Ecologically-based Management of Rodent Pests

ECOLOGICALLY-BASED MANAGEMENT OF RODENT PESTS

Edited by: **Grant R. Singleton, Lyn A. Hinds, Herwig Leirs and Zhibin Zhang**

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Abbreviations

ACIAR	Australian Centre for International Agricultural Research
AHF	Argentine haemorrhagic fever
AZRG	Agricultural Zoology Research Group (Thailand)
CIAP	Cambodia–IRRI–Australia Project
CRS	Catholic Relief Service
CSIRO	Commonwealth Scientific and Industrial Research Organisation (Australia)
EBRM	ecologically-based rodent management
ECC	endogenous circadian clock
ECTV	ectromelia virus
EWS	early wet season (crop)
GMO	genetically modified organism
GTZ	Deutsche Gesellschaft für Technische Zusammenarbeit (German Technical Cooperation)
HFRS	haemorrhagic fever with renal syndrome
HPS	hantavirus pulmonary syndrome
IPM	integrated pest management
IRD-ORSTOM	Institut de Recherche pour le Développement; the French Scientific Research Institute for Development through Cooperation
IRRI	International Rice Research Institute
Lao PDR	Lao People's Democratic Republic
MCMV	murine cytomegalovirus
MIA	Murrumbidgee Irrigation Area (Australia)
PICA	Predict, Inform, Control, Assess (strategy)
RPM	rodent pest management
SNV	Sin Nombre virus
TBS	trap–barrier system
TBS+TC	TBS plus trap crop
TBW	total body water
VVIC	viral-vectored immunocontraception
ZP	zona pellucida (glycoproteins)

List of Species

Species name	Common Name
Acomys cahirinus	spiny mouse
Apodemus agrarius	striped field mouse
Apodemus flavicollis	yellow-necked field mouse
Apodemus sylvaticus	wood mouse; long-tailed field mouse
Arvicanthis niloticus	unstriped grass rat; Nile grass rat
Bandicota bengalensis	lesser bandicoot rat
Bandicota indica	large bandicoot rat
Bandicota savilei	
Bolomys obscurus	dark field mouse
Brachyuromys ramirohitra	
Calomys callosus	"laucha grande"
Calomys musculinus	corn mouse
Castor canadensis	North American beaver
Castor fiber	Eurasian beaver
Citellus dauricus	Daure ground squirrel
Clethrionomys glareolus	bank vole
Clethrionomys rufocanus	red backed vole
Cricetomys gambianus	African giant pouched rat
Cricetulus barabensis	striped hamster
Cricetulus longicaudatus	lesser long-tailed hamster
Cricetulus triton	rat-like hamster
Cynomys ludovicianus	plains prairie dog
Dipodomys panamintinus	Panamint kangaroo rat
Geomys bursarius	eastern American pocket gopher; plains pocket gopher
Gerbillus nigeriae	Nigerian gerbil

Species name	Common Name
Hystrix cristata	crested porcupine
Hystrix indica	Indian crested porcupine
Liomys salvini	Salvin's spiny pocket mouse
Mastomys coucha	multimammate rat
Mastomys erythroleucus	multimammate rat
Mastomys huberti	multimammate rat
Mastomys natalensis	multimammate rat
Marmota himalayana	Himalayan marmot
Meriones unguiculatus	Mongolian gerbil; clawed jird
Micromys minutus	harvest mouse
Microtus brandti	Brandt's vole
Microtus californicus	California vole
Microtus fortis	oriental vole
Microtus mandarinus	brown vole
Microtus oeconomus	root vole
Microtus pennsylvanicus	meadow vole
Mus caroli	rice mouse
Mus cervicolor	ryukyu mouse
Mus domesticus	house mouse
Mus musculus	house mouse
Muscardinus avellanarius	dormouse
Myocastor coypus	coypu; nutria
Myospalax baileyi	plateau zokor
Myospalax fontanieri	Chinese zokor
Nesokia indica	short-tailed bandicoot rat
Nesomys rufus	
Notomys alexis	spinifex hopping mouse
Ochotona cansus	Gansu pika
Ochotona curzoniae	plateau pika; black-lipped pika
Ochotona daurica	Daurian pika

Species name	**Common Name**
Oligoryzomys longicaudatus	long-tailed pygmy rice rat
Ondatra zibethicus	muskrat
Onychomys spp.	grasshopper mice
Perognathus parvus	Great Basin pocket mouse
Peromyscus boylii	
Peromyscus maniculatus	deer mouse
Peromyscus truei	big eared cliff mouse; Pinyon mouse
Pitymys irene	
Pseudomys hermannsburgensis	sandy inland mouse
Rattus argentiventer	rice-field rat
Rattus bowersi	Bower's rat
Rattus colletti	dusky rat
Rattus exulans	Polynesian rat
Rattus flavipectus	buff breasted rat
Rattus germaini	
Rattus koratensis	Sladen's rat
Rattus losea	lesser rice-field rat
Rattus nitidus	Himalayan rat
Rattus norvegicus	Norway rat; brown rat
Rattus rattoides	Synonym for lesser rice-field rat and Turkestan rat
Rattus rattus	black rat; house rat; roof rat

Species name	**Common Name**
Rattus rattus diardii	Malaysian house rat
Rattus tanezumi (formerly *Rattus rattus mindanensis)*	Philippine rice-field rat
Rattus tiomanicus	Malayan wood rat
Rattus villosissimus	long haired rat
Rhabdomys pumilio	
Sigmodon alstoni	Alston's cotton rat
Sigmodon hispidus	cotton rat; Hispid cotton rat
Solomys spp.	tree rats
Spalax ehrenbergi	blind mole-rat
Suncus murinus	common shrew
Tachyoryctes splendens	African mole rat
Tatera indica	
Taterillus gracilis	gerbil
Taterillus petteri	gerbil
Taterillus pygargus	gerbil
Thomomys bottae	western American pocket gopher; valley pocket gopher
Thomomys talpoides	northern pocket gopher
Thryonomys spp.	cane rat; cutting grass rat
Xerus erythropus	ground squirrel
Zygodontomys brevicauda	cane mouse

Preface

THE SEED FOR this book was sown in Morogoro, Tanzania, in 1996, following the strong ecological theme that emerged at an international workshop: Rodent Biology and Integrated Pest Management in Africa. Herwig Leirs and Grant Singleton were encouraged that the theme of ecologically-based rodent research came through strongly as the future direction for rodent management in developing countries in both Africa and Asia. The opportunity to germinate the seed arose in 1997 when Zhibin Zhang approached Grant Singleton and Lyn Hinds to co-convene an international conference on rodent biology and management. The focus would be broader than the Morogoro workshop and it was obvious that to augment the charm and appeal of Beijing in early autumn, an impressive line-up of international speakers would be required to attract participants to the conference. The Australian Centre for International Agricultural Research (ACIAR), the Chinese Academy of Sciences and the Commonwealth Scientific and Industrial Research Organisation (CSIRO) Wildlife and Ecology each pledged support for the conference. This led to a successful recruiting drive with all the speakers we approached accepting an invitation to present a paper at the First International Conference on Rodent Biology and Management held in Beijing in October 1998.

In January 1998, the editors approached ACIAR with the concept of a book on ecologically-based management that would bring together leading researchers of the basic biology of rodents and those charged with developing and implementing management strategies for rodent pests, especially in developing countries.

The book consists primarily of a selection of papers presented at the Beijing conference and comprises three sections. Section 1 sets the scene with contributions from leading small mammal biologists interested in theory and current paradigms of rodent biology and management. Section 2 covers state-of-the-art technologies of the different approaches to management of rodent pests—rodenticides, physical control, urban management and biological control. Section 3 describes regional case studies of rodent pest problems and progress with their management for a selection of developing countries in Asia and Africa.

Internationally, there have been two previous books of note on rodent pest management: one edited by Ishwar Prakash, published in 1988, the other edited by Alan Buckle and Robert Smith, published in 1994. Both provided a good mix of papers on the principles and practices of rodent pest management, and are compulsory reading for students and practitioners of rodent biology and management. Our book differs from these two books in providing a considerably stronger emphasis on (i) ecologically-based management, (ii) recent developments in innovative approaches to biological control, and (iii) the problems, progress and challenges of rodent pest management in developing countries. One important element missing in our book, and in the previous two books, is a substantial contribution on rodent management in Central and South America. We hope that this void is filled in the near future. In the interim, we hope that our book is of interest and practical value to researchers in that region of the world.

This has been a challenging project with more than half of the contributing authors not having English as their native language. We thank these authors for their perseverance in the face of obvious frustration in not being able to write in Bahasa, Cantonese, Flemish, French, Kiswahili, Lao, Mandarin, Thai, Vietnamese etc. We commend them for their responsiveness to our requests for many points of clarification and in keeping to a tight schedule.

All chapters were refereed by two people and then edited. We thank fellow authors for their contributions to the reviewing and editing process as well as David Spratt, Abigail Smith, Wang Zuwang, Lam Yuet Ming, David Freudenberger, Alison Mills, Christopher Hardy and Geoffrey Shellam. The support and enthusiasm of John Copland and Peter Lynch have ensured that the seed of an idea developed into a bountiful crop—a crop which it is hoped will be eyed despairingly by rodents in our ecologically-led quest to battle their impact on our lives.

Grant Singleton
Lyn Hinds
Herwig Leirs
Zhibin Zhang

March 1999

1. Ecologically-based Management of Rodent Pests—Re-evaluating Our Approach to an Old Problem

Grant R. Singleton, Herwig Leirs, Lyn A. Hinds and Zhibin Zhang

Abstract

Rodent pest management has gone through a period of stagnation mainly because there has been too little research effort to understand the biology, behaviour and habitat use of the species we are attempting to manage. There is a growing demand, particularly in developing countries, for rodent control strategies that either have less reliance on chemical rodenticides or can better target their use. Similar concerns exist with the control of insect and weed pests. This has led to the development of the concept of ecologically-based pest management (EBPM) which builds on the progress made with integrated pest management (IPM). We analyse this idea for rodent pests and provide examples where research on the basic biology and ecology of rodent pests has provided management strategies that are more sustainable and environmentally benign. The theme of ecologically-based rodent management (EBRM) was foremost in our minds when we invited people to contribute to this book. The other significant considerations were a focus on rodent pest management in developing countries and the importance of marrying basic and applied research on rodents. If in developing countries we can foster the importance of population ecology and an emphasis on management directed at the agro-ecosystem level, then we are confident that the next decade will see rapid advances in rodent pest management.

Keywords

Rodent management; IPM; rodent ecology; ecologically-based rodent management

INTRODUCTION

THE GENESIS of this book was a common concern on the lack of progress in rodent pest management over the past 20 years in both developing countries and elsewhere. This has occurred despite the advent in the 1970s of sophisticated chemical rodenticides and effective strategies for their use (see Buckle 1988; Buckle and Smith 1994).

We contend that rodent pest management has gone through a period of stagnation for four primary reasons. First, there has been too great an emphasis on how to develop, use, compare and market rodenticides, with particular attention on commensal rodents in industrialised countries. In developing countries, on the other hand, the lack of a critical approach to the use of rodenticides for particular species has in some instances led to an unreasonable aversion to rodenticide use. Second, the development of rodent control strategies generally has been based on short-term experiments where immediate declines in rodent numbers were seen as a success, without much consideration of long-term consequences or ecosystem effects. Third, field studies have rarely progressed beyond alpha-level, descriptive population studies (see Krebs, Chapter 2). Fourth, the recommended management protocols have been too prescriptive. They rarely take into account the particular characteristics of the pest species or of the socioeconomic constraints of the end-users of the technology.

What has been lacking is a solid understanding of the biology, behaviour and habitat use of the respective species we are attempting to manage. Armed with such knowledge we will be able to focus on disentangling the major factors that limit the growth of pest populations. This requires experimental field studies conducted at an appropriate scale and for an appropriate length of time. Recently there has been some progress in the assessment of rodent management methods using replicated, manipulative field studies based on our understanding of the ecology of the pest species (e.g. Singleton and Chambers 1996; Brown et al. 1998; White et al. 1998; Fan et al., Chapter 13), but there is still much to be done.

In the interim, there has been a marked attrition in the number of wildlife researchers working on rodent pests. Ishwar Prakash (1988) noted this trend in his introduction to the pioneering book *Rodent Pest Management*.

> It is also felt that this work ... will trigger more research effort for the benefit of mankind, ... (which) it appears has dampened during the last few years.

Unfortunately, his plea did not arrest this trend.

Since 1993 there has been encouraging evidence of an increase in the number of young wildlife researchers interested in the biology and management of rodent pests in developing countries. This has been due primarily to funding support provided by the Australian Centre for International Agricultural Research in Southeast Asia, the European Union, Belgium and Denmark in eastern Africa and ORSTOM (French Scientific Research Institute for Development through Cooperation) in Western Africa. We are pleased that some of these researchers have been able to contribute to this book.

China, through necessity, also has seen a marked increase in research effort on rodent pests. Rodent problems increased in severity in the 1980s resulting in rodent control being listed as one of the top three priorities for the national plant protection program in 1985. Since 1985, rodent control has been listed in three successive national five-year-plans (1985–1990; 1991–1995; 1996–2000). There are now approximately 100 scientists with the Chinese Academy of Sciences, Ministry of Agriculture and universities working on rodent control. Many of these are young scientists, who received their degree in biology or post-graduate qualifications in the 1990s.

In this opening chapter we will set the scene with a brief overview of the magnitude of the impact of rodent pests, the concept of ecologically-based management and the aims and structure of the book.

RODENT PESTS—STILL A PROBLEM

The quest to control the depredations of rodents, especially in agricultural systems, has been ongoing for thousands of years. Aristotle (384–322 BC) recounts

> The rate of propagation of field mice in country places, and the destruction that they cause, are beyond all telling.

Although the last 50 years in particular have provided good progress with rodent pest management, rural people in many countries still rank rodents in the top three of their most important pests. Of particular concern are the losses caused in developing countries where rodents are literally competing with humans for food.

A meeting on rodent pest management in Southeast Asia was held in early 1998 at the International Rice Research Institute (IRRI) in the Philippines. Reports of present-day rodent problems were presented for Australia, Cambodia, East Africa, Indonesia, Lao People's Democratic Republic (PDR), Malaysia, Philippines, Thailand and Vietnam; the accounts were impressive in their extent and impact. Rodent problems ranged from eruptive populations of mice in south-eastern Australia and rats in the uplands of Lao PDR, to the chronic problems that occur annually in the rice fields of most Southeast Asian countries.

There were two telling commentaries from the meeting in the Philippines, which place in context the impact of rodent pests in developing countries. One reported that although rodents were not the most important pre-harvest pest to Laotian farmers, they were the pest they felt they had the least control over. The other presented losses caused by rodents in Cambodia not in monetary terms but in how much rice could have been available for annual human consumption if not for rat depredations. If we apply this line of reasoning to Indonesia where rats cause annual pre-harvest losses of approximately 17%, then rats consume enough rice annually to feed more than 25 million Indonesians for a year. In countries such as Indonesia, rice provides 50–60% of the daily energy requirements for people.

In some cases, the 'official' national level of annual pre-harvest losses caused by rodents is not high. For example, 3–5% losses are reported in Malaysia (Singleton and Petch 1994) and 1–3% in the Philippines (Sumangil 1990; Wilma Cuaterno, April 1998, pers. comm.). However, when detailed damage assessment is conducted, the damage caused by rats generally is more severe. For example, Buckle (1994b) reported a conservative loss estimate of 7.3% in the entire Penang State of Malaysia. Also, both in the Philippines and Malaysia, the patchy nature of rodent damage often results in farmers losing more than 60% of their crop, which means that rodents are still a significant national problem (Lam 1990). In other places, rodent damage may vary widely with limited damage in most years, and the most extreme losses of more than 80% of the harvest in outbreak years (e.g. Boonaphol and Schiller 1996). In countries that live at the brink of subsistence, such figures are a constant threat to food security.

This book contains detailed accounts of the magnitude and importance of the impact of rodent pests, particularly in agricultural systems. This information in itself is important because it provides a spotlight on rodent problems that generally have a lower profile than insect, weed and disease impacts on agricultural crops. The latter group of problems has a higher profile for two reasons. One is that, in developing countries, there are many entomologists, botanists and plant pathologists who are able to identify, quantify and sell the need for research, education, extension and action in their respective fields. In comparison, there are few rodent biologists; most of these have an entomological training and there is a poor infrastructure for research on rodent pests.

The second reason is that farmers have a stronger identity with rodents than other pests. Rodents are perceived as 'intelligent' pests, which learn to counter whichever control measures farmers use. Over the centuries, farmers have learned to accept the depredations caused by rats. A common response is,

> for every eight rows of rice we sow for our family, we sow two for the rats.

Unfortunately, with the increasing human population and the shortage of food in developing countries, this level of loss can no longer be tolerated.

Clearly, rodents are still an important problem, and this is without consideration of the losses they cause post-harvest, and the role they play as reservoirs for debilitating diseases of humans and their livestock.

IPM, RODENTICIDES AND ECOLOGICALLY-BASED MANAGEMENT

Integrated pest management (IPM) is simply the integration of a range of management practices that together provide more effective management of a pest species than if they are used separately. IPM was developed with the aim of promoting methods for managing insect pests and plant diseases that were least disruptive to the ecology of agricultural systems (Smith and van den Bosch 1967).

Ecologically-based pest management

In 1996, a review of pest management of insects and weeds by the Board on Agriculture of the National Research Council (NRC) of the United States of America, highlighted that the practice of IPM has generally not been consistent with the underlying philosophy of IPM. They contend that there has been too much focus on pest scouting and precise application of pesticides. They argue that there is a need to refocus objectives from pest control to pest management and this requires greater emphasis on ecological research and a systems approach (National Research Council 1996). This extension and refocusing of the ecological aspects of IPM led the NRC to develop a concept termed 'ecologically-based pest management' (EBPM). The fundamental goals of EBPM are threefold. One is to minimise adverse effects on non-target species and the environment. The second is to develop an approach that is economic for end-users, particularly farmers, in both the developed and developing world. The third is to establish an approach that is durable.

The development of IPM for rodents has followed a similar path to IPM for insects. The primary foci have been the development of simple monitoring systems to decide whether or not to instigate a baiting campaign, and the development of effective patterns of use for particular rodenticides. Generally, the focus in rodent control has been mostly to achieve a visible increase in mortality, without appropriate attention to other demographic processes or ecological compensation mechanisms. There have been attempts to develop rodent IPM based on an understanding of the habitat use and population dynamics of rodent pests (see Wood and Liau 1984 a,b; Redhead and Singleton 1989; Whisson 1996; Brown et al. 1998; White et al. 1998) or the use of biological control (e.g. Lenton 1980; Singleton and Chambers 1996), but with the possible exception of *Rattus tiomanicus* in oil palm plantations (Wood and Liau 1984a,b), these have not been adopted successfully over a large area. The progress of rodent IPM in Southeast Asia and Australia has been reviewed by Singleton (1997).

Also, biological control needs to be viewed in the context of ecologically-based management of pests because often it is limited in its specificity and efficacy. This is supported by a review of one of the success stories of biological control, the weevil — *Cyrtobagous salviniae*, for controlling the floating fern salvinia (*Salvinia molesta*). Following its establishment in South Asia in 1939, salvinia was spread by man to Southeast Asia and Australasia. It severely disrupts the lives of people by forming dense mats a metre thick, choking slow moving waterways, rice fields and lakes (see Thomas and Room 1986 for details). Efforts to develop biological control were thwarted initially because the fern was incorrectly identified, resulting in the testing of the wrong herbivores. In 1978, salvinia was found in Brazil where it is relatively rare. Field studies identified three potential herbivores and one of these, *C. salviniae*, was released into a lake in northern Queensland and destroyed 30,000 t of salvinia within a year (Room et al. 1981).

When tested in other waterways the weevil was not a success. Subsequently, a combination of ecological and laboratory studies revealed that, if the level of nitrogen was too low in the fern, the weevil population declined. Nitrogen was added to waterways which increased the weevil population, until it eventually reached a critical density at which the damage it caused to the plant resulted in a sufficient increase in nitrogen in the plant itself for the weevil population to be self-sustaining (Room 1990). This was an unexpected result because higher levels of nitrogen generally make weed problems worse. The salvinia story highlights how taxonomic and ecological research provided a strong basis for a successful systems approach for pest management.

Ecologically-based rodent management

For rodents, an ecological basis for control was suggested many years ago (Hansson and Nilsson 1975; see also Redhead and Singleton 1988) but the implementation of those early ideas has been largely overlooked. One success was the eradication of coypu (*Myocastor coypus*), an introduced rodent pest, in Britain in the 1980s. After several decades of unsuccessful control, a new strategy was developed based on a long-term population dynamics study and biological simulations. A complete solution of the problem was obtained in less than six years through integrating knowledge about the animal's biology and behaviour with a well-organised control scheme with attractive incentives for trappers (Gosling and Baker 1989). There are other good examples in the rodent literature which illustrate the importance of ecological, taxonomic and behavioural studies for developing effective strategies for managing rodent pests. We provide some further examples later in this chapter, with more detailed case studies provided in the ensuing chapters (Macdonald et al., Chapter 3; Leung et al., Chapter 14).

The advantages of viewing biological control of rodents as part of an integrated ecologically-based approach to rodent management rather than a single panacea for control has been reviewed by Singleton and Brown (1999). For simplicity, we propose that this strategy be termed 'ecologically-based rodent management' (EBRM). The contributions by Pech et al. (Chapter 4) and Hinds et al. (Chapter 10) further portray the advantage of having a strong ecological understanding of the biology of both the rodent pest and the disease agent when developing techniques for biological control. In this instance, the focus is on developing fertility control of house mice. Without a multi-disciplinary approach, the requisite knowledge of reproductive biology, social behaviour patterns and population dynamics of the wild house mouse could not be consolidated to allow full development of a product which can then be tested for efficacy.

Rodenticide-based control strategies have a clear need for a good biological basis to build upon. Toxicity of active ingredients and bait palatability are obvious factors which have been studied under laboratory conditions for many decades (see e.g. Buckle 1994a; Johnson and Prescott 1994). Less common, but equally important, is a proper understanding of how poisons can be delivered. For example, rodenticides in Hawaiian macadamia orchards were commonly distributed by broadcasting on the ground. Recently, population and behavioural studies of the black rat, *Rattus rattus*, revealed that those rats which damage the nuts forage only in the trees. This information led to placement of bait stations in trees leading to more efficient use of rodenticides for controlling damage (Tobin et al. 1997).

In China, chemical rodenticides, mostly anticoagulants, are still the routine weapons for controlling rodents in farmland and grassland. However, such rodent control campaigns in the absence of a sound ecological knowledge of the pest species have generally only achieved short periods (6–9 months) of respite from the ravages of the rodents. In the rice fields of southern China the effects have been even shorter (Huang and Feng 1998). Indeed, many studies (Liang 1982; Liang et al. 1984; Zhang 1996; Huang and Feng 1998; Qi et al. 1998) have shown that the response of rodent populations after chemical control is non-linear. Killing some individuals may reduce the population numbers initially, but the remaining animals compensate with better survival and better breeding performance. For example, following an 88% reduction in a population of the Mongolian gerbil (*Meriones unguiculatus*), the body mass at first pregnancy was reduced from 58 g to 35–50 g (Wang et al. 1998).

In Malaysia, populations of the Malayan wood rat (*R. tiomanicus*) also showed a rapid population response after control, with a full recovery in population density occurring over 12–18 months. In this case, knowledge of the population dynamics and factors limiting population growth resulted in an effective management program of rats in oil palm plantations. Management consisted of an intensive baiting campaign followed by recurrent placement of baits every six months (see Wood and Liau 1984a).

Re-invasion is another factor resulting in populations returning quickly to pre-control densities (e.g. Guruprasad 1992). This is particularly a problem in developing countries where farmers often manage their own rodent problems on small plots of land (0.25–2 ha) at different times to their neighbours. The land use patterns on these small holdings also generally result in a patchy landscape. We therefore need ecological studies to examine the relative demographic importance of each patch and the timing and rates of movements by rats between patches (Singleton and Petch 1994). This metapopulation approach to rodent control is achieving more attention (see Smith 1994), but appropriate field studies of the spatial dynamics of rodent populations in agro-ecosystems in developing countries (e.g. Leirs et al. 1997b) are few.

Ethology in rodent pest management

The development of resistance by rodent pest species to first and second generation anticoagulants explicitly necessitated an integrated approach to rodent management, where use of one poison type was complemented or alternated with the use of other poison types, physical control methods, exclusion, or other control measures (Greaves 1994). Here again, more attention was paid to short-term, and indeed often urgently needed, quick solutions like changing to a stronger poison. Much less effort has been directed towards preventing the development of, or containing the geographical distribution of, resistance. So-called 'behavioural resistance', where rodents refuse to eat the poisonous baits, poses other challenges. In the Birmingham restaurant area, house mice were impossible to control until detailed studies revealed that they had difficulties in digesting starch and were therefore unlikely to eat grain-based baits; changing to fish baits solved the problem quickly (Humphries et al. 1996).

The Chinese zokor (*Myospalax fontanieri*) provides another practical example of the importance of understanding rodent behaviour in developing effective management. In the farmland of Northwest Loess Plateau, the zokor, which lives underground, shows a cautious response to chemical baits. Less than 70% of a zokor population can be killed by using the best possible baiting technique for this species: setting baits in their underground tunnels (Zou et al. 1998). Further improvement in this kill rate depends on a better understanding of the behavioural aspects of feeding for this species, particularly in overcoming its neophobic response to baits (Zhang and Wan 1997) or perhaps whether they show social learning of food preferences (see Galef 1994; Berdoy 1994 for reviews).

A good ecological basis to management strategies can help to provide excellent rodent damage control without interfering with rodent demography. Wood mice (*Apodemus sylvaticus*) in Germany can be lured away from sugar beet seeds during the short period after sowing when they are prone to rodent damage by providing an attractive, unpoisoned alternative food in the periphery of the fields (Pelz 1989). As all the above examples show, however, solutions are often specific and require a detailed knowledge of the biology, ecology and behaviour of the pest species. Obtaining such knowledge is a laborious yet rewarding task that will allow the development of new damage control strategies.

Further examples of the benefits of combining knowledge of the ecology and ethology of rodent species for developing better integrated control are provided by Santini (1994) for three European species of rodents in agriculture and forestry, and Buckle et al. (1997) for the Malayan wood rat in oil palm plantations.

RE-EMERGENCE OF POPULATION ECOLOGY OF RODENT PESTS

The current book builds on the strong ecological theme that emerged at an international workshop on rodent biology and integrated pest management in Africa, held in Morogoro, Tanzania, in 1996 (for published proceedings see Belgian Journal of Zoology Volume 127, Supplement). Africa is an economically poor continent and control strategies which rely primarily on rodenticides are unrealistic. This has sparked interest in a more integrated ecological approach to rodent pest management. One of the conclusions of the workshop was, however, that such strategies cannot materialise without the availability of population data from long-term studies (more than three years) (Leirs 1997). In West Africa, much information was collected by Hubert and co-workers in the 1970s (e.g. Hubert 1982), while in East Africa it is only in the past few years that long-term ecological studies have begun to provide insights into the main factors driving rodent population dynamics (Leirs et al. 1996, 1997a). Building on these insights, the focus has now switched to experimental field studies.

The workshop in Morogoro formulated recommendations, many of which are relevant to the present book (Leirs 1997a). The key recommendations are as follows:

- The taxonomy of many pest rodents must be clarified so that control actions can target the correct species.
- Life-history studies and physiological comparisons between these species are imperative.

- Experimental ecological studies, properly designed with appropriate controls, must be set up to evaluate management strategies and, in the first place, test our hypotheses (or, rather, unsubstantiated beliefs) about rodent population dynamics.
- Poisons in this framework are not considered as something to avoid, but as only one of the possible approaches which should be used more effectively and integrated with other approaches.

The development of the concept of EBPM is important, because it builds on the solid foundations developed by IPM. In effect, EBPM is refocusing IPM towards understanding the population biology of the pest and the agro-ecosystem in which it lives. From the viewpoint of a population ecologist, one wonders what all the fuss is about; EBPM is self-evident. However, when one moves into applied wildlife management, especially of rodents, then the need to sell a concept such as ecologically-based management of rodent pests becomes a reality (Singleton and Brown 1999). Unfortunately, too often there is a divide between practitioners, who are more concerned with the details of how to apply specific control technologies, and wildlife researchers who focus on understanding the theory and the context of the problem (Sinclair 1991). We have provided a mix of pure (Section 1 and parts of 2) and applied (Sections 2 and 3) rodent biology in this book in an attempt to bridge this divide.

AIMS AND STRUCTURE OF THE BOOK

This book has four broad aims:

- to raise the profile of the importance of basic research for developing effective, applied management of rodent pests;
- to argue the need for an ecologically-based approach to rodent pest management;
- to raise the profile of rodent pest management in developing countries; and
- to spark interest in prospective students in a challenging but rewarding field of endeavour.

The book begins with a section on theory and current paradigms of rodent biology and management.

This section includes contributions from leading small mammal ecologists. Krebs (Chapter 2) provides a thought-provoking paper on the different phases of small mammal ecology and concomitant shifts in research paradigms. Macdonald and coworkers (Chapter 3) present the results of a series of novel studies used to disentangle the interesting social behaviour of Norway rats. Dickman (Chapter 5) examines, at the ecosystem level, the positive role rodents play as 'ecosystem engineers' through their impact on the chemical and structural attributes of the environment. Mills in his chapter on arenaviruses and hantaviruses (Chapter 6), and Pech and his coworkers through their synthesis of models for predicting mouse plagues in Australia (Chapter 4), both provide a different perspective of the need for strongly focused population studies of rodents.

One common theme is addressed by all authors—the importance of basic research for developing effective management of rodents.

The second section covers broad methods of management—rodenticides, physical control and biological control. This section provides overviews on the state-of-the-art technologies for fertility control (Chambers et al., Chapter 10), chemical control (Buckle, Chapter 7) and the control of rodent pests in urban environments (Colvin and Jackson, Chapter 11). Reviews are provided also on physical methods of control, particularly in rice agro-ecosystems in developing countries (Singleton and coworkers, Chapter 8) and on the ecological management of Brandt's vole in the grassland of Inner Mongolia (Zhong and coworkers, Chapter 9). The common theme for this section is ecologically-based pest management.

In a conscious effort to ensure the book is relevant to developing countries, regional case studies of rodent problems and the progress with associated research are provided for Asia and Africa in Section 3. This section has contributions from selected countries edited by G.R. Singleton and Z. Zhang (Asia—contributions from Cambodia, China, Indonesia, Lao PDR, Thailand and Vietnam) and H. Leirs (Africa—contributions from Burkina Faso, Kenya, Madagascar, Mali and Tanzania). The information on the biology and management of rodent pests in developing countries, and the infrastructure for research and extension, varies considerably. In some countries, such as Cambodia and Lao PDR, the problem is only just being defined and it is still not known which species cause the major problems in the different agro-ecosystems (see contribution by Schiller et al., Chapter 18). The contributions in this section comprise a mix of biological studies aimed directly at management, and general overviews of rodent problems and how they are currently being managed in various developing countries.

In seeking contributions for this book we were heartened by the enthusiasm that it generated from researchers across the spectrum of pure and applied research. We received no 'knock backs' from contributors we targeted. Indeed, we had to limit the contributions that were on offer. What pleasantly surprised us was the strong interest by 'pure' scientists in hoping their work would not only be of heuristic value. They were keen for their findings to be accessible to researchers in developing countries because they felt their research could make a significant contribution to tackling the problem of rodent pests in these regions. So perhaps Denis Chitty is indeed correct in stating "pure and applied science differ mainly in aims, not methods". If this book acts as a catalyst for pure and applied scientists to work together towards a common aim of reducing the impact of rodent pests in agricultural ecosystems of developed and developing countries, then we will be more than satisfied with our toil.

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Section 1

Basic Research — the Foundation for Sound Management

Pure and applied science differ mainly in aims, not methods

Chitty 1996

2. Current Paradigms of Rodent Population Dynamics — What Are We Missing?

Charles J. Krebs

Abstract

Rodent population studies have played a key role in developing our understanding of population dynamics. The proximal stimulus to this understanding is to alleviate problems of rodent pests in agriculture and disease transmission to humans.

Ideas about rodent population dynamics have gone through three phases. In the 1930s there were almost no quantitative data, and population control was believed to be caused by biotic agents that operated in a density-dependent manner. By the 1950s a new paradigm of social control of numbers emerged with emphasis on physiological stress and social aggression within populations. By the 1970s a synthesis of sorts had emerged suggesting that multiple factors caused population changes. Experimental manipulation of field populations in the 1960s enlarged our outlook on the complexities of rodent populations, and the emergence of modelling and rigorous statistical analyses of survival and reproduction in the 1980s and 1990s has shown again that rodents have been the *Drosophila* of population ecology. But as precision has increased over time, generality and simplicity have declined to near extinction.

What is missing and what do we need to do in the next 20 years? Experimentation is the key to understanding, and no study should be undertaken without a clear set of experimental predictions. The era of alpha-level descriptive population studies should be over. We need large-scale, extensive studies coupled with short-term experimental studies. Rodents are good candidates for studies of spatial dynamics, a strongly emerging subdiscipline in ecology. Also, rodent management should focus on the factors limiting populations and use an experimental approach. The era of pest eradication via killing alone should be over and we need to be smarter in developing our management options. The development of genetic resistance to anticoagulants and chemical poisons is a call to the ecologists of the 21st century to think more clearly about how we might outwit rodent pests. The accumulated knowledge of the physiology, behaviour, and genetics of rodents needs to be integrated into our management options. There is much to be done both to understand and to outsmart these clever mammals.

Keywords

Population regulation, population limitation, food, predation, social behaviour, rodents, pest management

INTRODUCTION

POPULATION DYNAMICS is without question the most highly developed of the subdisciplines of ecology. From abstract mathematical models to field experiments, ecologists have made progress over the last 50 years in analysing population changes in many species. In particular, rodents have been model organisms for studies of population dynamics for three reasons. First, they are conveniently short-lived so that a scientist or a postgraduate student can accomplish something within the constraints of a 3–4 year time window. Second, they are ubiquitous, occur in abundance nearly everywhere, and are relatively cheap to study, and are often of economic importance (Singleton et al., Chapter 1). Third, they do interesting things such as have population outbreaks that occur frequently enough that even politicians think that something must be done about them, at least when they are superabundant. All these features have combined to produce a very large literature on rodent population dynamics that is somewhat overwhelming to the novice. It is important therefore to step back and ask what we have accomplished with these studies, how useful it has been for pest control, and what is to be done next. This book brings together ecologists, physiologists, and ethologists with a common interest in rodent biology and thus provides an ideal time to address these larger issues for rodents.

After a historical overview I will summarise the three current paradigms of rodent population dynamics, assess their strengths and weaknesses, and suggest some paths for future growth.

WHAT ARE THE PROBLEMS?

Ecological questions are complex and one thing we have learned is to ask very specific questions about populations so that we can answer them clearly. Three major questions have formed the focus of population dynamics (Krebs 1994, p. 322; Krebs 1995):

- What stops population growth?
- What limits average abundance?
- What constrains geographical distributions?

To find out what stops population growth, we must compare a growing population to one that is not growing, and the usual approach is to look for some factors causing negative feedback in the form of density dependence. The second question is very broad and is answered by the use of the comparative approach in which a high-density population is compared with a low-density population to see what factors are associated with the observed differences in density. In both these cases an experimental approach is useful to answering the question most quickly and avoiding spurious correlations (Underwood 1997).

Most academic rodent ecologists have addressed the first question—the problem of regulation (Berryman 1986; Sinclair 1989), and this has engendered much discussion about density dependence in natural populations. Fewer ecologists have worked on the second question—limitation of numbers, and yet this is the critical question for pest management. In a simple world, the same ecological factors would limit and regulate a population, but this has never been found in the real world. Limitation often comes from habitat factors that students of regulation seldom consider, as we shall see. In a sense these two aspects of population dynamics correspond to the two statistical concepts of the mean and the variance of a set of measurements. We shall be repeating history to complain, as do many statisticians, that scientists are often preoccupied with the mean and tend to forget about the variance.

The question of what constrains geographic distributions has fallen out of favour until fairly recently when the consequences of global warming on north–south geographical distribution boundaries became a hot topic of worry. It is an important issue that I cannot deal with here, and there has been much discussion of the consequences of these biological invasions (Ehrlich 1989; Ruesink et al. 1995; Vitousek et al. 1996).

HISTORICAL OVERVIEW

Population dynamics has gone through three phases during the last 75 years. They have overlapped little in time but have phased into one another, with an abundance of outliers of the 'flat-earth' society type that bedevils ecology in general.

Phase I

The first phase began with the debate in the 1920s and 1930s about the role of biotic and abiotic factors in population regulation. The champions were A.J. Nicholson (1933) for the biotic school and a variety of opponents for the abiotic school (e.g. Thompson 1929; Uvarov 1931). The winners were the Nicholsonians with their focus on regulation via density-dependent processes, in which the main agents were predators, parasites, diseases, and food shortage. The habitat was nowhere to be seen, and weather was noise for population dynamics. Most of this early discussion was about insect populations, and rodents were not a part of the discussions. This was an age of data-free ecology, and the arguments were typically theoretical in the bad sense of this word with no experiments on natural populations available. I have referred to the Nicholsonian world-view as the density-dependent paradigm (Krebs 1995).

It is important to remember that from the start all ecologists implicitly believed that a population can be identified, that community interactions are all direct and easily definable, and that population processes are repeatable in space and in time. These are three gigantic leaps of faith that came back later to challenge simplistic models.

Phase II

The second phase of population dynamics began in the 1940s when ecologists began to realise that social processes could affect births, deaths and movements. Among the leaders of this phase were David E. Davis and John Christian in the United States and Dennis Chitty in England (Christian 1950; Chitty 1952; Davis 1987). Rodents were the key to this new phase, which built partly on the earlier recognition by some ornithologists that territoriality could regulate the breeding density of some bird species. Attention turned in this phase to studying the physiological and behavioural impacts of individuals on one another. One of the early striking experiments was done on rats in Baltimore by Davis and Christian (1956, 1958) who showed that one could reduce the population of rats in a city block by *adding* rats to the population (Figure 1), a completely counterintuitive result for the 1950s. Social strife for breeding space in rodents became a hot topic, and John Calhoun suggested crowded mice and rats as potential models for people in cities (Calhoun 1949). Much of this early work was done on house mice and rats in enclosures, and one of the dominant themes of criticism was that these enclosures were very high density, artificial environments and of little relevance to what went on in natural populations.

Social regulation of population size arose as an alternative explanation of population changes in populations that did not seem to be regulated by the conventional Nicholsonian predators, parasites, or food shortages (Chitty 1960). These studies interfaced well with emerging work in ethology and behavioural ecology, which indicated the complex social structure of many mammal populations, and the interest population geneticists began to show in the dynamics of natural populations (Ford 1975). There was, among many ecologists, considerable scepticism that social processes, in contrast to the extrinsic factors of predators, food supplies and parasites, might explain changes in numbers. A series of elegant experiments on bird populations (e.g. Watson and Moss 1970; Moss and Watson 1980) helped to convince some sceptics, and parallel work on rodents (e.g. Krebs et al. 1969; Tamarin and Krebs 1969; Gaines and Krebs 1971) strongly supported the concept of social limitation of population density.

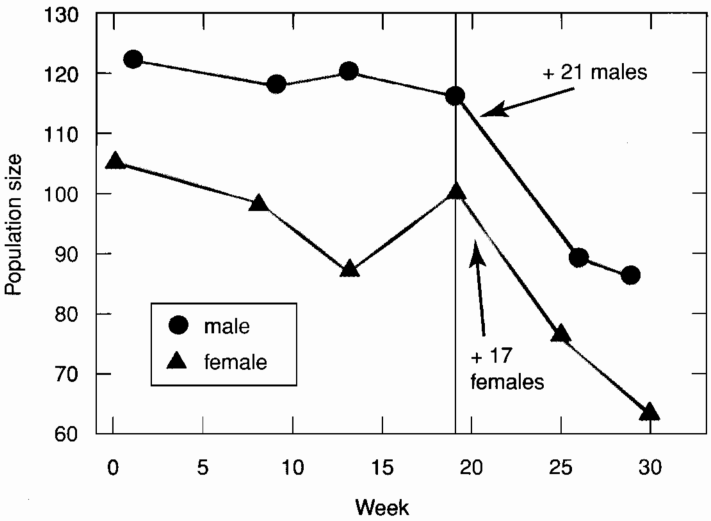

Figure 1.
Introduction experiments of Norway rats (*Rattus norvegicus*) into two city blocks in Baltimore in 1954. Adding rats to a stationary population did not increase numbers but caused them to drop (after Davis and Christian 1956).

Phase III

By 1970 nearly all the ideas about population regulation and limitation were on the table for consideration and a synthesis began by suggesting that everyone might be correct, that multiple factors could be involved in both regulation and limitation (Lidicker 1973, 1988). Two developments accompanied this phase of population studies. First, experimental testing of hypotheses in field situations became the norm in ecology. Second, mathematical models began to be applied to specific questions about rodent systems in order to explore assumptions with rigour (e.g. Stenseth 1978, 1981b). The question then became how to articulate multiple factor hypotheses within the paradigm of experimental ecology. All ecologists are happy to conclude that the world is a complex multivariate system, but almost all agree that we must abstract from this complexity to some order to make progress.

Many multiple-factor hypotheses suffer from three deficiencies. Excessive complexity is the first lethal deficiency. A good example occurs with many flow chart models of population processes. Batzli (1992), for example, lists 22 hypotheses for rodent population cycles and gives a complex flow chart to illustrate some of the interrelationships involved. Limited predictability is a second problem with multiple-factor hypotheses. It does us no service to tell managers that we cannot predict anything about their potential pest problems because the world is complex. Third, many multiple-factor hypotheses are impossible to test experimentally. Without an experimental approach rodent ecology will make little progress.

The solution to these problems is fairly straightforward. We should encourage multifactor models of limited complexity, quantitative predictability, and feasible experimental tests. Note that there are two distinct types of multi-factor models of population limitation.

Several independent factors limit average abundance

The key point in this alternative is that the several factors that affect abundance are independent in a statistical sense. In practice this means hypothetically that if you change factor A and double numbers, and change factor B and triple numbers, you expect that if you change both factor A and factor B at the same time you will change numbers by the simple multiple (2 × 3) or 6 times.

Several interacting factors limit average abundance

This is the most complex alternative hypothesis since it postulates a statistical interaction between some factors. In practice you would recognise an interactive explanation by the fact that changing factor A and factor B at the same time does not result in their joint effect being predictable. In the above example, changing factor A and factor B might change numbers much less than 6 times, or much more than 6 times. If this hypothesis applies to your rodent population, interest centres on exactly how the ecological interaction of factor A and factor B operates mechanistically.

A straw poll among rodent ecologists would probably find most of them supporting multi-factor hypotheses of regulation and limitation. If this turns out to be the most frequent model for rodents, it raises the multifactor dilemma that it is difficult to deal with more than three factors in any realistic model. There are two possible solutions to this dilemma. First, we can hope that all factors operate independently (hypothesis 1 above), so that if we have four or five significant factors for a particular herbivore, the factors do not interact. Second, we can hope that for systems with interactions only two or at most three factors show interactive effects (hypothesis 2).

The recent history of rodent population studies has been a history of reduced generality, increased precision, and decreased simplicity. Philosophers would be appalled at this, but ecologists should be happy to see us move away from superficial generality and simplicity. The touchstone of our progress must be the management of rodent pests, and we must try to answer this important question:

> how much have our ivory tower studies of rodents in the laboratory and in the field helped us to solve problems of rodent pests?

THREE CURRENT PARADIGMS

There are three current paradigms that represent the dominant focus of work today on small rodent populations.

The food paradigm

The food paradigm states that both the quantity and the quality of food supplies regulate rodent population density. Food supplies also limit the average density of populations, and outbreaks of rodents are caused by changes in their food supplies. The most important thing you need to know, under this paradigm, is what do your rodents eat and how much of it is out there in their habitat. These are themselves complex issues since diets change seasonally and may be affected by an individual's sex and age and also by changes in plant productivity from year to year and season to season. A test of the food paradigm is done most easily by supplementing food supplies artificially, although these experiments themselves can be called into question if the food given is not adequate nutritionally.

The food paradigm cannot be tested as a unit and needs to be applied to specific cases to make predictions that can be falsified. For example, the average abundance of a rodent pest might be higher where more food is available. Ecologists often pyramid hypotheses about food supplies. A recent example is the hypothesis about Lyme disease in eastern United States of America (Ostfeld 1997; Jones et al. 1998): food supplies in the form of acorns from oak trees are postulated to limit the average abundance of deer mice (*Peromyscus maniculatus*), trigger outbreaks of these mice (when acorn crops are heavy), and regulate density through starvation. Boutin (1990) concluded in his review of feeding experiments that, by adding food to terrestrial herbivore populations, one could increase density two to three-fold but not more, so that clearly for some populations food limits density over some restricted range only. Ecologists tend to despair when their favourite explanation does not apply to all species in all situations. We should be more modest in our aims. Food is clearly one of the dominant ecological factors limiting and regulating rodent populations, and the question is which populations and under exactly what conditions.

The predator paradigm

Many things eat rodents and some ecologists look to these trophic links to explain regulation and limitation of populations. The predator paradigm states that mortality caused by predation regulates rodent populations, that generalist predators limit the average density of populations below the limits that might be set by food supplies, and that outbreaks of rodents are caused by predator control activities, artificial or natural. The most important thing you need to know, under this paradigm, is who eats whom in your community. Since this can vary seasonally, and predators are often selective for sex and age groups, obtaining this information with quantitative rigour is not easy.

Paul Errington presented the most serious challenge to the predator paradigm more than 50 years ago by suggesting that predators consumed only the doomed surplus from rodent populations (Errington 1946). This question has been restated more recently as the question of whether predation mortality is *additive* or *compensatory* (e.g. Bartmann et al. 1992). Errington suggested that it was often compensatory. This question can be answered directly by removing predators or indirectly by showing what fraction of mortality is due to predation kills. There are considerable problems with inferring predation limitation from predator kills alone. If territoriality causes dispersal movements, or parasites cause debilitation, or food shortage causes poor condition, predators may be the executioners rather than the primary cause of population changes (Murray et al. 1997).

The usual argument against predation as a regulating factor has been that rodents have such a high rate of reproduction, that it is impossible for predators to kill enough of them (e.g. Chitty 1938, 1996; but see Korpimäki and Norrdahl 1998). It is certainly correct that sufficient numerical and functional responses must be present for predation to be a potential regulator of rodent populations (Hanski and Korpimäki 1995). From a practical viewpoint the key is to manipulate predator numbers. For example, to see if they could reduce crop damage by house mice in Australia, Kay et al. (1994) provided perches in agricultural crops for raptors. The important point is not to be convinced that predators are limiting or regulating numbers just because predators kill many rodents. It is convenient politically to show lots of dead rodents to our political masters, but scientifically dubious to infer from these piles of dead bodies that predators are helping to alleviate pest problems.

The social paradigm

The social structure of a rodent population can affect its ecology. The social paradigm states that social interactions between individuals can lead to changes in physiology and behaviour that reduce births, and increase deaths, and thereby regulate populations. In particular, territoriality may limit the average density of rodent populations. Outbreaks of rodents are postulated in this paradigm to be caused by changes in the social environment (e.g. Krebs et al. 1995). The social paradigm is the least popular of the three paradigms under which population ecologists operate. This is usually because ecologists assume that the social environment is primarily determined by habitat which is highly correlated with food supplies. Thus, for example, food supplies determine territory size and territory size limits population density. The problem is that other factors may influence social behaviour as well, and thus the linkage of habitat to social processes can be very loose.

Practical problems of rat and mouse control had highlighted already by the 1940s that killing of rats and mice often did not result in control, especially when the pests were at high density (Chitty 1954, p. 6; Elton 1954). Achieving controls in rat populations has typically involved intensive large-scale campaigns of killing rats either directly or by poisoning (see Singleton et al., Chapter 8). Only recently has the possibility of using other methods of control like parasites (Singleton and McCallum 1990) or immunocontraception (Caughley et al. 1992; Chambers et al. 1997) been able to be explored.

The social paradigm has highlighted the role of immigration in local population dynamics. Removal experiments on rodents and other small mammals have illustrated the difficulties of controlling rodents by increasing mortality. Figure 2 illustrates one of the first experimental field removal studies on voles. In spite of very high and continuous mortality imposed by removals, the vole population continued to maintain high density and grow via immigration. Sullivan and Sullivan (1986) obtained a similar result for snowshoe hares. After a series of laboratory and field studies it became clear to ecologists that pest species with high turnover (high reproduction, high mortality, short generation times) are most sensitive to reductions in fecundity rather than increases in mortality rates (Figure 3) (Stenseth 1981a; Lebreton and Clobert 1991).

The fence effect (Krebs et al. 1969) is one example of an experimental result that was completely unanticipated by the food or the predator paradigms (Krebs 1996). If fencing a vole population without altering the food supply or the predator fauna could produce a 3–4-fold increase in population density, what role are immigration and emigration playing in population regulation? Lidicker (1962) had raised this question long ago but few rodent workers have responded to analyse this phenomenon (Ostfeld 1994). Unfortunately if you are interested in pest control you do not wish to find a procedure that will increase rodent density! My point is that surprise results that are unexpected under the conventional wisdom can result from ignoring social processes in rodent populations.

I do not wish to argue the merits of the social paradigm here. The important point for those interested in pest control is whether or not it suggests any kinds of manipulations that could reduce pest numbers. To date the major contribution of the social paradigm to rodent pest management has been to show that dispersal and social structure can render useless simple forms of pest control via mortality (e.g. Sullivan and Sullivan 1986).

OPTIMAL POPULATION STUDIES

Given these three paradigms, what ought we to be doing in rodent population studies? We can start by asking what an ideal world of population data would look like. It would have four components.

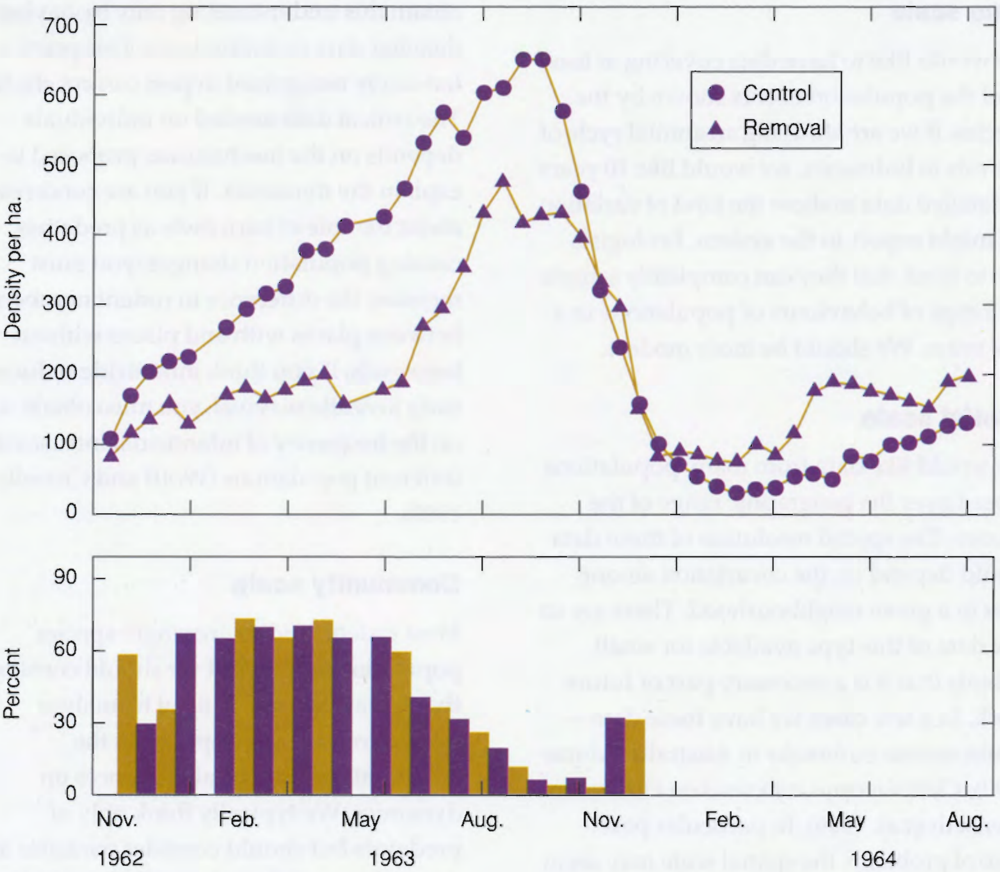

Figure 2.
A removal experiment on the California vole (*Microtus californicus*). All adult voles were removed every two weeks from the removal area of 0.8 ha. From November 1962 to July 1963 an average of 62% of the population was removed every two weeks with little impact on population growth because of immigration (after Krebs 1966).

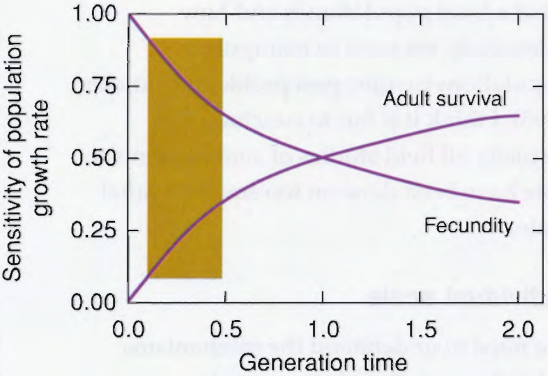

Figure 3.
Relative sensitivity of the population growth rate to survival after weaning and to fecundity for mammal populations. The shaded area is the zone occupied by many rodent pests (modified after Lebreton and Clobert 1991).

Time scale

We would like to have data covering at least 10 of the population events shown by the species. If we are studying an annual cycle of rice rats in Indonesia, we would like 10 years of detailed data to show the kind of variation we might expect in the system. Ecologists like to think that they can completely sample the range of behaviours of populations in a few years. We should be more modest.

Spatial scale

We would like data from many populations spread over the geographic range of the species. The spatial resolution of these data would depend on the covariation among sites in a given neighbourhood. There are so few data of this type available for small rodents that it is a necessary part of future work. In a few cases we have these data—house mouse outbreaks in Australia (Mutze 1990), *Clethrionomys rufocanus* on Hokkaido (Stenseth et al. 1996). In particular pest control problems the spatial scale may seem to be irrelevant, but it is not if we remember that the local spatial scale can also be critical (Stenseth 1981a). The concern about dispersal and population structure has focused attention on the need to find out what a local population is and how extensively we need to manipulate populations to solve pest problems (Lidicker 1995). I think it is fair to conclude that virtually all field studies of small rodents to date have been done on too small a spatial scale.

Individual scale

We need to understand the mechanisms behind population changes, and we can obtain this understanding only by having detailed data on individuals. This point is too rarely recognised in pest control studies. The critical data needed on individuals depends on the mechanisms proposed to explain the dynamics. If you are concerned about the role of barn owls as predators causing population changes, you must measure the difference in rodent numbers between places with and places without barn owls. If you think infanticide reduces early juvenile survival, you must obtain data on the frequency of infanticidal intrusions in different populations (Wolff and Cicirello 1989).

Community scale

Most rodent studies are single-species population studies but we should consider that it may be more fruitful to analyse interactions between species in the community as potential influences on dynamics. We typically think only of predators but should consider parasites and diseases as well (Saitoh and Takahashi 1998). In most pest rodent studies, competition for resources between species is presumed to be minimal and single-species interactions are paramount so that these community interactions can be ignored. Generalist predators are perhaps the most common factor operating on small mammals in which community interactions, including indirect effects (Menge 1997), need to be considered.

WHAT DO WE HAVE ALREADY?

Given this ideal world, we should take stock of what we have already accomplished and then move on to what we are lacking. Three strengths stand out.

- Population ecologists are fortunate in having a set of good quantitative methods for dealing with the arithmetic of population change. From the Leslie matrix to metapopulation models, there is quantitative rigour in abundance. The importance of this is not always appreciated by population ecologists, yet it is one of the great intellectual achievements of this century. We can use this arithmetic to balance the books. If we know the birth rates and death rates of a population (as well as immigration and emigration) we can compute exactly the rate of population increase or decrease. We need to use this more often to check on our estimates of these parameters (e.g. Haydon et al. 1999). For many rodent pests, control through increasing mortality is the only option available. For these cases quantitative demographic models can estimate the mortality required to reduce a population a specified amount in order to plan an optimal control program.
- Second, we have a set of good paradigms for analysing population regulation and limitation. I have outlined these above, and others can be articulated. The importance of being able to articulate clear, testable hypotheses is underappreciated in ecology (Platt 1964; Underwood 1997). Prediction, absolutely essential for scientific respectability, is almost unknown in population ecology (Peters 1991).
- Third, we have good field methods for estimating population parameters to feed into quantitative models and into statistical analysis of our experiments. Population estimation methods have been extensively improved (Pollock et al. 1990), elegant methods for analysing survival rates are available (Lebreton et al. 1993), and statistical methods for analysing reproductive changes and separating immigration from births are being developed (Nichols and Pollock 1990; Nichols et al. 1994). We have the demographic tools to understand rodent populations with a level of precision that was not available 25 years ago.

WHAT ARE WE LACKING?

I address here six problems that I think are central to future studies on rodent populations. They are not in any particular order of importance, since some are more relevant than others to particular situations.

Good methods for spatial dynamics

One of the contributions of the social paradigm to rodent population dynamics has been the stress on the importance of immigration and emigration for understanding population changes. But we still lack good methods for studying the spatial aspects of populations. Radio-telemetry has made it possible to get some data on individual movements, but we are rarely able to do it on a scale that would be sufficient to get a broad picture of landscape dynamics. We know too little about how we should structure our studies of spatial processes. Should we have many small trapping grids or a few very large grids? How large an area should we attempt to study? What fraction of movements that we can document are genetically effective (i.e. the immigrant individual survives, breeds and leaves offspring rather than dies after immigrating)? We have much to learn about just how to study spatial dynamics successfully in rodents, yet spatial processes underlie all of the problems of pest management. If we can reduce rats on one rice farm, will the neighbouring farms be affected or not? Much empirical work needs to be done on these questions. We can model pest populations as metapopulations in space but if we do not know the linkage parameters for these populations, our models will not be very useful.

Long-term experiments on limitation

There are no long term experiments on population limitation in any rodent species. If we feed a population for two years, we often get a population increase (Boutin 1990). What happens if we continue this experiment for 10 years? Is the system in equilibrium after two years so that we will learn nothing more from the longer study? There are numerous examples in ecology of short-term effects that were not sustained or even were reversed in the longer term (Norby et al. 1992; Wilsey 1996). There are also many examples from pest control in which initial encouraging results were followed by failures (DDT resistance, anticoagulants). The message is to be cautious about long-term conclusions.

Good interplay of models and field studies

Many ecologists have lamented the lack of interaction between field ecologists and modellers (e.g. Kareiva 1989). There are signs that this is finally breaking down (Stenseth and Saitoh 1998) but I think it is a failure on both sides that holds back progress. Models can help us to explore the logical consequences of assumptions we make in field experiments, and provide a quantitative estimation of the anticipated effect sizes. I think it is particularly important that rodent pest control studies incorporate both adequate controls and modelling studies as part of their overall approach.

Methods for evaluating weather-driven hypotheses

Climatic change is the wave of the future and we should be more concerned that our understanding of rodent systems will be transient and modified by weather changes. Hypotheses about weather-driven events are difficult to test. Post-hoc correlational studies are useful but inconclusive. They test more the cleverness of the statistician than the reality of the biological cause. We need to state weather hypotheses clearly so they can be tested next year, not last year, and we need to abide by the simple rules of experimental falsification when our predictions fail. Ad hoc explanations are available by the shipload for ecological systems, and we should not get in the habit of using them to bail out our failures of understanding. The exact mechanisms by which weather acts on populations need to be determined, since we need to know whether births or deaths are driving the change.

Economic and environmental analyses of pest control alternatives

This is not my area of specialty but I would like to think that we should aim in pest control work to achieve the best gain for the least cost—both environmental and economic. If we cannot achieve this, e.g. because the lowest economic cost method produces the highest environmental damage, we need to state this clearly so that the public can make an informed decision about alternatives.

Strategies for analysing the pest community of crops

In viewing rodent pests as single-species populations we overlook the broader strategy of looking at the whole community of pests of a particular crop. If the pests are truly independent, we can work on them one by one. But community interactions have ways of producing surprises via indirect effects (Holt 1987; Menge 1995), and we should be preemptive in looking for these possibilities.

CONCLUSION

The ivory tower of basic research studies on rodents has contributed little to the practical successes of rodent pest management, either short or long term. Much more insight has flowed in the opposite direction, and our understanding of rodent dynamics has been greatly improved by the practical studies of rodent pest control. What basic ecology can contribute to pest management is in the methods of study needed. The need for clear hypotheses, rigorous experimental tests based on good knowledge of natural history, a sceptical view of existing ideas, and the need to measure our successes and failures—all of these features of good science should be part and parcel of rodent management.

The major deficiencies of rodent population studies as we move into the new millennium are three. We need to apply the insights of theoretical ecology, behavioural ecology, physiology, and genetics to rodent pest problems. A promising start in this direction is immunocontraception, (Chambers et al. 1997; Chambers et al., Chapter 10). We need studies of tropical species in varied tropical environments, since much of our knowledge of rodent ecology comes from the Temperate Zone (c.f. Leirs et al. 1996). Finally, we need more studies of parasites and diseases in field populations. Conventional wisdom suggests that they are of little impact on highly fecund rodents, but their potential for biological control is largely untested (c.f. Singleton and McCallum 1990). There are many experiments waiting to be done and much promising modelling ahead with the goal of understanding population processes in rodents and at the same time alleviating the suffering caused by rodent pests around the world.

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3. The Behaviour and Ecology of *Rattus norvegicus*: from Opportunism to Kamikaze Tendencies

David W. Macdonald, Fiona Mathews and Manuel Berdoy

Abstract

While rat population management is clearly possible in the absence of a knowledge of rat biology, we aim to show in this review how control is likely to prove more effective if woven into a robust framework of understanding. For example, rats have flexible population dynamics and can delay the onset of fertility in times of food shortage. Detailed observations have demonstrated the presence of stable, near-linear dominance hierarchies, where male social status tends to be age-related. We discuss how the success of poisoning strategies are crucially dependent on the foraging decisions which are made against this background of dominance hierarchies and competition for mates. Feeding patterns also can be altered in order to avoid predators. Rats are notoriously neophobic, and poor bait uptake is one of the main reasons that control strategies fail. Our review highlights the importance of social cues and *Toxoplasma gondii* infection in the modulation of neophobic responses. The potential impact of ill-planned rat control operations on the spread of zoonotic diseases is also considered. Finally, we discuss the development of behavioural and physiological resistance by rats in the face of continued poisoning pressure, and the apparent evolution of a new type of resistance which benefits the rat even in the absence of poison.

Keywords

Rattus norvegicus, rats, behaviour, society, neophobia, resistance, disease

INTRODUCTION

EXPLOSIVE DEMOGRAPHY, adaptable ecology and opportunistic behaviour are capacities that cause rats to rank high amongst those mammals that have most affected the course of human history. Today rats exact an immense toll on society worldwide, whether through the costs of prophylactic or remedial control, or through disease transmission and damage to crops and stored food. Throughout Southeast Asia, for example, pre-harvest damage caused by the rice-field rat, *Rattus argentiventer*, is reckoned to reduce crop yields by 17%, a figure which translates into the squandered rice requirements of in the order of 20 million people (Singleton 1997). Such losses may also have indirect environmental costs; lower yields forcing larger areas into production and accelerating the cultivation of wilderness with consequent threats to biodiversity. More directly, rats threaten the survival of endemic fauna on a number of islands, from the Galapagos to Guam (e.g. Amarasekare 1993; Robertson et al. 1994; Cree et al. 1995); alien species are, second only to habitat loss, the greatest contemporary force for extinction. Finally, the enormity of the threat posed to humanity by rat-borne disease is heightened in the context of our huge populations, rapid transportation and antibiotic resistance. Amongst the emerging infectious diseases, the viral haemorrhagic fevers and Lassa fevers add to the already lengthy list of blights which can be transmitted by rodents. The 200,000 cases of haemorrhagic fever with renal syndrome diagnosed annually in Asia is doubtless just the tip of an epizootiological iceberg. These threats are not confined to the developing world: the 1973 wave of deaths through hantavirus with pulmonary syndrome amongst healthy young Americans led to the discovery of hantavirus in the deer mouse, *Peromyscus maniculatus* (Childs et al. 1987). Hantavirus infection has also been discovered in Norway rats in rural Britain (Webster and Macdonald 1995a).

Amongst the diversity of problems caused by rodents, the Norway rat (*Rattus norvegicus*), ranks high amongst the miscreant species. Originally from Southeast Asia, the Norway rat's versatility rivals mankind's and our two species have, in company, spread around the globe. Trawling bibliographic indices reveals that some 24,000 technical publications refer annually to *R. norvegicus* (Berdoy and Macdonald 1991). This stunning total is, however, neither a fitting tribute to the fascination of its adaptability nor recognition of the enormity of its pest status; rather it stems largely from the utility of its domestic form as a model for studies ranging from biochemistry to experimental psychology. Publications on wild-type Norway rats largely concern toxicological studies of candidate poisons, while the behaviour and ecology of the species in the wild—which is where it actually does damage—account for scarcely a handful of those 24,000 publications annually. Indeed, as we shall show, while a little is known of the ecology of wild rats in farmscapes and a few cities in a smattering of developed countries, they are perversely unstudied where they impact the most. Most startling of all, effectively nothing is known of the biology of the sewer-dwelling rat.

Our objective in this chapter is to review the behavioural ecology of wild rats, largely within the context of our own team's findings. Our contention is that while rat control is manifestly possible in the absence of much knowledge of rat biology, it is likely to be much more effective if woven into a robust framework of understanding. This proposition rests on the oft-proven wisdom of the maxim: 'know thyn enemy'. In particular, our aim is to reveal that seemingly disjunct, and perhaps even rarefied, research topics, such as dispersal, social status, feeding patterns and disease transmission are actually inextricably linked in formulating a biological basis for rat management.

POPULATIONS, DEMOGRAPHY AND DISPERSAL

Questions about the population biology of Norway rats were at the forefront of mammalian ecology in post-war years, thanks to the pioneering work by Elton and Chitty (Chitty 1954) and Davies (1949). Considering the enormity of the rat's agronomic and public health impact, it is remarkable that the momentum of these early investigations was soon dissipated.

Numerous studies on farmland (Errington 1935; Aisenstadt 1945; Emlen et al. 1948; Zapletal 1964; Hartley and Bishop 1979; Brodie 1981; Huson and Rennison 1981; Homolka 1983) in differing temperate climates indicate that hedges and fields are generally a marginal habitat for rats, except when crops are available as food. Middleton (1954) noted that all rat infestations in hedgerows at his study site in Berkshire (United Kingdom) were either short-lived or were associated with rat colonies in corn-ricks or field-barns. He suggested that scattered field colonies were themselves ephemeral, but were probably the main reservoirs from which infestation of farm buildings occurred in the autumn and winter.

Colonists tend to be rats that are approaching, or have recently achieved, sexual maturity (Zapletal 1964). Telle (1966) found that most colonists weighed between 160–250 g, while Farhang-Azad and Southwick (1979) reported a mean weight of 190 g for 26 rats collected from newly recolonised burrows. Both concluded that emigrants are mainly young animals, but neither reported the sex of new colonists. However, Bishop and Hartley (1976) found approximately twice as many 'new' adult males as females entering their hedgerow population. Similarly, Calhoun (1962) reported that more males than females were ejected, or at least departed, from more socially stable colonies. Kendall (1984) and Leslie et al. (1952) found that the sex ratio of rats in environments where they breed tended to be biased towards females.

Rat population dynamics, and thus the success of control operations, are intimately linked with the availability of food supplies. In the simplest case, bait uptake is most likely when other sources of food are unavailable. However, we have found that food supply, and other environmental factors, also produce concomitant changes in behavioural and reproductive ecology (D.W. Macdonald and M.G.P. Fenn, unpublished data). These changes in turn may be of fundamental importance to rat population size and to control efforts. We live-trapped and radio-tracked rats in three contrasting United Kingdom farmland habitats, all of which were surrounded by winter wheat: (i) a resource-rich agricultural tip; (ii) a woodland where grain was intermittently provided for pheasants; and (iii) an adjacent, resource-poor stream bank. Several salient findings emerge. First, and unsurprisingly, more rats occurred at the farm rubbish tip, where food was most abundant, and fewest along a stream where it was most scarce (Figure 1). Second, numbers varied at each site: in general, there was a cycle in rat abundance corresponding to seasonal changes in breeding activity—pregnant females were generally captured from March until October, and peak numbers of juveniles were found between November and December (see also Davies and Hall 1951; Farhang-Azad and Southwick 1979, who report a bimodal pregnancy rate, with highs in spring and late summer). There is also evidence that reproduction ceases in cold winters (Leslie et al. 1952; Andrews et al. 1972; Lattanzio and Chapman 1980). However, in our study (D.W. Macdonald and M.G.P. Fenn, unpublished data) breeding activity was not simply a function of season but also depended on food

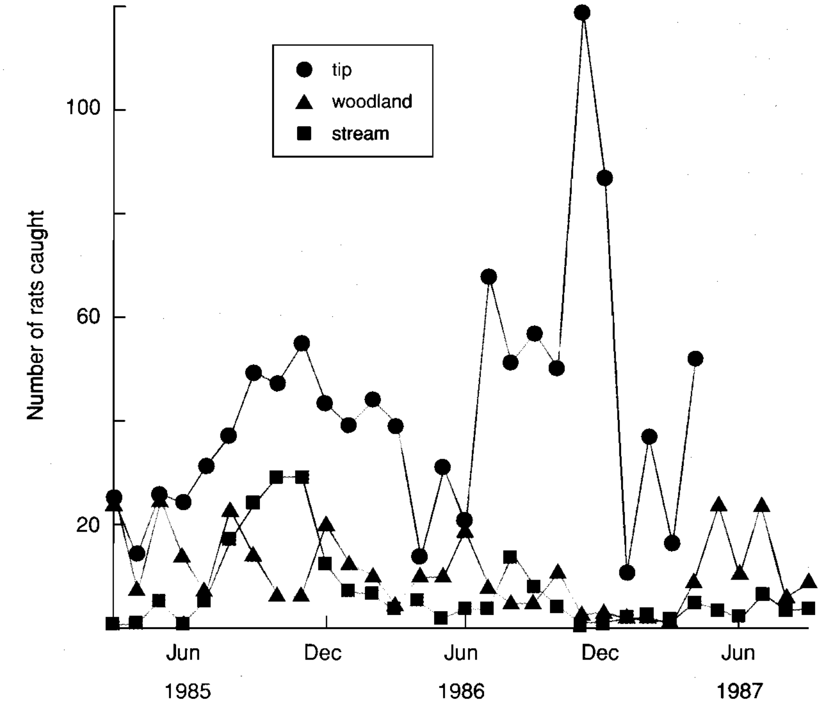

Figure 1.
Variation in rat abundance across time in three habitats with different food resources. The figure illustrates that more rats were captured in the resource-rich environment of the tip than in the woodland (moderate food availability) or stream (poor availability of resources). Cyclical fluctuations in abundance were also more marked in the resource-rich environment (D.W. Macdonald and M.G.P. Fenn, unpublished data).

availability. In the woodland site, winter breeding was stimulated by the provision of grain in January for the pheasants, with peak numbers of juvenile rats occurring in the population approximately three months later, in March and April.

Fertility in both sexes was affected by season. Using perforation as a measure of attainment of sexual maturity, the median weight of females at perforation at the rubbish-tip site was higher in the summer sample than the winter one. Fertility in males was also modulated by season and food supply, with evidence for delayed onset of sexual maturity and facultative cessation of spermatogenesis where food was scarce. For example, males achieved a greater weight before their testes became scrotal in winter than was the case in summer. Similarly, those animals living in the relatively poor environment of the stream delayed sexual maturity until they had achieved a greater weight than their counterparts in more productive habitats (Figure 2) (D.W. Macdonald and M.G.P. Fenn, unpublished data). Indeed, it was not unusual for males weighing more than 300 g to have abdominal testes [the median weight of rats with scrotal testes reported elsewhere was 136 g in rural rats (Davies 1949) and 145 g in rats living around Baltimore zoo (Farhang-Azad and Southwick 1979)]. Clearly, the control of food availability may have an important role in maintaining rat populations at manageable levels.

Movements

Farmland rats may either occupy stable home ranges or travel widely as transients. Hartley and Bishop (1979) estimated that three-quarters of rats fell in the former category and therefore were unlikely to have access to bait points positioned outside their home ranges. Within the home range, rats regularly retreat to rest sites (Orians and Pearson 1979; Galef 1988), which in arable areas tend to be located in hedge bottoms and banks (Brodie 1981).

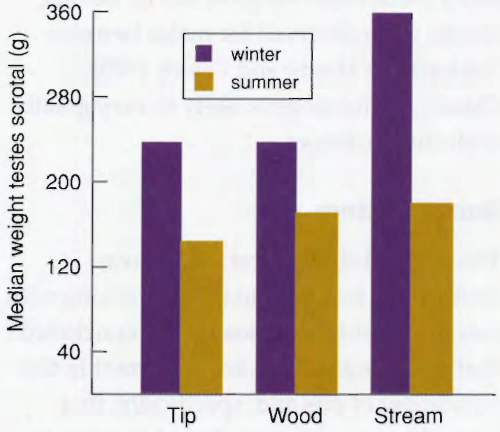

Figure 2.
Median weight at which testes became scrotal in winter and in summer at sites which differed in resource availability (tip = resource rich, wood = moderate, stream = poor). The figure illustrates that males achieved sexual maturity at lower weights in summer than in winter, and also in resource-rich environments ($p < 0.05$ for seasonal differences, $p < 0.001$ for resource differences) (D. W. Macdonald and M.G.P Fenn, unpublished data).

We radio-tracked rats in and around farms (Fenn et al. 1987; Macdonald and Fenn 1995). Males ranged widely through the fields when crop cover was available to provide protection from predators [mean linear home range = 678 m, standard deviation (SD) = 535]. However, their ranges contracted after harvest (90 m, SD = 28.2). This effect appeared not to apply to females,