields. Detailed accounts of the population dynamics of these two species and *Tatera* in the non-irrigated fields are reported in Chapter one.

Materials and Methods

Sampling in three contiguous localities (part of the 22,000 ha of the Kano River Project) at Karfi, Kura and Kadawa, was carried out using a random cluster technique (Rennison and Buckle, 1988). See Table 4.1 for samples drawn and approximate man-hours in labor expended. The cluster here refers to a small plot or planting bed (5 rows x 6 hills). Benigno (1979) recommends random selection of clusters of 25 hills as being optimal for sampling precision. In our study area the planting beds were clearly demarcated (akin to tiles on the floor) by small irrigation channels, and this helped to ease the problem with their numbering and random selection. Some plots were large and had more than 30 hills; in such cases only 30 hills were considered for tiller counting. The hills within each plot formed the basic sampling units, which were also defined physically with regular spacing of about 0.30m between one another, both in the case of replant and broadcast cereal crops. This pattern of planting was created by most farmers to facilitate accessibility and manual weeding in the fields. Damage to tillers was occasionally localized at the edges or in the center of fields but not sufficiently consistent to warrant the use of some other sampling technique. Moreover, uncultivated strips of land demarcating holdings of different ownership and fallow (uncultivated) farms, both of which served as rodent refugia, were scattered throughout the fields, thus spreading out what might otherwise be pockets of heavy damage. In all, 100 plots (hill clusters) each of rice and wheat were selected during each season, and within each plot the hills were examined for damage using the cut tiller count procedure developed by the Rodent

Table 4.1. Number of random cluster samples and man-hours labor input in counting rodent-damaged tillers in cereal crops in three contiguous localities in the Kano River Project, northern Nigeria. Note: sampling was done fortnightly in each crop from the fifth week of growth to maturity.

Cereal crop	Growing seasons	Locality	Number of plots sampled (1 plot = 30 hills)	Approximate labor input (Man-hours)
Rice	1990, 1991	Karfi	18	122
		Kura	50	338
		Kadawa	32	206
Wheat	1991, 1992	Karfi	30	358
		Kura	40	476
		Kadawa	30	358

Research Center in the Philippines for use in the Philippines National Rodent Survey of 1970 to 1973 (Sanchez, 1974). Its utility and shortcomings have been discussed in Jackson (1977) and Lavoie, Swink and Sumangil (1970). In brief, the method is one of painstaking labor, requiring careful examination and counts of tillers in each selected plot. The numbers of damaged and undamaged tillers in each sample were counted each fortnight, beginning from the time when the crop was five weeks old until it reached the "dough" stage, 11 for rice and 15 weeks for wheat. The mean percent damage from the total number of hills at the end of each sampling period was calculated. At maturity of the crop, one final sampling was done to determine yield loss from damage done at that period. It was assumed that the percent loss of tillers determined during a sampling period two to three weeks before harvest approximates the magnitude of percent crop yield loss at harvest because there is little or no growth compensation for damage done to tillers after this period (Jackson, 1977; Buckle and Rowe, 1981). Percent Yield Loss in a mature crop was estimated using the Rennison and Buckle (1988) formula:

$$PL = 100 (A - B)/A$$

Where PL = Percent tiller loss, A = number of tillers per hill in undamaged hills, and B = tillers per hill in damaged and undamaged hills. No yield loss estimates were determined from damage done in earlier growth stages prior to crop maturation. Mean percent values of crop tillers damaged were transformed by arcsin square root prior to any statistical testing. Then, a two-way factorial analysis of variance was used to test the effect of differences of year (period) of cultivation, stage of development of the crop (stage), and year x stage interaction on the proportions of tiller damage for both rice and wheat crop. Level of significance in the differences between the mean values were determined using Ryan-Einot-Gabriel-Welsh Multiple Range Test (REGWQ).

Results

The rodent species causing damage in the irrigated fields (Chapters one and two) were *Arvicanthis* and *Mastomys*. (see also Chapters three). Percentages of tiller damage during the premature stages of rice were generally low, less than 10% during any premature growth stage in both 1990 and 1991 growing seasons (Table 4.2). In 1990, the mean percent tiller damage steadily increased from 2.05% up until the rice was booting at nine weeks old, when damage reached 6.11%. The rate dropped two weeks later to 4.25%. The damage levels in 1991 were less than those of 1990 but did not show any decline after the crop was 11 weeks old, as in the previous year. In 1990, the mean percent yield loss was 4.81%, lower than the 12.69% during 1991 growing season (Table 4.2) These damages are generally lower than in wheat (Table 4.3).

Results of a two-way factorial ANOVA revealed that levels of damage to rice tillers (Table 4.4) were affected by the year of cultivation, ($F=4.21$; $df=1$; $P=0.04$); hence damage to rice tillers in 1991 growing season was significantly higher than in 1990 (REGWQ test, $P<0.05$). The effects of developmental stage of the crop ($F=63.98$; $df=4$; $P<0.001$) and of year of cultivation x developmental stage interaction ($F=35.37$; $df=4$; $P<0.001$) on percent of tiller damage were highly significant.

By contrast to damage in rice, the rodents inflicted far more damage over longer periods in the wheat fields since this crop takes more weeks to mature (Table 4.3). In the 1991 growing season, the lowest damage rate of 10.21% was at the early tillering stage. This increased steadily to a high of 41.39% at the late booting stage. The mean percent of tillers damage fell to 38.16% and 31.93% when the wheat was 13 and 15 weeks old, respectively. The mean percentages of wheat tillers damaged at all stages of development during the growing season of 1991 were dramatically higher than the

Table 4.2. For rice, the Mean Percent of tillers damaged by rodents based on survey data of 100 plots (1 plot = 30 hills) at each sampling period (growth stages) in fields near Kano, northern Nigeria. Figures in parentheses are standard error values. Note: Percent damage at the mature stage directly translates into percent yield loss. Low=low damage, Mod.=Moderate damage, High= high damage, using the criteria in Benigno (1979).

Age (Weeks)	Growth Stage	Percent Tiller Damaged		Damage Status	
		1990	1991	1990	1991
5	Tillering	2.05 (0.30)	0.75 (0.11)	Low	Low
7	Tillering	2.90 (0.17)	1.70 (0.14)	Low	Low
9	Booting	6.11 (1.06)	2.40 (0.25)	Mod.	Low
11	Dough	4.25 (0.35)	5.00 (0.42)	Mod.	Mod.
14	Mature	4.81 (0.41)	12.69 (0.92)	Mod.	High

Table 4.3. For wheat, the Mean Percent of tillers damaged by rodents based on survey data of 100 plots (1 plot = 30 hills) during each sampling period (growth stages) in fields near Kano, northern Nigeria. Figures in parentheses are standard error values. Note: Percent damage at the mature stage directly translates into percent yield loss. Low=low damage, Mod.=Moderate damage, High=high damage, Sev.=Severe damage, using the criteria in Benigno (1979).

Age (Weeks)	Growth Stage	Percent Tiller Damaged		Damage Status	
		1991	1992	1991	1992
5	Tillering	10.21 (1.67)	5.07 (1.15)	High	Mod.
7	Tillering	29.18 (2.24)	2.75 (0.53)	Sev.	Low
9	Booting	31.65 (2.37)	7.59 (0.99)	Sev.	Mod.
11	Booting	41.39 (2.26)	13.01 (0.70)	Sev.	High
13	Dough	4.81 (0.41)	12.69 (0.92)	Mod.	High
15	Dough	31.93 (2.33)	18.49 (0.90)	Sev.	High
17	Mature	30.03 (2.73)	21.79 (2.33)	Sev.	High

Table 4.4. Results of two-way factorial ANOVA testing the effect of year of cultivation (Year), rice developmental stage (Stage), and stage x year interaction on mean percent rice tiller damage caused by rodents during the two growing seasons of 1990 - 1991 in fields near Kano, northern Nigeria. Damage to mature crops in 1991 was greater than in 1990.

Source	df	MS	F	P
Year	1	112.896	4.21	0.040
Stage	4	1716.956	63.98	<0.001
Year x stage	4	949.008	35.37	<0.001
Error	990	26.843		

corresponding growth stages in 1992, during which damage to five-weeks old wheat was 5.07%, and increased steadily to 19.50% at the dough stage (Table 4.3). This fell slightly to 18.49% two weeks later. Rodent damage to the mature rice crop (yield loss) was generally moderate. In 1991 percent yield loss in wheat (30.03%) was higher than the 21.79% of 1992.

Comparable results for the wheat crop (Table 4.5) showed the effects of year of cultivation ($F=319.65$; $df=1$; $P<0.001$), of developmental stage ($F=33.35$; $df=6$; $P<0.001$) and of their interaction ($F=11.99$; $df=6$; $P<0.001$); all had highly significant effects on the mean percentages of damaged tillers. Thus, the damage to wheat tillers during the 1991 growing season was significantly higher than that recorded in 1992 (REGWQ test, $P<0.05$). As was the case in the rice crop, the percentages of damaged wheat tillers were significantly different among the various stages of development, the damage being higher at the mature stages (REGWQ test, $P<0.05$). Because rice and wheat were grown at different times, it is not possible to make comparisons of the extent of damage during the same period. Regardless, the magnitude of damage to wheat in both growing seasons was higher than those in rice (compare Tables 4.2 and 4.3).

A one-way ANOVA test using combined data of two growing seasons (composite year) each for rice (1990 and 1991), and for wheat (1991 and 1992) showed significant

Discussion

The highest mean percent tiller damage to rice was 6.11% at the ninth week of 1990. Thus, damage to rice may be considered to be low to moderate. Benigno (1979) ranks damage levels of less than 3% percent as low, 3-5% as moderate, and greater than 23% as severe. Damage at the premature stages of wheat was markedly higher than in rice, probably due to two reasons, namely that rice was grown for the most part during

Table 4.5. Results of two-way factorial ANOVA testing the effect of year of cultivation (Year), wheat developmental stage (Stage), and stage x year interaction on mean percent wheat tiller damage caused by rodents during the two growing seasons of 1991 - 1992 in fields near Kano, northern Nigeria. Damage was greater in 1991 than in 1992.

Source	df	MS	F	P
Year	1	110449.446	319.65	<0.001
Stage	6	11523.303	33.35	<0.001
Year x stage	6	4141.753	11.99	<0.001
Error	1386	345.535		

the rainy months when other food sources for rodents, including insects, were in relatively higher supply, and the rice fields often were somewhat water-logged (if not flooded), which may have helped to slow the invasion of rodent pests. Wheat, on the other hand, was grown by irrigation at a time when other food sources were declining in abundance.

Estimates of yield loss during earlier growth stages are more difficult to evaluate due to plant compensatory responses (Rennison and Buckle, 1988). To tackle this problem, agronomists (e.g., Poche *et al.*, 1981 Akhtar and Fulk, 1981; Haque and Fiedler, 1985), mostly working in the countries of southeast Asia, have conducted a number of simulation experiments of rodent damage to cereal crops and subsequently compared yields in damaged and undamaged crops. It is unclear whether the results of such experiments have wider application beyond southeast Asia, especially given the array of crop varieties and major differences in soil and local conditions amongst the various regions. However, experiments to the varieties of rice and wheat tested demonstrate that damage of less than 30% inflicted right up to the booting stage did not affect crop yield significantly (Poche *et al.*, 1981 ; Haque and Fiedler, 1985). In our study, damage to rice and wheat at all prematuration stages, excepting for wheat in 1991, was below 20%. The damage level to wheat in 1991 was especially high, up to 41.39% at the booting stage and remained above 30% at the dough stage. This may have caused some yield loss but we did not install the rodent-proof exclosures that would be needed to measure that loss.

It has already been noted that the percent tiller damage in mature crops translates directly into percent crop loss since there is little or no compensation for damage at the stage of maturation. Yield loss in rice in 1991 (12.69%) was nearly three times that in 1990 (4.81%). The rice variety was the same and so were the farming practices during

both years, and rather surprisingly there was more rain in 1991 than in 1990, which might have created flooded conditions unsuitable to rodents, and thereby reducing their damage levels. Yet, despite these conditions, the damage in 1991 was still higher than that of the previous year. Yield loss in mature wheat in 1991 (30.03%) was higher than in 1992 (21.79%) but the difference was not as dramatic as the annual differences in rice. It is clear that 1991 was a serious pest year for farmers of both rice and wheat. Using Benigno's (1979) scale for damage and yield loss, we may conclude that the yield losses were moderately high for rice and severe for wheat. Rodent population densities (Chapter one) during 1991 were not higher than either in 1990 or 1992. However, there was grass-slashing activities in the grass-orchard habitats during March - April 1991. It is possible that rodents evicted from these refugia had moved into crop fields and caused more damages than would normally be the case.

Percent yield loss expressed in terms of crop acreage and estimated cash value lost to rodent damage were substantial. For rice in 1990, this amounted to about 900 ha in the irrigation district, a crop value of N5.3 million (US \$0.60 million). In 1991, the total acreage of rice yield loss was 2700 ha with cash value of N19 million (US \$1 million). The percent wheat yield loss was the equivalent to about 3000 ha in 1991 with cash value of over N28 million (US \$1.56 million), and in 1992 was 2650 ha with cash value of N26 million (US \$1.25 million).

Damage to crops in the non-irrigated fields (which was not the main focus of the present study) was not quantified but from field observations and information gathered from farmers, the damage levels were generally considered very low even though farm holdings adjacent to rodent refugia might occasionally suffer some moderate to high levels of damage. The two rodent species in the present study, namely *Arvicanthis*, and *Mastomys*, plus *Tatera* (which was entirely absent from the irrigated fields) are involved

in depredation and damage to the crops. *Mastomys* and *Tatera* were probably more serious pests than *Arvicanthis*, as was evident from higher capture rates of the two species in the crop fields and their greater preference of seeds, grains and cereals (Chapter three). In an overall sense of "pest," the above assertion may not hold as true since the relative numbers of *Arvicanthis* in the fields were higher than those of the other two species (Chapter one). However, Happold (1987) characterizes *Tatera* as granivorous and *Arvicanthis* as herbivorous. Moreover, *Arvicanthis*, being a poor climber, was less likely to inflict any serious damage to standing crops as would, say, *Mastomys*.

Pre-storage crop losses to rodents in both irrigated and non-irrigated fields, although not investigated in the present study, appeared to be very important and call for some research. In most manually operated peasant farms (which constitute over 80% of the acreage in the districts), the harvested crops were left in the field for two to three days to dry before further processing and bagging. This provides ample opportunity for very high but unestimated rodent depredation and damage. Poor crop threshing and processing methods as well as slow evacuation from the fields also combine to make greater amounts of food available to rodents. These activities certainly reduce yields and might be important factors leading to rodent outbreaks.

We did observe that rats causing damage to crops live in burrows and grass nests in raised uncultivated patches of land near the crops fields in unweeded orchard fields and on ridges separating plots. Damage was also common in unweeded farms, which of course are substantial refugia for rodents. Taylor (1972) reports similar observations. Therefore, eliminating rodent refugia interspersed in irrigated crop fields and maintaining clean farms might help reduce the severity of rodent damage. Taylor (1968) and Green and Taylor (1975) also recommend such measures in the control of field rodents.

The steady increase in tiller damage to growing rice and wheat crops right from tillering to the booting stage seen in this study appeared to be similar to reports in other studies. For example, Lavoie *et al.* (1970) report increases in *Rattus* damage to growing rice from the vegetative stage to the reproductive and maturation stages. The report of the Philippines National Damage Survey to rice, 1970 (Sanchez, 1974) notes a similar pattern of little or no damage at the earlier growth stages of rice but heavy damage levels in later stages. The amount of vegetative density of the crop, hence the amount of cover, seems to be important in affecting the amount of damage to tillers (Poche, Haque, Mian, Sultana and Karim, 1981). The shoots of sprouting grasses are especially nutritious (Raay and Leeuw, 1974), and perhaps are even more nutritious at the dough or milk stage in such cultivated cereals as rice and wheat, presumably one of the reasons why damage levels increased at those stages.

In conclusion, our study has shown that damage levels caused by rodents to growing cereals in northern Nigeria, as in other regions, was affected by the developmental stage of the crop, being higher in the maturing stages. Damage levels at all pre-maturation and mature stages of wheat were higher (exceeding 20%, and characterized here as severe in terms of both acreage and cash value lost) than in rice (grown mainly during the rains), perhaps because wheat was grown by irrigation when other rodent foods were not as abundant as during the rains. Thus, irrigation projects provide the conditions for the survival of rodents that may later ravage crops. We have also seen some significant differences in crop damage levels between different years of cultivation, a fact which may or may not be related to the differences in rodent density. This study supports the indictment of *Arvicanthis* and *Mastomys* as major tropical agricultural pests.

SYNTHESIS

Concluding remarks for the dissertation.

Populations of three co-existing rodents, namely *Arvicanthis*, *Mastomys* and *Tatera* were studied in both natural and irrigated savannah fields near Kano, northern Nigeria during July 1990 to August 1992. *Tatera* was entirely absent from the irrigated fields where crops were grown during the dry season (November-April) and rainfed crops during May to October (Chapters one, two)

Reproduction in all three species in the natural fields was strictly seasonal, during the rains (Chapter two). *Mastomys* had the biggest litter size (mean of 8.61 embryos per mature female), followed by *Arvicanthis* (5.30 embryos per mature female) and *Tatera* (3.41 embryos per mature female. *Arvicanthis*, however, had the highest population density (despite lower reproductive capacity than *Mastomys*) of 218/ha during peak density (Chapter one). The relatively lower density for *Mastomys* was probably due to lower adult survival and recruitment rates, and to a lesser extent, probably greater dispersal (Chapter one). A good proportion of adult *Mastomys* would simply disappear soon after the breeding season. Reports (e.g. Delany, 1986; Telford, 1989) have described *Mastomys* as an annual species; thus, providing support for our data. Adult and young of both *Arvicanthis* and *Mastomys* showed decreased survival rates during the peak rains of July-September (Chapter one).

In contrast to seasonal reproduction in the natural fields, breeding in the irrigated fields was continuous although with greater vigor during the rains (Chapter two). Population sizes and recruitment rates in *Arvicanthis* in these fields exceeded those in the natural fields by 400-500%, for peak density was up to 1161 per ha. The densities for *Mastomys* were about three times those in the natural fields (Chapter one). It is evident,

therefore, that irrigation does enhance both reproduction and larger population sizes in some African rodents.

Analysis of stomach contents revealed that consumption of insects and fresh vegetative materials during the dry season were significantly higher in the irrigated fields. Consumption of seeds was also enhanced by irrigation, at least in the case of *Arvicanthis* (Chapter three). These food sources, which were abundant year round in the irrigated fields but scarce in the natural ones due to dry season drought (Chapters three and four) are known to sustain breeding in small mammals (Delany, 1986; Swanepoel, 1980, Taylor and Green, 1976). The effects of foods on breeding may be due to high protein content or the presence of chemicals that stimulate gonadal activities. Many authors (Delany, 1986; Poulet and Poupon, 1978; Taylor, 1968) attribute outbreaks of certain African rodents to improved habitat conditions directly caused by either greater amounts of or extended availability of moisture. Not surprisingly, we observed (and measured, Chapter V) extensive crop damages, especially in the dry seasons in the irrigated fields. Thus, there is ample support for the hypothesis that highly productive environments support high density rodent populations that may in turn ravage crops.

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AUTOBIOGRAPHICAL STATEMENT

Safianu Rabiū was born on August 15, 1959 at Zakirai, 50 km northeast of Kano city, Nigeria. He went to elementary school in the same village, and later, a government high school at Kazaure, Kano State. From there he went to the College of Advanced Studies from 1977 to 1979. In October 1979, Safianu enrolled in the freshman class at Bayero University, Kano and graduated in 1982 with a B.Sc. degree in Zoology.

After one year of National Service and working experience as Wildlife Officer, Safianu returned to Bayero University to teach and pursue a higher degree in animal ecology. He earned a Masters degree in 1986 and continued to teach for another two years before moving to the U.S. in the fall of 1988 to enroll in the ecological sciences doctoral program of the Old Dominion University. While at O.D.U. Safianu also attended the University of Virginia during part of 1989.

The African Dissertation Fellowship Program of the Rockefeller Foundation generously supported Safianu's Doctoral Research Project whose findings are contained in the present document. Safianu is married to Halimat-Sadia. They have two children.