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**THE MANAGEMENT OF RODENTS IN NORTH
QUEENSLAND CANEFIELDS**

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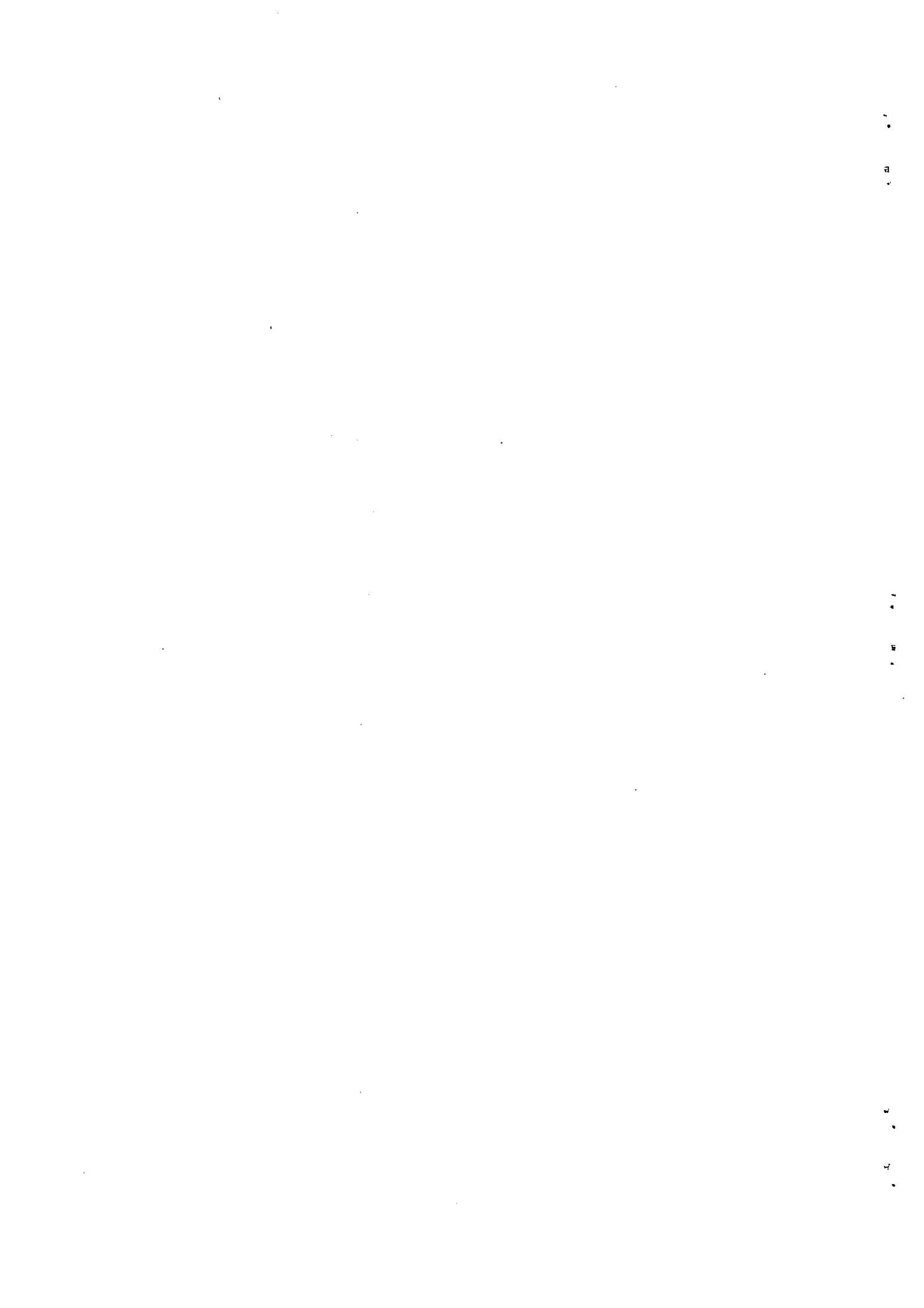
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PROJECT OVERVIEW

1.1 THE PROBLEM

Rodent damage to sugarcane has been of concern to the Australian sugar industry since the 1930's. In more recent times, annual surveys have indicated that damage by rodents occurs over approximately 50% (150 000 ha) of sugar producing areas resulting in annual losses of between two and four million dollars. A further \$0.6 million is expended on annual baiting programs. Rodents are therefore the second most important pest of the Australian sugar industry, the most important pest being the cane grub (Bureau of Sugar Experiment Stations Annual Reports 1984 - 1989).

On a regional basis, losses and associated control costs can be calculated from damage surveys conducted by the Mackay Cane Pest and Disease Control Board over the 1984 - 1986 period (Table 1.1).

Table 1.1

Summary of rodent baiting campaign costs and rodent-induced
crop losses at Mackay, 1984-1986

Year	Aerial baiting details ¹		Calculated crop losses ²	
	Hectares baited	Cost (\$A,000)	Tonnes sugar	Net value (\$A,000)
1984	22700	66	12900	1834
1985	37360	108	2600	308
1986	37140	130	4114	740

1 Collated from BSES Annual Reports 1984 - 1986.

2 Values calculated in \$A, using relevant market price for sugar less official estimated harvest costs and charges.

These estimates demonstrate the economic impact of rodents at the regional level but do not necessarily represent the extreme case. Northern regions regularly record stalk damage rates significantly higher than those occurring in the Mackay district (BSES Annual Reports 1984 - 1989).

Economic impact results from both a decrease in the yield of cane and a loss of sugar content. Although only one or two internodes of a stalk may be directly damaged by rodents, the sugar content can be reduced by 15% to 29% as a result of secondary damage by bacteria and fungi (Taylor 1972; Jackson 1977; Hampson 1982).

Cost-effectiveness is the ultimate test of any control strategy as control practices represent a cost to the industry that must be balanced by a benefit to production. Factors influencing the cost-effectiveness of rodent control programs in sugarcane crops include:

- . The severity of overall damage in a region;
- . The effectiveness of the control program;
- . The cost of the control program;
- . The current market value of sugar.

The influence of some of these factors on the likely cost-effectiveness of current rodent baiting campaigns at Mackay are illustrated in Table 1.2.

To be cost-effective, any control strategy must be able to provide answers to three questions:

- . What will be the overall level of damage within a district?

How will damage be distributed throughout a district?

What are the most effective methods to tackle the specific problems of a particular year?

Table 1.2

Estimated costs and monetary returns of a rodent-baiting campaign in sugarcane, using actual data from Mackay, 1984-1986

Year	% damaged stalks	Net return \$A/tonne sugar ¹	Baiting costs ² (\$A,000)	Estimated benefit (\$A,000) from damage reduction of			
				10%	20%	30%	40%
1984	16.0	142.2	190	204	459	786	1223
1985	3.4	118.5	190	34	77	132	205
1986	4.6	179.9	234	82	185	317	493

1 Values calculated in \$A, using relevant market price for sugar less official estimated harvest costs and charges.

2 Calculated cost of baiting the total Mackay crop of 65 000 ha based pro-rata on actual costs shown in Table 1.

The answers to these questions must be known well in advance of the occurrence of the problem. The high reproductive capacity of rodents dictates that it is more efficient to prevent the problem from occurring, than to commence control measures after the problem has arisen and damage has started to occur.

A reliable estimate of potential crop damage is essential if rational decisions are to be made regarding the extent of a control program. A system designed to provide early warning of potential crop damage must therefore form an integral part of any control strategy. If the timing, location and

intensity of rodent outbreaks can be predicted with adequate accuracy well in advance of the occurrence of damage, the most cost-effective prevention methods can be implemented.

1.2 THE SPECIES

Two Australian native rodent species are responsible for damage to cane (McDougall 1946a,b; Hitchcock 1973; Redhead 1973; Watts and Aslin 1981):

Rattus sordidus (Gould), the canefield rat;

Melomys burtoni (Ramsay), the climbing rat.

Some industry sources have assumed that damage caused by *R. sordidus* is of greater industry significance than that caused by the canefield rat (Bureau of Sugar Experiment Stations *pers comm*). In part, this view has arisen because damage due to the climbing rat occurs higher on the cane stalks and is more visible to the casual observer.

Trapping and damage surveys undertaken by the Bureau of Sugar Experiment Stations (BSES) and the Cane Pest and Disease Control Boards throughout the sugar-growing districts of North Queensland have shown that *R. sordidus* is the major cause of damage (greater than 90%) in areas south of the Herbert River district (BSES Annual Reports 1984 - 1989).

These trapping and damage surveys have indicated that *R. sordidus* is also responsible for a large proportion of the damage inflicted in the flat, extensive canegrowing areas to the north of the Herbert River district. The climbing rat is the major offender in the highly dissected, narrow valleys of

the more northerly areas where many canefields are adjacent to densely forested areas or vegetated creek banks.

Approximately 75% of land assigned to canegrowing is in areas where the canefield rat is responsible for over 90% of total rodent damage. Therefore, damage caused by this species is of far greater economic significance to the sugar industry than damage caused by the climbing rat.

R. sordidus is a grassland animal that favours areas with close ground cover and friable soil. Favoured habitats include grasslands, grassy fringes of forests, open forests bordering closed forests and the edges of swamps and watercourses (McDougall 1944a,b; Taylor and Horner 1973; Lavery and Grimes 1974). Plantations of cane closely resemble the preferred native habitat, providing good ground cover and friable soil able to support the extensive burrow networks constructed by this colonial species (Watts and Aslin 1981).

In its native habitat, the diet of *R. sordidus* consists mainly of grasses together with small amounts of seed and insects (Watts and Aslin 1981). In sugarcane growing regions it has extended its diet to include sugarcane (Harrison 1962; Woods 1966).

This species has one of the highest reproductive potentials of any native *Rattus* species. The oestrus cycle is six days and the gestation period is about 22 days. Average litter size is six and the young are independent at 18 days of age. Females are capable of having their first litter when they are approximately 65 days old (McDougall 1946a,b; Taylor and Horner 1973; Breed 1978).

1.3 CURRENT CONTROL PROCEDURES

The current method of control relies entirely on the widespread aerial application of packeted thallium sulphate (0.3% thallium sulphate on a grain substrate). Trials in the Herbert River District (Hitchcock 1973; Hitchcock and Kerkwyk 1975; Redhead 1973) have shown that although this procedure can significantly reduce the incidence of rat-bitten stalks, results are extremely variable and success depends on:

- . The severity of the rodent infestation;
- . The timing of the control procedure.

Major limitations of the current procedure include:

- . Aerial distribution is non-selective and therefore costly, with baits being applied at the same rate regardless of the level of infestation. Normally, rodent damage within a district is patchy;
- . Thallium treated wheat is unpalatable to *R. sordidus* during the breeding season and therefore baiting must be delayed until the end of the breeding season. At this stage, population levels are high and damage has started to occur (Bureau of Sugar Experiment Stations *pers comm*);
- . Following baiting, invasion from non-crop habitats results in the rapid recovery of crop populations (Redhead and Saunders 1980);
- . In its present form, the thallium sulphate baits are accessible to a wide range of non-target species.

The timing of baiting programs is critical to their success. A simple simulation based on the following characteristics:

- . Sex ratio 1:1 (McDougall 1946a; Redhead 1973);
- . Survival per month 0.5 (assumed - no data available);
- . Embryos per female 5.6 (McDougall 1946a);
- . Pregnancy rate 0.35 in months 1 to 6, zero in months 7 to 12 (McDougall 1946a; Taylor and Horner 1973);
- . Linear relationship between population size and damage (assumed - no data available);

shows that without control, the population initially increases exponentially due to breeding (Figure 1.1).

During the increase phase, a population level is reached where damage first becomes apparent in the field. In the absence of control, the population then starts to decline as breeding has ceased but mortality continues (Figure 1.1(a)). Early in the cycle, cumulative damage increases with population size and then asymptotes as population size decreases.

If a successful baiting program (80% mortality) is implemented when the population is at its peak, the control program achieves little over what was about to happen in the normal course of events. In this situation it is possible to believe that the control procedure has been successful and that the expenditure has been justified, when actually no major change in either population trajectory or cumulative damage has occurred (Figure 1.1(a)).

If the same control procedure were to be implemented at the first appearance of crop damage (Figure 1.1(b)) the level of damage would be reduced. Unfortunately, any delay in implementing the control procedure would quickly cause the situation to revert to that of Figure 1.1(a).

A simulation of the effect of baiting on populations of *Sigmodon hispidus* (Montague *et al* 1990) showed a similar relationship between the timing of the control procedure and its effectiveness.

Despite baiting programs at Mackay during 1984 - 1986, significant rodent damage still occurred (Table 1.2).

1.4 AN ALTERNATIVE APPROACH TO CONTROL

An alternative approach to control involves predicting population levels well in advance of crop damage and implementing cost-efficient responses when and where necessary. These responses may include:

- . Reducing the extent of breeding;
- . Reducing the potential for crop colonisation and establishment;
- . Applying additional control (bait treatment) to specific areas.

Regular monitoring of population levels could allow the potential for damage to be assessed well in advance of the problem occurring. In turn, this would allow a response to be initiated before damage was apparent. In this case, the population would attain peak density after the control program was implemented as the population would still be in the active increase phase and surviving animals would still breed. However, population levels would be substantially reduced.

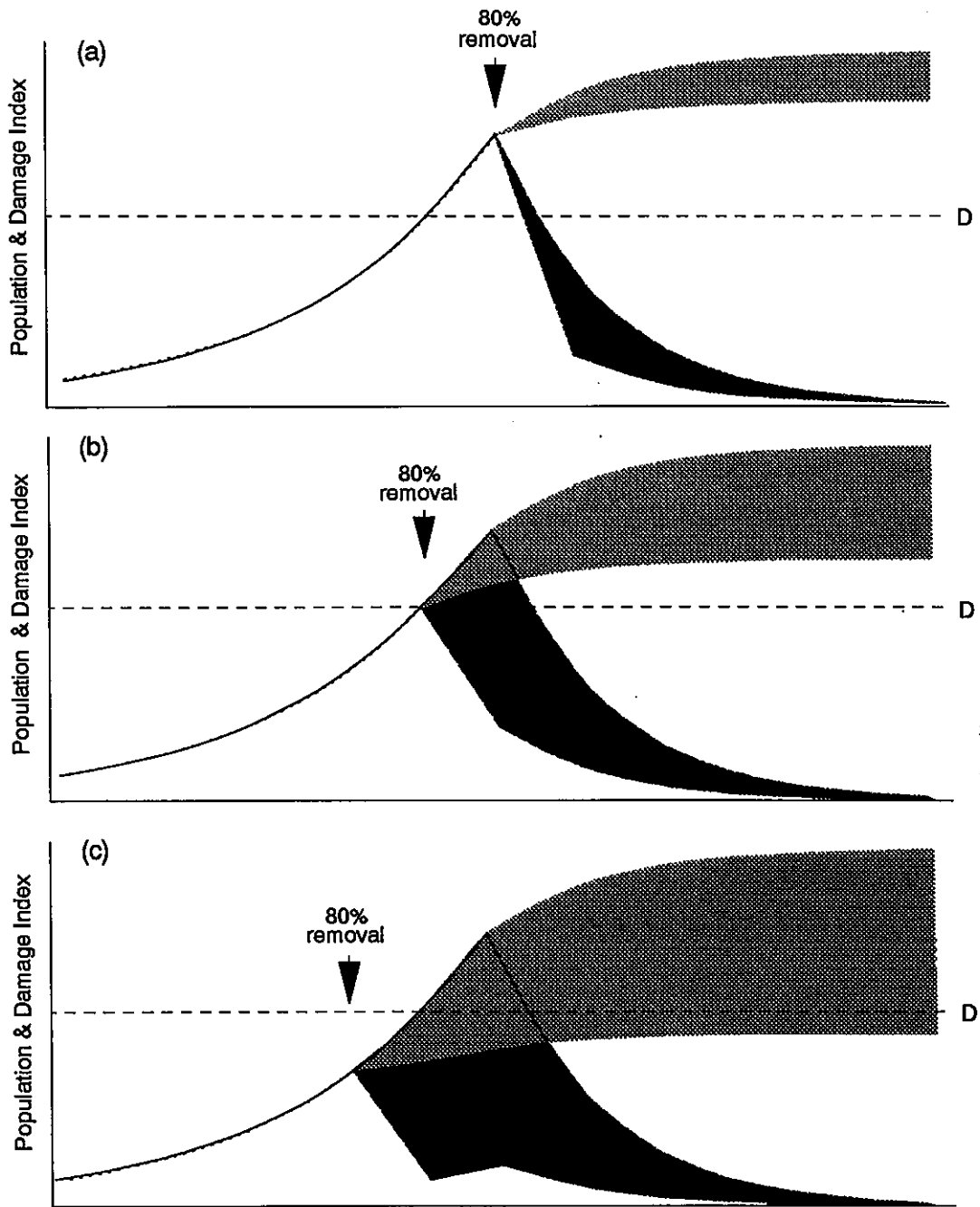


Figure 1.1 Simulated growth of a rodent population with removal at a) peak density; b) when significant damage is first observed; and c) in anticipation of significant damage.



Change in population trajectory due to control procedure.



Change in cumulative damage trajectory due to control procedure.

D represents the population level at which significant damage is first observed.

If the success of breeding and the potential for crop colonisation could be reduced by modifying the habitat to remove factors that are necessary for high breeding success and (b) reduce the size of non-crop populations that form the basis of future colonising populations, then the population would be suppressed and crop damage significantly reduced.

If these methods result in the population being reduced by the same amount as in the previous simulation (80%), but two to three months earlier (Figure 1.1(c)), the population would be reduced during the early stages of the breeding season. In this case, the population would not reach a critical size and crop damage would not be significant.

This alternative approach is an integrated control strategy combining both biological and chemical methods in an orderly sequence, based on an understanding of the population cycle of the target species.

1.5 OBJECTIVES

Given the philosophy outlined above, the objectives of this study are:

- . To provide an understanding of the population cycle of *R. sordidus* in sugarcane growing areas;
- . To identify critical organism - organism and/or organism - environment interactions that give rise to the high reproductive success of this species and, if possible, manipulate the environment to reduce breeding success;
- . To identify those landscape factors that determine the spatial distribution of rodent damage within a district;

If possible, to integrate the above studies into a practical, cost-effective and environmentally-acceptable management strategy for the control of rodents in sugarcane-growing areas.

Each of these objectives is addressed in a subsequent chapter of this report.

Obviously, the first objective is critical to the development of the others as it provides the ecological framework within which to evaluate both the problem and the solution. It is only with a thorough understanding of the population ecology of the animal that effective control may be achieved.

1.6 THE STUDY AREA

The Herbert River district, centred on Ingham, North Queensland (Figure 1.2) and covering an area of approximately 2700 km² was selected as the primary location for this study for the following reasons:

- . The presence of all major non-crop habitats that occur throughout the northern sugarcane growing areas;
- . A history of substantial, widespread rodent activity;
- . A diversity of agricultural practices that are representative of the practices followed in most sugarcane growing areas.

The Mackay District was chosen as the secondary location for the study because it possesses all of the above characteristics and is geographically isolated from the primary location (Figure 1.2).

Studies undertaken in the primary location were designed to determine the

significant organism/organism and organism/environment interactions that regulate the damage process. The secondary location was then used to provide independent validation of the importance of these interactions.

The two phase approach of (a) determining the processes responsible for damage and then (b) providing validation of the importance of the processes independently in a geographically isolated area was chosen to ensure that the results from the study do not simply relate to local populations but that they are applicable to populations throughout the sugarcane growing areas.

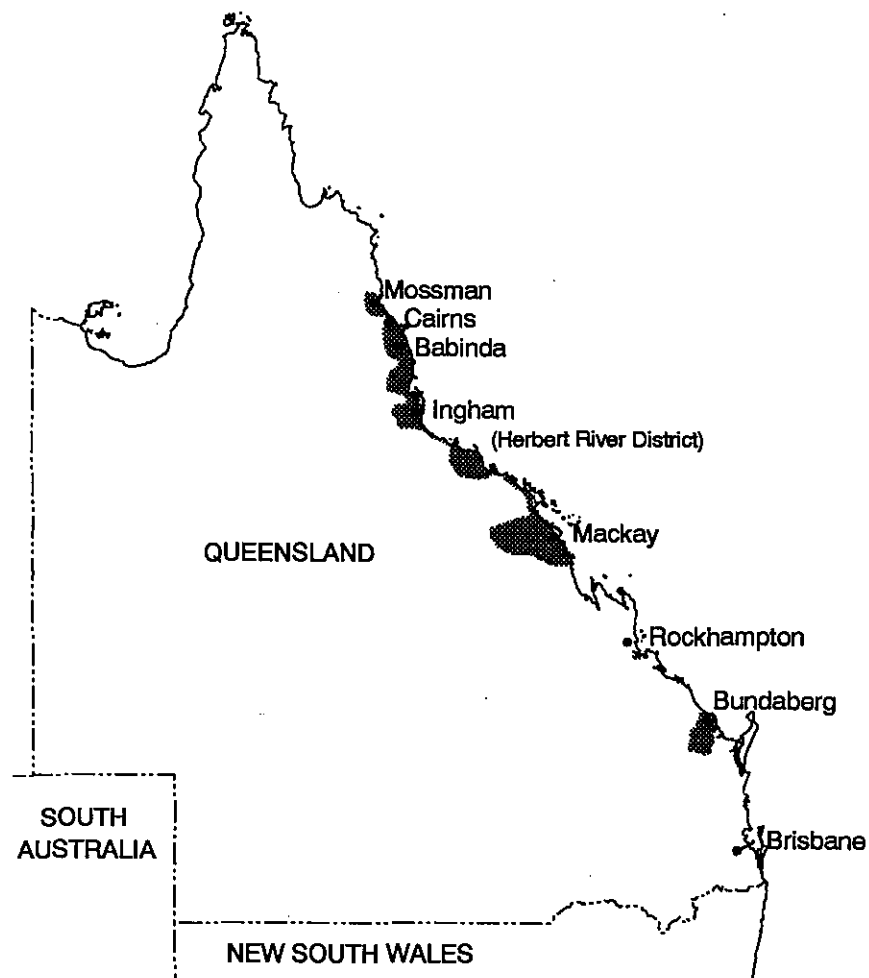


Figure 1.2 Map of Queensland showing sugarcane growing areas and location of study areas

 Sugarcane

RODENTS AS AGRICULTURAL PESTS

Many rodent populations are characterised by large fluctuations in density, the amplitude of these fluctuations depending on the species, environmental conditions and habitat quality. As man pursues more intensive and innovative agricultural practices, a host of new habitats have been made available to rodents (Drummond 1970). The planting of large monocultures has in many cases, resulted in a magnification of the normal population fluctuations to an extent where some species have become agricultural pests (Hampson 1982).

The murid rodents are the least specialised and consequently the most adaptable of rodents and it is mainly members of this group that have been favoured by the development of agricultural habitats. Polyoestrus breeding, early sexual maturity, a short gestation period and large litter size allow the population to respond rapidly to a favourable environmental change giving rise to what appears to be a "spontaneous" plague (Taylor and Horner 1973).

This life history strategy has allowed rodents to become a domestic and commercial problem of worldwide significance (Taylor 1972; Sanchez 1976; Jackson 1977; Wood and Liau 1978; Hampson 1982; Elias 1988; Fiedler 1988). In some developing countries, rodent damage has resulted in localised famine (Taylor 1972) or losses to vital export income (Sanchez 1976). Crops susceptible to rodent damage include sugarcane, coconuts, rice, cereals (including wheat, barley, maize and sorghum), cocoa, oil-palms, nut crops and occasionally tea and coffee (Taylor 1972). In addition to direct crop losses, rodents are often responsible for structural damage and may also constitute a significant public health risk as they are known vectors for more than twenty disease organisms (Sanchez 1976). These secondary effects of rodent infestation are rarely included in cost estimates

even though they may be of greater economic significance than the direct crop loss and so estimates of the actual cost of rodent damage are usually imprecise and conservative (Hampson 1982).

2.1 THE AUSTRALIAN SITUATION

In Australia, plagues of rodents have a long history and are still continuing (Plomley 1970). Four rodent species are responsible for the majority of crop damage in Australian agricultural systems, namely: *Rattus villosissimus* (the long-haired rat), *Mus domesticus*, (the house mouse), *Melomys burtoni* (the climbing rat) and *Rattus sordidus* (the canefield rat). Plagues of *R. villosissimus* have caused considerable damage to crops in Western Queensland and the Barkley Tablelands (Carstairs 1976). The house mouse is responsible for extensive damage to cereal crops in the Darling Downs region of Queensland (Williams *et al* 1978) and in the cereal growing areas of Victoria, New South Wales and South Australia (Newsome 1969 a,b; Saunders and Giles 1977; Redhead 1988; Mutze 1989; Singleton 1989). *M. burtoni* and *R. sordidus* are the major pest species in North Queensland where they are responsible for extensive damage to sugarcane (Gard 1935; McDougall 1944a; Redhead 1968, 1973, 1980). Redhead (1973) considered *M. burtoni* to be the major pest of the highly dissected sugarcane growing areas in the Cairns/Babinda area whilst McDougall (1944a) and Hitchcock (1973) showed that *R. sordidus* was the major pest south of this region.

2.2 RODENTS IN SUGARCANE

Sugarcane is particularly susceptible to rodent attack. The mature crop provides good cover, is a readily available food source and is grown as a large monoculture, providing rodents with a hitherto unavailable area of favourable habitat (Hampson 1982). Losses of 10% to 30% of the potential

yield are common and result from both a decrease in the yield of cane and loss of sugar content. Even though only one or two internodes of a particular stalk may be damaged, the sugar content may be reduced by 15% - 20% as a result of secondary damage by bacteria and fungi (Taylor 1972; Jackson 1977; Hampson 1982). Assuming a sugar price of \$0.32/kg (average from 1977 to 1981) and a 3% loss due to rodent damage, Hampson (1982) estimated the worldwide loss of sugar to be as high as \$518 million per year. This represents an average loss of \$40 per hectare of sugar grown.

Early interest in *R. sordidus* as a pest of Australian sugarcane centred on the role of the animal in the transmission of leptospirosis (Weil's disease) (Sawers 1938). The extent of rodent infestations in sugarcane and their economic impact on the Australian sugar industry was not fully realised until McDougall (1944a,b; 1946a,b; 1947) provided information on the biology of the pest species. In an attempt to reduce the economic impact of rodent damage, most research to date has concentrated on developing control strategies based on the use of rodenticides (Hitchcock 1973; Hitchcock and Kerkwyk 1975, 1978; Hitchcock, Kerkwyk and Hetherington 1983). The extensive biological study of Redhead (1973) was the exception. This study concentrated on *M. burtoni*, the species causing the most obvious damage in the far northern sugarcane growing regions.

R. sordidus is a native rodent with a predominantly coastal distribution in Queensland and northern New South Wales. It is most common in sugarcane growing areas north of Bundaberg although specimens have been collected in north eastern New South Wales (Keith 1976).

It is a grassland animal, favouring areas of friable soil with medium to dense groundcover of grasses and/or sedges. It rarely occurs in closed forests except where breaks in the canopy allow sufficient light to penetrate

for a cover of grass to establish. Favoured habitats include the grassy fringes of closed forests, open forests and the grassed edges of swamps and watercourses (McDougall 1944b; Taylor and Horner 1973; Lavery and Grimes 1974).

R. sordidus constructs extensive burrows five to ten centimetres in diameter, often sloping downwards to a nest chamber about fifteen centimetres in diameter. It is a colonial species and networks of runways are formed between burrow entrances. Burrow systems are usually less than 40 centimetres below the surface (McDougall 1944b).

Plantations of sugarcane closely resemble the natural habitat of *R. sordidus*, providing good cover and a readily accessible food source (Hampson 1982). Woods (1966) found *R. sordidus* to be more prevalent in cultivation than in adjacent grasslands, eucalypt forests and closed forests. Taylor and Horner (1973) also recorded higher trap successes in sugarcane than in adjacent natural habitats.

In its native habitat, the diet of *R. sordidus* consists mainly of grasses and includes a small quantity of seeds and insects (Taylor and Horner 1973; Watts 1977). In sugarcane growing areas, it has extended its diet to include sugarcane (Harrison 1962). The utilisation of sugarcane as a food source varies throughout the year. Woods (1966) found that non-cane vegetation predominated in stomach contents over the November - March period whereas sugarcane was the major food source for the remainder of the year. No attempt was made to correlate the change in diet to the population cycle.

Most of the information on the reproductive biology of *R. sordidus* has come from studies of captive populations (Table 1.1).

These reproductive characteristics place *R. sordidus* in a group of species that possesses the highest reproductive potential of any native Australian *Rattus* species (McDougall 1946a; Taylor and Horner 1973; Breed 1978).

Table 2.1

Characteristics of the reproductive biology of <i>R. sordidus</i>	
Mammary formula	3,3=12 _a
Vaginal perforation	37 days _b
First oestrus ¹	63-70 days _b
Length of oestrus cycle	4.3 _b , 6.0 _c days
Post-partum oestrus	Yes _{b,c}
Gestation period	20-27 days _{b,c}
Mean litter size	6 _b , 7.5 _d , 5 _e
Range of litter size	3 to 14 _{b,d}
Minimum period between litters	21 days _b
Number of litters per year ²	10 _b
Number of litters per lifespan ²	25 _b
Number of young/litter reared to weaning ²	8+ _b
First descent of testes ³	65-70 days _b

a Thomas (1923)

b McDougall (1946a)

c Taylor and Horner (1973)

d Sawers (1938)

e Gard (1935)

- 1 at an average body weight of 50-55g
- 2 based on incidental observations of an unspecified number of individuals
- 3 testes normally ascend during winter without undue loss of fertility and descend with the onset of warmer weather in spring

Although rodent control has been of concern for many years, most control programs are still applied in a haphazard manner and result only in a temporary reduction of population size. Ideally, the objective of a control

program should be to lower the overall carrying capacity of an area and thereby provide a more permanent solution to the problem (Stenseth 1981; Davis and Jackson 1982). It follows that a thorough understanding of the mechanisms that regulate population processes is essential to the effective control of rodents in agricultural systems.

2.3 REGULATING MECHANISMS IN SMALL MAMMAL POPULATIONS

The regulation of small mammal populations depends on feedback mechanisms that involve the three main population processes - reproduction, survival and colonisation/dispersal. These mechanisms can include both organism-organism and organism-environment interactions, resulting in an enormous diversity and complexity of regulating mechanisms. It is not surprising therefore, that many authors concentrate on specific population processes or interactions when attempting to describe the mechanisms that regulate small mammal populations.

Many small mammal populations exhibit seasonal variability in both the intensity and duration of breeding periods and a host of factors have been implicated in the control of reproductive processes. Photoperiod, rainfall, availability of food resources, ambient temperature and agonistic stimuli have all been shown to either induce or depress the reproductive effort of small mammal populations. In most cases, regulation is achieved by the action of a combination of factors (Bronson 1979b). It is an advantage for opportunistic rodent populations that exist in disturbed, temporally unstable habitats to possess a strategy whereby reproduction can be controlled by local food levels, shelter and social conditions rather than by seasonal change (DeLong 1978).

Photoperiod has pronounced effects on reproduction in small mammals,

influencing body weight (Canguilhem *et al* 1988); development of reproductive organs (Meyer and Meyer 1944); weight of gonads (Ashman and Seed 1974); hormone secretion and sexual behaviour (Fantie *et al* 1984) and feeding rhythms (Haynes and Cooper 1972).

There is considerable evidence to suggest that photoperiod does not act directly to suppress reproduction but that it provides a cue that indicates the onset of environmental conditions that are favourable for reproduction (Sadlier 1969 for review).

In many instances, the effect of photoperiod is only significant when considered together with diet (Nelson *et al* 1983; Irby *et al* 1984; Pinter 1968).

Temperature may regulate reproduction via a direct physiological effect or indirectly by affecting the quality and quantity of available food. In laboratory studies, temperature has been shown to exert a direct effect on reproduction by regulating the size of reproductive organs (Goertz 1965); time to puberty, length of the oestrus cycle and the interval between parturition (Barnett 1962; Barnett and Coleman 1959; Batt 1980; Pelikan 1981) and net reproductive effort (Pennycuik *et al* 1986). Temperature also plays a role in determining the rate of embryo resorption (Sod-Moriah 1971) and the energy available for lactation (Barnett and Coleman 1959; Sadleir *et al* 1973).

The effect of temperature on reproduction in wild populations is extremely difficult to determine because of the seasonal linkage between temperature, rainfall, food resources and photoperiod. For example, Bomford (1987a) suggested that low winter temperatures inhibited breeding in wild populations of *M. domesticus*. However in a subsequent study, Bomford (1987b) suggested that the reduction in breeding intensity was not directly

related to temperature but rather to a decrease in the quality of food resources.

The breeding season of many small mammals correlates with rainfall pattern (Ghobrial and Hodlieb 1982; Williams 1987; Fiedler 1988; Mutze *et al* 1990) hence rainfall has often been considered a major factor in the regulation of reproductive processes.

In most instances, rainfall acts in the same manner as photoperiod, synchronising reproduction to food supply and environmental conditions. Rainfall, acting via this mechanism can be responsible for an extension of the breeding season (Taylor and Green 1976; Rowe-Rowe and Meester 1982; Advani 1983), increased survival by delaying the harvesting of crops (Taylor 1968) or the timing and success of seasonal reproduction (Newsome and Corbett 1975; Breed 1982; Kenagy and Bartholomew 1985; Williams 1987). Gard (1935), McDougall (1946a) and Redhead (1973) have suggested that rainfall is a determinant of the breeding success of *R. sordidus* populations.

Apart from determining the availability of food resources, unseasonal rainfall can improve habitat quality by providing suitable conditions for burrowing (Newsome 1969 a,b) and shelter (Redhead 1973) at a time when these factors normally limit reproductive processes.

Energetically, there should be a direct relationship between the abundance of a food resource and the reproductive process where the seasonal variation in reproduction is related to the excess energy available after thermoregulatory and locomotor energy costs have been satisfied (Bronson and Perrigo 1987).

Studies have linked food availability (and the coincident environmental

variables of temperature, rainfall and photoperiod) to reproductive activity (Ghobrial and Hodiab 1982; King 1983), onset of reproduction (Rowe-Rowe and Meester 1982) and the extension of the breeding period (Ashby 1967). In general, the annual occurrence of reproduction is synchronised with environmental factors to ensure that energy and nutritional states are high so that an appropriate amount of resources can be devoted to reproduction (Kenagy and Bartholomew 1985).

The effect of food availability (or shortage) on reproduction has been evaluated by comparing life histories with and without supplemental food (Bendell 1959; Flowerdew 1972; Fordham 1971; Desy and Thompson 1983; Singleton 1985; Bomford 1987b). The results of these types of studies are varied, appear to be species or location specific and show no consistent relationship between food supply and reproductive processes. This variability in outcome is to be expected as many factors such as photoperiod, temperature and food availability vary seasonally and a change in one variable without the corresponding changes in related variables that would normally occur coincidentally, may completely disrupt the mechanisms that are regulating the system. Given the complexity of the interactions, there is little likelihood of separating the effects of each factor in studies of wild populations (Bronson 1979b).

Female fertility may be stimulated by small supplements of a food source and is inhibited by larger supplements (Alhibai 1985). The stimulatory effect of very small dietary supplements suggests that minor constituents of food sources may also play an important role in the regulation of reproductive processes (Negus and Pinter 1966; Negus *et al* 1977).

Various compounds have been isolated from plant material that influence the onset (Berger *et al* 1981;), duration (Negus and Pinter 1966; Alhibai 1985), intensity (Berger *et al* 1981; Olsen 1981; Bomford 1987a) and

cessation (Berger *et al* 1981; Sanders *et al* 1981) of reproduction in rodent populations. These compounds change in concentration during plant growth and therefore exert considerable influence on the timing of the breeding season.

Reproductive processes can also be inhibited by social interactions associated with high population density even when food supplies are abundant. Crowding may result in the inhibition of sexual maturation, growth and development of reproductive organs, ovulation and spermatogenesis, inhibition of oestrus, delay in implantation, prolonged gestation, reduction in litter frequency, increased resorption of fetuses and damage to surviving embryo *in utero* (DeLong 1967; Newsome 1969 a,b; Lloyd 1975; Adamczyk 1977; DeLong 1978; Stueck and Barrett 1978; Van Zegeren 1980; Lee and McDonald 1985; Jamon 1986; Massey 1986; Boyce and Boyce 1988).

Litter size and frequency are important determinants of overall reproductive potential. Chronological age (Goertz 1965; Maibenco and Krehbiel 1973; Beg *et al* 1983), age at puberty or first oestrus (Drickamer 1988), habitat quality (Pryor and Bronson 1981; Catling 1984) and population density (DeLong 1978; Stueck and Barrett 1978; Van Zegeren 1980; Rampaud 1984; Lee and McDonald 1985) have all been shown to influence litter size and/or the frequency of litters in rodent populations.

In many small mammal populations, survival has an inverse relationship with density and may vary between different strata of the population (DeLong 1967; Tamarin and Malecha 1971; Lee and McDonald 1985). In order to determine the significance of factors affecting survival it is common to stratify the population into three discrete strata - nestlings, juveniles and adults.

A breakdown of normal maternal behaviour resulting in increased nestling

mortality has been associated with large litter sizes (Priestnall 1972; Stueck and Barrett 1978; Rampaud 1984; Lee and McDonald 1985) or as a consequence of increased population densities (Lloyd 1975; DeLong 1978; Stueck and Barrett 1978; Van Zegeren 1980; Rampaud 1984; Lee and McDonald 1984). McDougall (1946a) suggested that nestling mortality may have a role in the regulation of *R. sordidus* populations.

As the recruitment of juveniles usually varies seasonally and from year to year, juveniles have often been considered as the most sensitive stratum on which both intrinsic and environmental regulating mechanisms act (DeLong 1967; King 1982; Pennycuik *et al* 1986). Increased juvenile survival has been associated with increased availability of nutritional food resources (Bendell 1959; Flowerdew 1972; Williams 1987) and the occurrence of warm weather (Pennycuik *et al* 1986). Recruitment, growth and survival of juveniles may also be severely affected by agonistic behaviour of adult resident individuals (Tanton 1969; Flowerdew 1974; Adamczyk 1977; Fordham 1971; Gurnell 1978; Green 1979). Increased juvenile survival often coincides with the death of older individuals from the preceding generation (Tanton 1969).

The stress related mortality of adults associated with reproductive effort has been well documented for *Antechinus* species and several authors have suggested that a less intense version of this phenomenon may also occur in some small mammal species (Braithwaite and Lee 1979; Fairbairn 1976; Gurnell 1978). Braithwaite and Lee (1979) suggested that low adult survival may favour selection for early maturation and high reproductive rates.

Changes in the probability of adult survival have been correlated with the availability of food resources. Coincident changes in other environmental variables such as temperature and photoperiod have a profound effect on other population processes (eg breeding and juvenile recruitment) and so it

is difficult to establish whether the change in adult survival is due to the availability of food or is a consequence of another population process (Gurnell 1978; Braithwaite and Lee 1979; Green 1979).

The male and female strata of small mammal populations often exhibit significantly different mortality schedules. These differences have been attributed to a wide diversity of causes from differential exposure during dispersal (Lidicker 1975) to aggression and territoriality (Kondo 1982). The mechanisms that give rise to this situation appear to be unique to each case and no underlying concept is apparent although Giesel (1972) suggested that species in which males suffered higher mortality than females would be better able to track short-term environmental changes and be more efficient colonisers of new environments. Similarly, Clark (1980) and Cockburn (1981) both suggest that populations with a sex ratio biased towards females during the breeding season have the capacity to rapidly respond to fluctuations in food resources.

Resources such as shelter, food supply and breeding space are rarely constant over time in many of the natural habitats occupied by small mammals. This is certainly the case in agricultural systems where cultivation and the crop cycle impose a high degree of temporal instability on habitats within the system. Under these circumstances, intra-specific competition may result in a more efficient utilisation of resources (Lidicker 1965). In many small mammal populations, intra-specific competition results in either the dispersal of juveniles or an extension (or shift) of the home range of adults (Bronson 1979a).

2.4 SPATIAL CONSIDERATIONS

In unstable agricultural environments, mobility has been cited as being of prime importance for the success of a species. Stickel (1979) documented

high turnover rates of house mice in a cropped area subject to continuous disturbance. Populations tracked the spatial and temporal crop mosaic and were characterised by low survival and high productivity. McDougall (1946b) also detected large movement patterns in *R. sordidus* populations that coincided with crop disturbance.

Lidicker (1975) identified three main prompts for dispersal processes in small mammal populations namely, the high breeding rate of the resident population, a saturated environment and aggression by dominant animals. Under these conditions, the objective of dispersal is to make more efficient use of remaining resources by optimising the division of energy invested in both dispersal and breeding activities. Consequently, at high population densities, individual fitness may be improved by leaving rather than by continuing to utilise available resources (Grant 1978) and in some instances, may result in a species being able to persist in an area where it might otherwise be eliminated (Hastings 1982).

Two main types of dispersal behaviour have been described (Lidicker 1975). Saturation dispersal (density-dependent dispersal) occurs from populations at or near carrying capacity. Dispersing individuals are usually juveniles or are from a stratum of the population that is in poor physical condition. The result of saturation dispersal is often a breeding population with fewer young than would be expected on the basis of recruitment rates (Tanton 1969; Williams and Cameron 1984). Pre-saturation dispersal is the movement of animals from the population before the habitat becomes saturated. In this instance, individuals are usually in good physical condition as there is still a surplus of resources in the home environment. All sex/age groups including pregnant females can be included in the dispersing stratum.

Newsome (1969a,b) described saturation dispersal in populations of house mice in an agricultural area but pre-saturation dispersal is more often the

case in small mammal populations (Grant 1978). Pre-saturation dispersal may favour a species by rapidly extending the range of the species as favourable habitats become available (Howard 1960). It would also tend to reduce intraspecific conflict and bring about more efficient utilisation of resources (Butler 1980; Stafford and Stout 1983).

Dispersal is of particular concern in the control of rodents in agricultural systems. Most agricultural systems consist of a mosaic of crop and refuge habitats. Within a typical Australian agricultural system, rodents are faced with a diversity of cropping systems and refuge habitats, each of which have their own temporal cycle of food- and shelter- availability. Consequently, pest rodents have developed strategies to cope with both the spatial and temporal elements of the agricultural mosaic.

The complexity of these strategies is typified in the model of Newsome (1969 a,b) that describes the dynamics of the house mouse in a South Australian wheat system. Mice establish permanent colonies in refuge areas, or donor habitats (Hansson 1977), and survive in these habitats during periods of environmental stress. When breeding commences and these areas attain carrying capacity, juveniles move (or are forced) from the donor habitats into receptor habitats such as crops if they are available. Once established in the receptor habitats, a complex system of cues (Bronson 1979a) ensures that breeding commences only if conditions in the receptor habitats are favourable for the establishment of nest sites. Population density in the area as a whole increases until cessation of breeding in autumn and, as food supply abruptly decreases in the crops (due to harvest), animals die or return to the refuge areas and establish an overwintering population which then primes the system for the next crop cycle.

Crop harvest results in a sudden decrease in food supply and shelter,

causing rapid movement of rodents from crops to refuge areas (Newsome (1969 a,b). This is not typical saturation dispersal as animals are not necessarily in poor physical condition. Nor is it typical presaturation dispersal as it is induced by a rapid decline in the carrying capacity of the area. Such *responsive* dispersal is of great importance in the management of rodents in agricultural systems as the relative distribution of habitat types (including crops at differing stages of development) will regulate the total production of the species (Hansson 1977). It follows that the *spatial* dynamics of the system is just as important as the *temporal* dynamics of the species.

The concept of spatial dynamics (or landscape ecology) was an integral of Singleton's (1989) explanation of the population dynamics of the house mouse in a Victorian agricultural system. It was suggested that fencelines, channel banks and similar areas which provide a constant source of food and shelter for mice throughout the year act as donor habitats. In contrast, crops were only a good source of food after they had formed seedheads in late October. Once this occurred, vast areas rapidly changed from low- to high- quality habitats. Dispersal of mice from donor habitats to receptor crops began in spring and breeding began within three weeks, converting a large area into an induced-donor habitat. The timing of onset of reproduction, the length of the breeding season and the proportion of adult females breeding, varied between the different habitats. It was therefore suggested that the spatial distribution of donor, receptor and induced-donor habitats was a critical element of the dynamics of the system.

Spatial dynamics is now recognised as an essential element in the understanding of the success of a species in a heterogeneous environment and is being incorporated into models for conservation management as well as pest species management (Gilpin and Hanski 1991 for review).

The critical organism/organism and organism/environment interactions that give rise to high reproductive success or a high probability of survival can only be identified through an understanding of the mechanisms that govern population processes at both the local and regional levels of scale. Once identified, it may be possible to manipulate these interactions to reduce the success of the population and so provide long-term population control.

THE POPULATION DYNAMICS OF *RATTUS SORDIDUS* IN NORTH QUEENSLAND SUGARCANE GROWING AREAS

3.0 INTRODUCTION

There is considerable uncertainty regarding the factors that regulate populations of *R. sordidus* in north Queensland sugarcane growing areas. The only extensive investigation of rodent pests in sugarcane was undertaken by McDougall (1944a,b; 1946a,b; 1947). Although this research provided significant information on the biology of *R. sordidus* under laboratory conditions, the description of the dynamics of *R. sordidus* populations in the field and the factors that regulate the populations was largely anecdotal and inconclusive. Additional research by Redhead (1973) concentrated on the ecology of *Melomys spp.*, the evaluation of baiting strategies and the prediction of annual damage levels. Incidental studies have addressed distribution, breeding and diet of *R. sordidus* in sugarcane growing regions (Harrison 1962; Woods 1966; Taylor and Horner 1973; Watts 1977; Breed 1978).

Patchy distribution of *R. sordidus* populations and crop damage levels throughout a canegrowing district have been reported (McDougall 1946b; Redhead and Saunders 1980), however the factors causing this pattern of distribution are poorly understood. In a study of *R. sordidus* in the Mackay district, McDougall (1944b) concluded that soil conditions were the most important factor determining population density. The presence and type of non-cane habitats have also been reported to influence local population levels (Redhead and Saunders 1980). Woods (1966) found *R. sordidus* to be more prevalent in cultivated areas (sugarcane and cowpeas) than in adjacent non-crop habitats. He recorded 18% trap success in cane, 33.3% trap success in cowpeas, and only 9.8%, 5.8% and 0% trap success in adjacent grasslands, eucalypt forests and closed forests respectively. Taylor

and Horner (1973) also recorded higher population densities of *R. sordidus* in sugarcane than in natural habitats with 9.8% and 2.3% trap success respectively.

McDougall (1947) considered that survival, productivity and distribution of *R. sordidus* populations were not influenced to any great extent by the presence of non-cane habitats (eg. grassland, swamp or open forest habitat). It was suggested that sugarcane fields comprise a significantly greater proportion of the district compared to non-cane areas, and so provide a more important habitat. However, the disturbances associated with cultivation ensure that sugarcane crops can only be considered as a temporary habitat in comparison to the permanent nature of non-cane areas (Redhead 1973). Elevated damage levels in crops adjacent to wastelands (undisturbed grasslands) or weed infested drains indicates that the presence of these habitats in canegrowing areas may influence population levels and dynamics (Redhead 1973; Redhead and Saunders 1980). Redhead (1973) suggested that these habitats act as refuges for *R. sordidus* during the harvest period and are thus reservoirs for reinvasion of crops as they become available.

Life-history characteristics including early independence and sexual maturity, a short gestation period, post partum oestrus and large litter size place *R. sordidus* in a group of species having the highest reproductive potential of any native Australian *Rattus* species (McDougall 1946a; Taylor and Horner 1973; Breed 1978). Maximum reproductive potential is rarely achieved under field conditions due to seasonal breeding and variable litter sizes (McDougall 1946a). Gard (1935) observed a decrease in litter size throughout the breeding period with a litter size ranging from four to eleven in the first litters of the season and rarely exceeding six in subsequent litters, whereas McDougall (1946a) reported no sequence or regularity in the size of successive litters of individuals under laboratory conditions. In

field populations there was no relationship between adult age and breeding or between weight of young at birth and size of the litter. McDougall (1946a) observed that up to one sixth of a *R. sordidus* litter can be killed by the male or female within the first few hours after birth in laboratory populations and therefore suggested that nestling mortality may have a role in regulating wild populations of *R. sordidus*.

Although *R. sordidus* will breed throughout the year in captive populations (McDougall 1946a), seasonal breeding is a characteristic of field populations (McDougall 1946a; Taylor and Horner 1973). McDougall (1946a) observed breeding in the Mackay district to decline from July through November with no pregnancies in December or January. Taylor and Horner (1973) also reported seasonal breeding in *R. sordidus* populations in the Herbert River and Mackay districts. They recorded pregnancies over the period November to May with 71 of births occurring between March and May and none occurring in mid-September and October.

Emphasis has been placed on the role of rainfall as the prompt that cues breeding in *R. sordidus* populations. However, there is considerable uncertainty about the mechanism by which rainfall regulates reproduction in this species. Gard (1935) observed *R. sordidus* to breed soon after the onset of a wet period and suggested that breeding was in response to an increase in the availability of young, green plant food after rain. Following observations of low breeding intensity during periods when lush food sources were abundant; or in years of early, long, or heavy wet seasons, McDougall (1946a) concluded the extent of reproductive effort to be dependent on spring rainfall. It was suggested that an increase in both the quantity and quality of food resources following spring rainfall allowed spring breeding, and improved physiological condition of individuals for future breeding. It was further proposed that although an increase in breeding may follow rain, the breeding rate observed by Gard (1935) was probably

influenced by a "carry-over of conditioning for breeding" from the previous spring.

Redhead (1973, 1980) suggested that spring rainfall may also result in larger populations in the following year by promoting conditions which result in advanced young cane being present before completion of harvesting of the old crop. Increased survival would result from rodents not needing to leave the canefields and survive in non-cane areas which may already support populations. Increased survival might also result from drains and headlands, which would normally be managed to reduce grass growth, being overgrown, effectively increasing the availability of favourable non-cane habitat and therefore survival of rodent populations.

Although McDougall (1946b) and Redhead (1973) each discussed survival, growth and decline of *R. sordidus* populations, factors affecting these processes were not critically evaluated. McDougall (1946b) observed a steady turnover of *R. sordidus* throughout the year. This was coupled with an increase in population density in areas where the environment remained suitable for continued habitation. Marked increases in activity and general movements together with sharp changes in population density were observed in late June, July and August and again after November. However, considerable variation in the timing of these movements was also recognised. Periods of least movement coincided with the actual or potential peaks of the breeding seasons.

Increases in population density to "plague" proportions were attributed to the population encountering "mild" conditions during several high movement periods (non-breeding period). McDougall (1946a) suggested that these conditions may lead to increased survival as indicated by the presence of very old animals (over two years of age) as well as young individuals in the population. It was further suggested that the extent of population build-up

would be dependent on the time interval over which such a population composition existed and indicated a 5 - 6 year cycle. However, no attempt was made to validate this cycle or to incorporate this information into a predictive system for management purposes.

Despite fluctuations in annual losses due to *R. sordidus*, control costs are similar each year. Redhead (1973, 1980) considered that a predictive system may allow control costs to be tailored according to the predicted damage potential. He suggested that a prediction of damage would be available if observed damage intensity could be related to a measurable factor by means of a regression equation. As weather has been implicated as being the prime factor governing fluctuations in *R. sordidus* numbers (McDougall 1946a), Redhead (1973, 1980) investigated a possible relationship between rainfall and damage intensity the following year in the Herbert River District. It was suggested that rainfall during the April - December period may contribute to increased damage in the following year by:

- i) prolonging the optimum conditions for plant growth resulting in increased reproduction leading to higher rodent numbers in the following year;
- ii) promoting conditions which result in advanced young cane being present before completion of harvesting of the old crop. This may lead to increased survival as rodents no longer need to leave the canefields and surviving in non-cane areas which may already support populations. Damage may also occur earlier than in years when crop growth is delayed by low rainfall; and

- iii) resulting in drains and headlands, which would normally be managed to reduce grass growth, being overgrown, effectively increasing the availability of non-cane harbourage.

Using crop loss estimates maintained by the Victoria Mill for the years 1942 to 1963, Redhead (1980) found a significant correlation between rainfall in April and May and damage intensity in the following year ($r=0.71$). The following regression equation was derived:

$$\arcsin\sqrt{P_n} = 2.282\log_e R - 7.744$$

where P_n = Percent. loss in year n
 R = Rainfall in April and May of the previous year ($n-1$)

However, the limitations of this predictive model for use by the sugar industry were recognised:

- i) The result is only sufficient to predict a high or low level of damage. The regression only accounts for 50% of the variation in the data and is therefore not very reliable for management purposes.
- ii) The relationship between damage level and distribution throughout a mill area has not been established. Elevated damage levels may represent more intensive damage on fields which usually suffer damage, an increase in the number of fields with damage, or both. Relating control costs to the predicted level of damage is therefore not possible.
- iii) The model may only be applicable to the Victoria Mill area of the Herbert River District.

Consequently, control of *R. sordidus* in North Queensland canegrowing areas has relied entirely on the widespread application of thallium treated

wheat baits at a cost of approximately \$0.6M to the industry each year. As rodent damage throughout a district is generally patchy, non-selective aerial distribution of baits is therefore costly, with baits being applied at the same rate regardless of the level of infestation (Taylor 1972; Redhead and Saunders 1980).

Stenseth and Hansson (1981) suggested that control programs which rely solely on increasing mortality by lethal techniques are seldom cost-effective in the long-term. They suggested that optimal control may only be achieved by reducing rates of reproduction and immigration into depopulated patches (ie. colonisation). Development of a control strategy therefore relies on an understanding of the population dynamics of the pest species and should involve:

- i) the identification of critical habitats;
- ii) an understanding of the specific use made of each habitat, and
- iii) the relationship between environmental parameters and the reproductive cycle of the organism.

As most research on *R. sordidus* in North Queensland sugarcane growing areas has focussed on the development of baiting strategies, factors affecting the distribution and the population cycle of this species in canegrowing areas has not been documented.

The objectives of this study were:

- i) to determine the relative utilisation of habitats by *R. sordidus* within the Herbert River canegrowing district;

- ii) to provide an understanding of the population fluctuations of *R. sordidus* in the sugarcane growing area of the Herbert River District, based on results of a three year extensive rodent monitoring program (1985 - 1988);
- iii) to develop a temporal model for the prediction of *R. sordidus* population and damage levels in the Herbert River District; and
- iv) to validate this model in the Mackay district to ensure that the results are relevant to all major sugarcane growing districts.

3.1 THE HERBERT RIVER DISTRICT

3.1.1 Methods

The Herbert River District encompasses six geographic areas:

- . Abergowrie;
- . Stone river;
- . Fairford;
- . Macknade;
- . Estate;
- . Ingham Line.

Six study sites were selected within each geographic area. Each study site consisted of three zones:

- . a non-crop habitat adjacent to a canefield;
- . a crop margin (approximately two metres inside the crop);
- . a crop interior (greater than two metres from the crop boundary).

Sites were chosen in each area such that they included the six most prevalent non-crop habitats within the area (Table 3.1). This resulted in a total of 36 sites throughout the entire district (Figure 3.1).

Table 3.1

Major non-crop habitats in the Herbert River District

Habitat type	Description
Grassland	Grass species include guinea (<i>Panicum maximum</i>), para (<i>Brachiaria mutica</i>), and summergrasses (<i>Brachiaria miliformis</i> and <i>Digitaria ciliaris</i>). These areas are generally dry and occasionally cleared by slashing or burning.
Open woodland	An upper storey of <i>Acacia</i> , <i>Casuarina</i> and <i>Eucalypt</i> species with a ground layer of predominantly blady grass (<i>Imperata cylindrica</i>) which is periodically burnt.
Closed forest	Vine or river scrub along the banks of creeks and rivers.
Grazing land	Paddocks are grazed for most of the year. Grasses include couch (<i>Cynodon dactylon</i>) and improved pasture species that support an average of two head per hectare.
Swamp Drainage channels	Vegetation is predominantly para grass (<i>Brachiaria mutica</i>). Water levels fluctuate throughout the year. Marginal vegetation is occasionally maintained by burning.

Source: Hinchinbrook Shire Handbook. Queensland Department of Primary Industries, 1975.

On one night per month from May 1985 to September 1988, a line of twenty snap traps baited with paper soaked in linseed oil were set in each zone of each site. Traps were laid at ten metre intervals within each trapline.

All animals were autopsied and the following data collected:

Location

Sex and reproductive condition:

Males:	testes abdominal	- immature
	testes scrotal	- mature
Females	immature -	Vaginal perforation occurs at an age of approximately 37 days although first oestrus does not occur until an age of approximately 70 days, corresponding to a head-body length of 125mm (McDougall 1946b). A head-body length of 125mm was therefore assumed as the upper limit of the immature female stratum.
	mature-	Greater than 125 mm
	pregnant -	Determined by dissection. The number of embryos per female was also recorded.

Head-body length (mm)

Weight (g)

Stomach contents: The amount of sugarcane, seed, non-cane vegetation and other material was estimated as a volume percentage of the total stomach contents (to the nearest 10%).

Non-cane vegetation in each of the crop zones was sampled monthly. Five 0.625m² quadrats were placed at random within each zone and the above-ground vegetation harvested. Total wet weight (g) and the wet weight (g) of the dominant species were recorded. Any major perturbations or farm management practices occurring since the previous trapping session were also recorded.

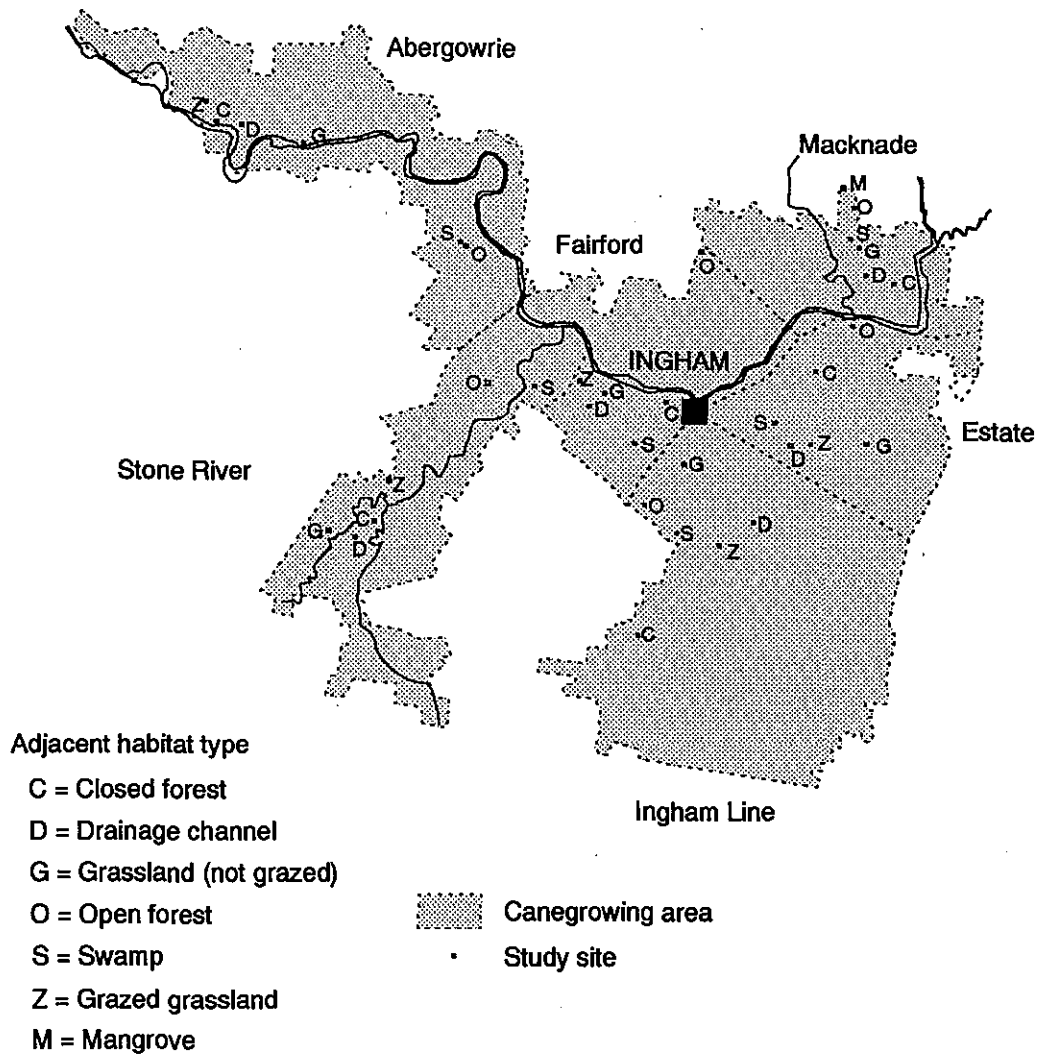


Figure 3.1 Location of study sites in the Herbert River District. (Letter beside site indicates adjacent habitat type)

3.1.2 Results

In-crop weeds

The percentage of crops with in-crop weed cover varied throughout the crop cycle, increasing from less than 20% of sites in September/October to more than 70% of sites in February/March each year (Figure 3.2).

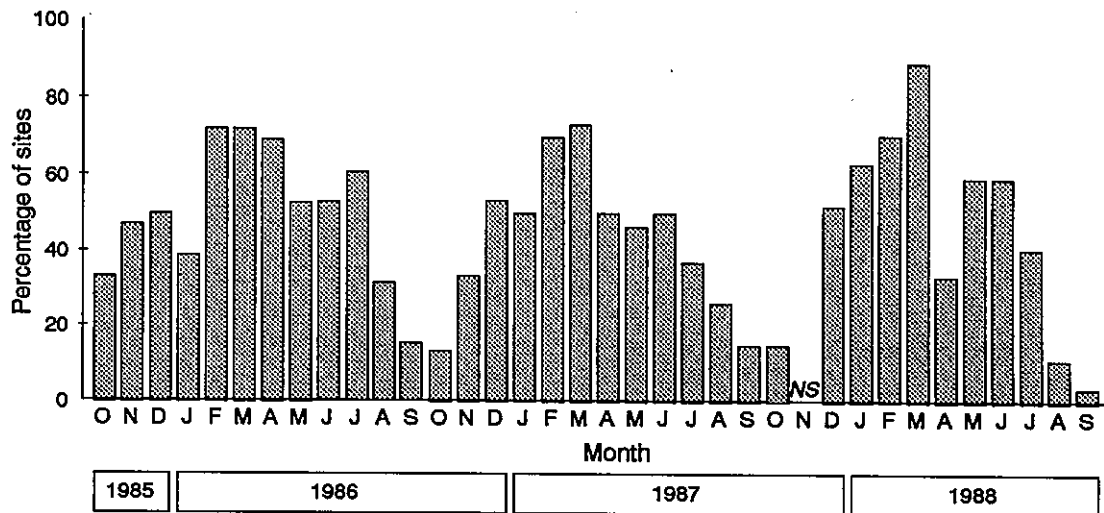


Figure 3.2 Percentage of crops with in-crop weed cover

NS No sample taken

Number of sites = 36 each month

Species composition changed throughout the crop cycle. Nutgrass (*Cyperus rotundus*), green summer grass¹ (*Brachiaria subquadripara*), summer grass¹ (*Digitaria ciliaris*) barnyard grass¹ (*Echinochloa crus-gali*) and awnless barnyard grass¹ (*Echinochloa colona*) were dominant during the November - May period whilst blue top (*Ageratum spp.*) was dominant during the later half of the crop cycle (May - September) each year. Guinea grass (*Panicum maximum*) was the dominant species in a small percentage of crops throughout each crop cycle (Figure 3.3).

¹ These four species are collectively termed "summergrasses".

At sites where summergrasses were present, maximum biomass occurred in January 1986, April 1987 and March 1988 (Figure 3.4). There was considerable variability in both the abundance and timing of peak abundance of summergrasses each year.

Habitat utilisation

Over the period of the study, May 1985 to September 1988, 2842 *R. sordidus* and 234 *M. burtoni* were captured. Incidental captures were made of *R. rattus* (black rat), *Mus domesticus* (house mouse), *Hydromys chrysogaster* (water rat), *Uromys caudimaculatus* (giant white-tailed rat) and *Antechinus flavipes* (yellow-footed antechinus). *R. sordidus* and *M. burtoni* represented 91% and 7.5% of total captures respectively.

In all years, percentage trap success was highest in grassland habitats (Table 3.2). The interior of sugarcane crops also supported significant populations although crop margins were not utilised to the same extent. Closed forest and grazing habitats were poorly utilised.

The temporal utilisation of the margin and interior of crops by *R. sordidus* is shown in Figure 3.5a. Percentage trap success was consistently higher in the interior of the crop throughout the entire period of the study (Wilcoxon's signed-ranks test, $p=5.21 \times 10^{-8}$).

In 26 of the 40 months of the study, percentage trap success was higher in grasslands than in crops (Wilcoxon's signed-ranks test, $p=0.009$) (Figure 3.5b). Low monthly trap success in other non-crop habitats precluded them from this type of comparison.

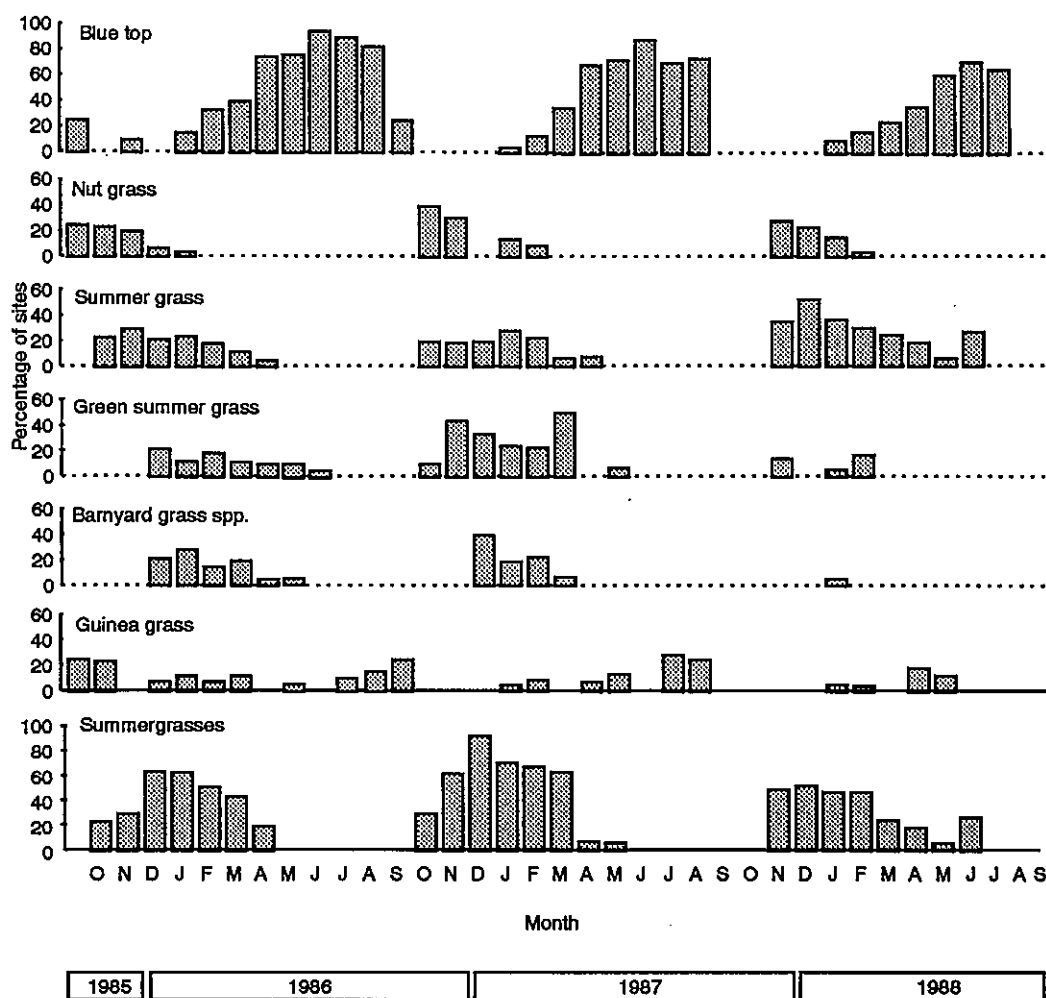


Figure 3.3 Percentage of crops in which each weed species was dominant over the study period

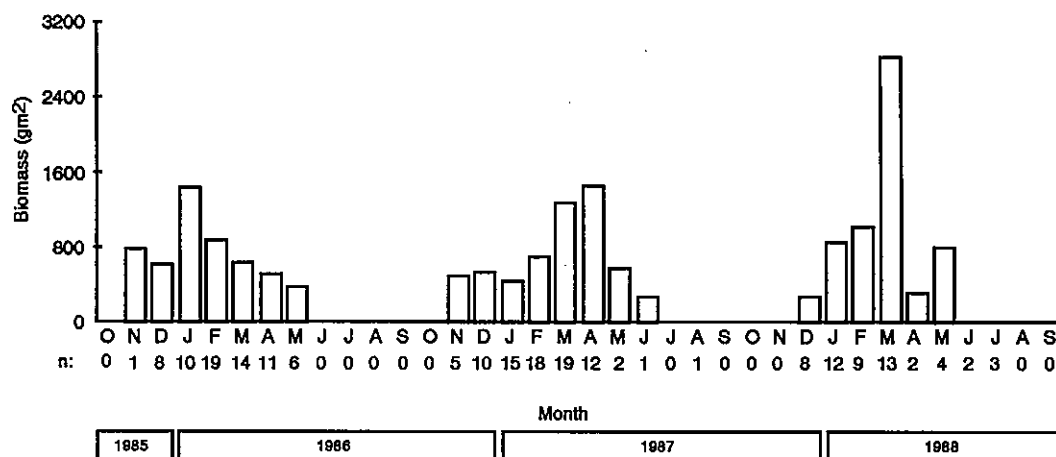


Figure 3.4 Mean biomass of summergrasses in crops (only crops with summergrasses are included)
n: number of crops

At sites where summergrasses were present, maximum biomass occurred in January 1986, April 1987 and March 1988 (Figure 3.4). There was considerable variability in both the abundance and timing of peak abundance of summergrasses each year.

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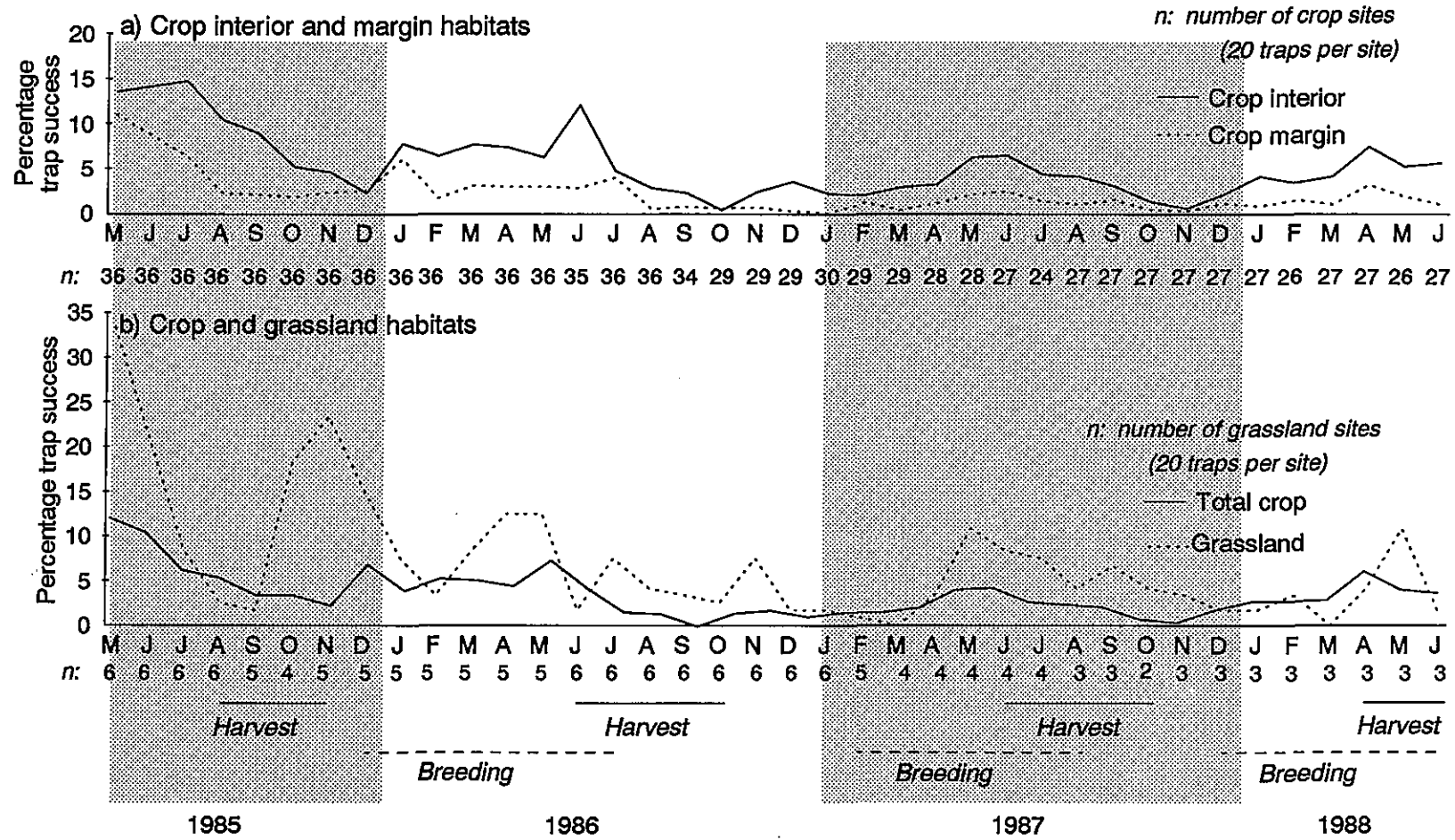


Figure 3.5 Percentage trap success of *R. sordidus* in (a) crops - interior and margin and (b) crop (pooled data for interior and margin) and grassland habitats

Table 3.2

Percentage trap success of *R. sordidus* in the major habitats of the Herbert River District

Habitat	Year			
	1985	1986	1987	1988
Grassland	14.64 (840)	6.21 (1400)	6.18 (1020)	5.47 (605)
Crop interior	8.53 (5020)	5.50 (8160)	3.24 (6520)	4.41 (4512)
Drainage	5.12 (840)	4.30 (1400)	1.52 (1320)	- (0)
Open forest	4.40 (840)	2.32 (1420)	0.93 (1080)	- (0)
Crop margin	4.06 (5020)	2.25 (8160)	1.06 (6520)	1.48 (4512)
Swamp	3.10 (840)	2.11 (1420)	1.52 (1320)	- (0)
Closed forest	2.26 (840)	0.77 (1420)	0.86 (1160)	- (0)
Grazing	0.51 (780)	0.38 (1060)	- (0)	- (0)
χ^2	286.15 (7df)	242.65 (7df)	175.98 (6df)	77.50 (2df)

() Number of trap nights per year

Dotted lines indicate the division of the data into significant subsets (χ^2 simultaneous test procedure, $p_{\alpha,05}$)

In all years of the study, the populations in each habitat type possessed similar structures with respect to the proportion of juveniles (Table 3.3) and the proportion of mature females (Table 3.4).

The effect of adjacent non-crop habitats on the structure of crop populations is shown in Tables 3.5 and 3.6. The proportion of juveniles in crop populations was independent of the adjacent non-crop habitat in all years except 1987 (Table 3.5). The proportion of mature females in crop populations was also independent of the adjacent non-crop habitat in all years except 1988 when a higher than expected proportion of females were captured in grasslands (Table 3.6), (χ^2 simultaneous test procedure, $p_{0.05}$).

Table 3.3

The proportion of juveniles in each habitat

Habitat	1985	1986	1987	1988
Crop interior	0.21 (428)	0.17 (443)	0.17 (208)	0.17 (197)
Crop margin	0.23 (204)	0.18 (179)	0.17 (66)	0.25 (65)
Grassland	0.18 (123)	0.16 (87)	0.17 (63)	0.15 (34)
Drainage	0.26 (43)	0.12 (60)	0.30 (20)	- (-)
Open forest	0.03 (37)	0.15 (33)	0.30 (10)	- (-)
Swamp	0.19 (26)	0.13 (30)	0.21 (19)	- (-)
Closed forest	0.32 (19)	0.27 (11)	0.20 (10)	- (-)
Grazing	1.00 (4)	0.25 (4)	- (-)	- (-)
χ^2	9.27, $p > 0.05$ (4df)	1.60, $p > 0.05$ (5df)	0.02, $p > 0.05$ (2df)	2.35, $p > 0.05$ (2df)

* Where sample size was less than 30, data for these habitats were not included in the analysis

- No trapping undertaken

() Number of captures

Table 3.4

The proportion of mature females in each habitat

Habitat	1985	1986	1987	1988
Crop interior	0.54 (338)	0.59 (368)	0.58 (173)	0.60 (164)
Crop margin	0.65 (157)	0.62 (147)	0.62 (55)	0.65 (49)
Grassland	0.60 (101)	0.68 (73)	0.62 (52)	0.69 (29)
Drainage	0.63 (32)	0.66 (53)	0.50 (14)	- (-)
Open forest	0.64 (36)	0.46 (28)	0.57 (7)	- (-)
Swamp	0.71 (21)	0.46 (26)	0.67 (15)	- (-)
Closed forest	0.46 (13)	0.88 (8)	0.63 (8)	- (-)
Grazing	(0)	0.33 (3)	- (-)	- (-)
χ^2	8.04, $p > 0.05$ (6df)	7.61, $p > 0.05$ (5df)	1.25, $p > 0.05$ (4df)	1.00, $p > 0.05$ (2df)

* Where sample size was less than 30, data for these habitats were not included in the analysis

- No trapping undertaken

() Number of captures

Table 3.5

Proportion of juveniles in crops adjacent to non-crop habitats

Adjacent habitat	1985	1986	1987	1988*
Grassland	0.22 (108)	0.16 (76)	0.12 (51)	0.29 (51)
Drainage	0.26 (90)	0.20 (58)	0.30 (46)	0.15 (32)
Open forest	0.15 (53)	0.15 (66)	0.22 (32)	0.19 (27)
Swamp	0.26 (70)	0.18 (100)	0.08 (38)	0.09 (46)
Closed forest	0.22 (64)	0.16 (43)	0.15 (41)	0.10 (41)
Grazing	0.12 (44)	0.16 (100)	- (-)	- (-)
χ^2	5.63, p>0.05 (5df)	0.96, p>0.05 (5df)	9.66, p=0.047 (4df)	9.53, p>0.05 (4df)

() Number of captures

- No trapping undertaken

* Trapping occurred in crops but not in adjacent non-crop habitat

Table 3.6

The proportion of mature females in crops adjacent to non-crop habitats

Adjacent habitat	1985	1986	1987	1988*
Grassland	0.59 (84)	0.59 (64)	0.60 (45)	0.83 (36)
Drainage	0.57 (67)	0.65 (46)	0.69 (32)	0.52 (27)
Open forest	0.44 (45)	0.52 (56)	0.56 (25)	0.41 (22)
Swamp	0.63 (52)	0.51 (82)	0.57 (35)	0.55 (42)
Closed forest	0.48 (50)	0.75 (36)	0.46 (35)	0.59 (37)
Grazing	0.51 (39)	0.61 (84)	- (-)	- (-)
χ^2	5.51, p>0.05 (5df)	7.91, p>0.05 (5df)	3.79, p>0.05 (4df)	12.71, p<0.05 (4df)

* Trapping was discontinued in adjacent non-crop habitat except for grasslands however trapping continued in crops.

- No trapping undertaken

() Number of captures

Percentage trap success in crops varied with adjacent non-crop habitat type (Table 3.7). In all years except 1986, percentage trap success was higher in crops adjacent to grasslands (χ^2 simultaneous test procedure, $p_{0.05}$). In 1986, higher trap success was associated with grazing and swamp habitats.

Table 3.7

Percentage trap success in crops adjacent to non-crop habitats

Adjacent habitat	1985	1986*	1987	1988*
Grassland	13.57 (42)	5.43 (70)	5.00 (51)	7.73 (33)
Drainage	11.43 (42)	4.23 (70)	3.33 (72)	3.14 (51)
Swamp	8.33 (42)	7.11 (71)	2.68 (71)	4.51 (51)
Closed forest	8.10 (42)	3.17 (71)	2.97 (69)	4.02 (51)
Open forest	6.79 (42)	5.07 (71)	2.50 (64)	3.21 (42)
Grazing	5.61 (41)	9.26 (54)	- (0)	- (0)
χ^2	40.11 p<0.05 (5df)	58.99 p<0.05 (5df)	14.03 p<0.05 (4df)	24.34 p<0.05 (4df)

Dotted lines indicate the division of the data into significant subsets (χ^2 simultaneous test procedure, $p_{0.05}$)

* Trapping was discontinued in adjacent non-crop habitats except for grasslands

() Number of crops trapped (40 traps per crop)

+ (Grazing=Swamp)>(Grassland=Open forest=Drainage=Closed forest)

Crop populations

In all years of the study, both mature crops awaiting harvest and newly planted crops were present over the July - December period due to staggered harvesting throughout the district (Figure 3.6). Consequently, there was also overlap between the three population cycles documented in this study (November 1985 to October 1986; September 1986 to October 1987; and October 1987 to September 1988). Population trends during the three cycles are shown in Figure 3.6.

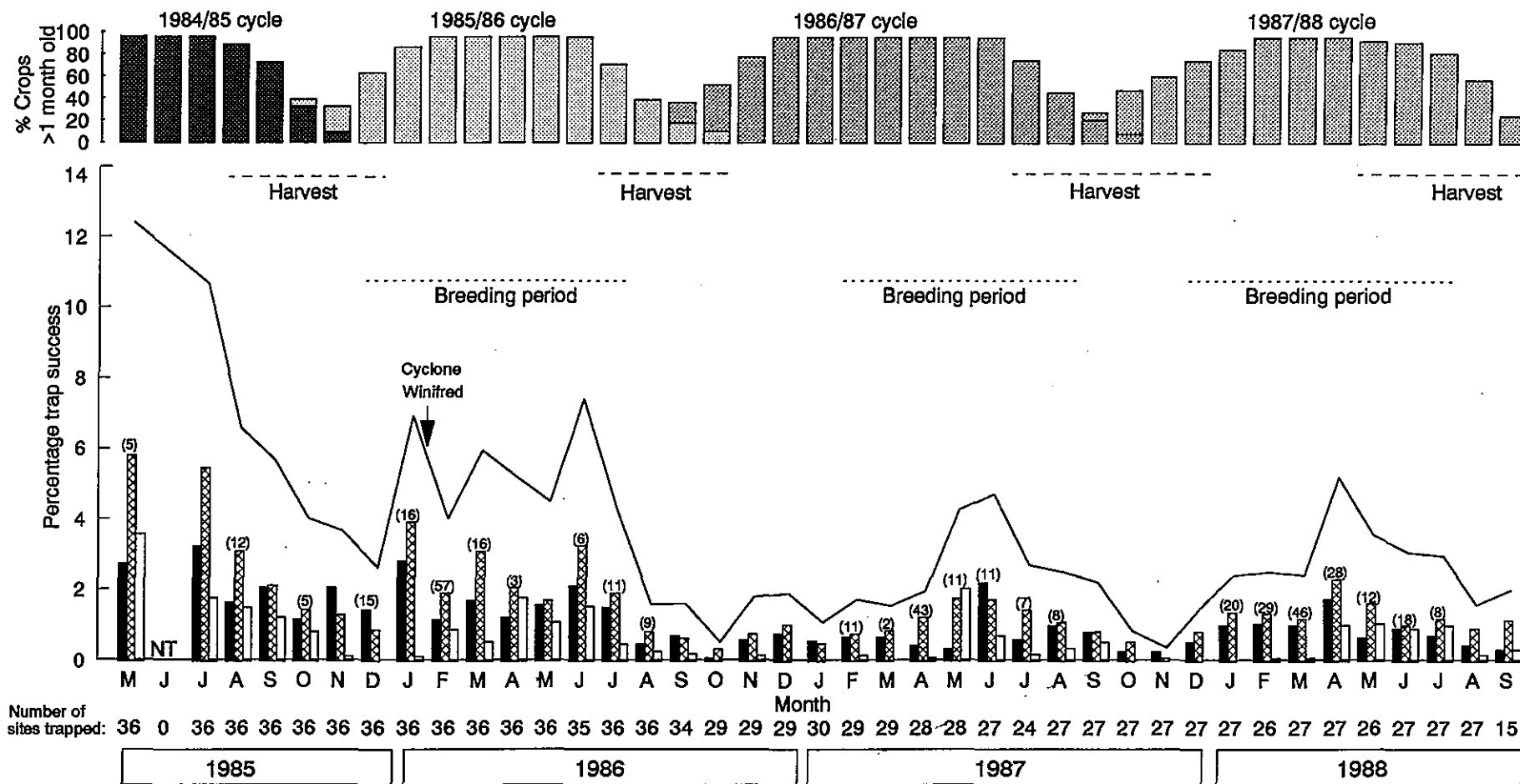


Figure 3.6 Population characteristics of *R. sordidus* in crops of the Herbert River District (Includes data for fallow fields)

Mature males
 Mature females
 Juveniles
 — Total population index
 NT No trapping undertaken () Percentage of mature females pregnant

Percentage trap success never exceeded 0.5% in recently harvested crops or fallow fields (fields without grass or legume cover) (Table 3.8). Over the entire study period, only 18 captures (in 4880 trap nights) were made in these fields indicating that crops are colonised annually.

Table 3.8

Percentage trap success of *R. sordidus* in crops of each age class

Crop age (months)	1986		1987		1988	
0 (bare fallow)	0.38	(2080)	0.24	(1640)	0.50	(1160)
1	3.42	(1200)	1.12	(1160)	1.30	(920)
2	8.42*	(1200)	1.75	(1200)	2.61	(920)
3 - 4	7.45*	(2120)	2.32	(2200)	1.13*	(1680)
>4	7.2*	(6800)	4.19*	(7760)	4.33*	(6560)
grassed fallow	0.43	(920)	0.28	(360)	0.12	(840)

* Pregnancies recorded in sample

() Number of trap nights per year

Table 3.9 shows that the majority of crops were not colonised until at least two months following harvest and/or planting. In the 1986/87 and 1987/88 crop cycles, the majority of crops were not colonised until they were five months old.

The two month period following harvest for a ratoon crop or planting of a new crop was defined as the colonisation period (Tables 3.8 and 3.9). Three periods of crop colonisation occurred between 1985 and 1988. Due to the staggered harvesting of sites throughout the district over the June - December period each year, the period during which sites were colonised varied between years: October 1985 to January 1986; September to December 1986; and August to December 1988.

Table 3.9

The percentage of crops¹ where *R. sordidus* were trapped and crop age during each crop cycle

Crop age (months)	Percentage of crops in which <i>R. sordidus</i> had been trapped		
	1985/86	1986/87	1987/88
0	13	9	4
1	33	13	4
2	70	16	22
3	87	28	22
4	90	34	26
5	90	44	39
6	93	53	61
>6	97	84	91
Total number of crops	30	32	23

1 Greater than one capture of *R. sordidus* was required to avoid including incidental captures

Colonists were defined as those animals trapped during the two months following harvest (for a ratoon crop) or planting (for a new crop). Conversely, established populations were from mature crops awaiting harvest. A comparison of the structure of colonising and established populations over the entire study period showed that the colonising population comprised a higher than expected proportion of mature males ($\chi^2_2 = 14.02$, $p < 0.05$) (Table 3.10). Comparisons for each crop cycle were not possible due to insufficient data.

Over the study period 97 pregnancies were recorded (Figure 3.6). A well defined breeding period occurred during each crop cycle, with greater than 95% of pregnancies being recorded during December 1985 - July 1986 (1985/86 cycle); February - August 1987 (1986/87 cycle) and January 1988 - July 1988 (1987/88 cycle).

Table 3.10

The structure of colonising and established populations during each crop cycle

Year	Population	Number of captures		
		Juveniles	Mature males	Mature females
1985/86	Colonising	3 (0.06)	29 (0.60)	16 (0.33)
	Established	67 (0.19)	122 (0.34)	172 (0.48)
1986/87	Colonising	0	1	1
	Established	32 (0.15)	72 (0.34)	96 (0.45)
1987/88	Colonising	3	5	2
	Established	31 (0.16)	65 (0.33)	99 (0.51)
All years	Colonising	6 (0.10)	35 (0.58)	19 (0.32)
	Established	130 (0.17)	259 (0.34)	367 (0.49)

() Proportion of population

Total reproductive effort over the December - August period of each cycle did not vary significantly between years ($\chi^2_2 = 2.4746$, $p > 0.05$) with a mean of 16.6% (15.5% to 21.4%) of mature females present during this period being pregnant (Table 3.11). There was a consistent trend in breeding intensity within each of the three breeding periods, with the highest percentage of mature females being pregnant in the third month of the breeding period each year. There was also no significant difference in the proportion of mature females pregnant at the peak of the breeding season in each year ($\chi^2_2 = 0.91$, $p > 0.05$) when approximately 50% of the mature female stratum was pregnant (Table 3.11).

Onset of breeding varied between years, occurring in December of the 1985/6, February of the 1986/87 and January of the 1987/88 cycle. Breeding periods corresponded to the period when summergrasses were present in the crop (Figure 3.7). Maximum breeding intensity occurred in February (1985/86 cycle), April (1986/87 cycle) and March (1987/88 cycle),

in each case, one month after the peak in summergrass biomass. Breeding ceased in July/August each year.

The number of embryos per pregnant female ranged from 1 to 13 with a mean of 6.44 ± 0.30 , and was constant during the breeding period (all years combined, $F_{8,75} = 2.043$, $p = 0.0525$). There was a weak positive correlation between the number of embryos and the head-body length of mature females ($r_s = 0.3019$; $n=82$; $p=0.0066$). However, there was no significant correlation between the number of embryos and the weight of females ($r_s = 0.1160$; $n=82$; $p=0.2963$).

Pregnancies were only recorded for females with a head-body length exceeding 125mm (Table 3.12). Pregnancies were most frequently recorded for individuals having a head-body length greater than 150mm.

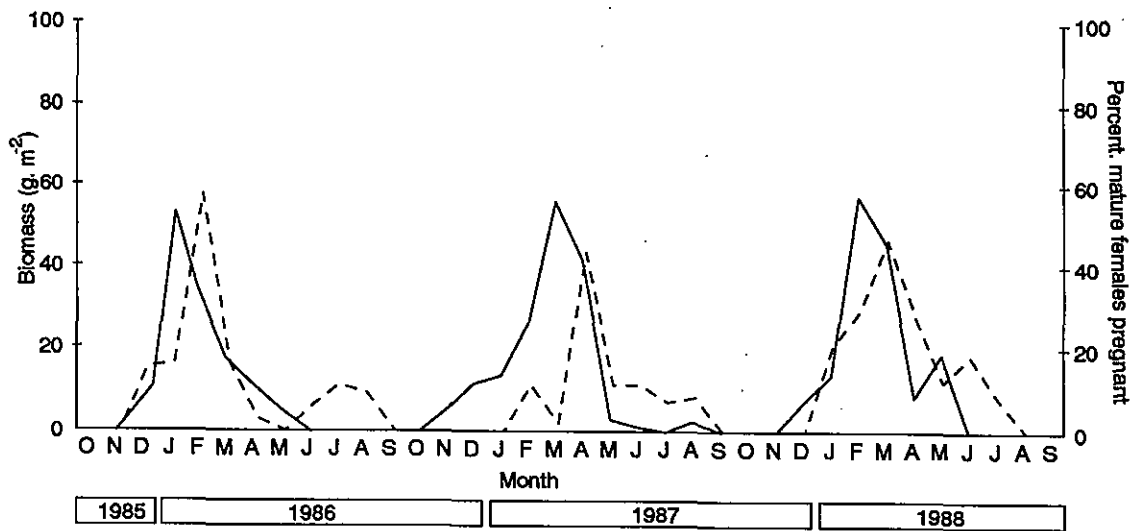


Figure 3.7 Relationship between biomass of summergrasses and breeding intensity (no. sites as for Figure 3.6)

— Biomass of summergrasses - - - - Percent mature females pregnant

Table 3.11

Reproductive effort of *R. sordidus* over the study period

Cycle	Month of breeding period	Number of mature females	Percentage of mature females pregnant (number of pregnancies)	Number of embryos	
				Mean	Range
1985/86	1 (Dec)	13	15 (2)		
	2 (Jan)	55	16 (9)	6.11	2 - 11
	3 (Feb)	28	57 (16)	7.59	3 - 12
	4 (Mar)	44	16 (7)	8.29	5 - 13
	5 (Apr)	29	3 (1)	4.5	3 - 6
	6 (May)	25	0 (0)		
	7 (Jun)	47	6 (3)	5.33	3 - 7
	8 (Jul)	27	11 (3)	4.33	2 - 6
	9 (Aug)	11	9 (1)	6.0	6
1986/87	(Dec)	11	0 (0)		
	(Jan)	7	0 (0)		
	1 (Feb)	9	11 (1)	6.0	6
	2 (Mar)	10	2 (5)	6.60	4 - 8
	3 (Apr)	14	43 (6)	6.83	4 - 10
	4 (May)	19	11 (2)	3.0	2 - 4
	5 (Jun)	19	11 (2)	6.50	6 - 7
	6 (Jul)	14	7 (1)	5.0	5
7 (Aug)	12	8 (1)	2.0	2	
1987/88	(Dec)	9	0 (0)		
	1 (Jan)	15	20 (3)	7.33	2 - 12
	2 (Feb)	14	29 (4)	3.75	1 - 7
	3 (Mar)	13	46 (6)	7.83	3 - 11
	4 (Apr)	25	28 (7)	7.71	4 - 12
	5 (May)	17	12 (2)	3.50	3 - 4
	6 (Jun)	11	18 (2)	4.50	4 - 5
	7 (Jul)	13	8 (1)	6.0	6
(Aug)	0	0 (0)			
Total	1	37	16 (6)	7.0	2 - 12
	2	79	22 (17)	5.72	1 - 11
	3	55	51 (28)	7.43	3 - 12
	4	88	18 (16)	7.38	2 - 13
	5	65	8 (5)	4.60	3 - 7
	6	50	6 (3)	4.67	4 - 5
	7	72	7 (5)	4.80	2 - 7
	8	27	15 (4)	4.25	2 - 6
	9	11	9 (1)	6.0	6

Table 3.12

Number of females and percentage pregnant
within each head-body length class

Population cycle	Head-body length class (mm)					
	≤125		126 - 149		≥150	
	Percentage pregnant	Total females*	Percentage pregnant	Total females*	Percentage pregnant	Total females*
1985/86	0	29	2.99	67	18.87	212
1986/87	0	10	5.71	35	25.81	62
1987/88	0	18	11.11	36	29.17	72

* Total number trapped during the breeding period of each cycle.

The proportion of mature females in the most productive head-body length class (≥ 150 mm) during the breeding period varied significantly between years, being highest in the 1985/86 cycle (76.0%) and lowest in the 1986/87 cycle (63.9%) ($\chi^2_2 = 7.728$, $p < 0.05$). In the 1987/88 cycle, this class included 66.7% of the mature female stratum.

An index of physiological condition was calculated for each mature female as the ratio of head-body length to eviscerated body weight. This index therefore increases with decreasing body condition. The physiological condition of pregnant females was significantly higher (ie lower index) than that of non-breeding mature females during each population cycle (Table 3.13).

Testes weight in mature males was significantly correlated with eviscerated body weight ($r_s = 0.706$, $n=589$, $p < 0.0001$). An index of reproductive condition for mature males was calculated as the ratio of testes weight (mg) to eviscerated body weight (g). This index increases with increasing reproductive condition.

Table 3.13

Median body condition indices of breeding and non-breeding mature females during each population cycle

Population cycle	Breeding status	Sample size	Median	Lower quartile	Upper quartile	Kruskal-Wallis χ^2_1	p
1985/86	Breeding	40	1.6050	1.4327	1.7541	20.40	6.3×10^{-6}
	Non-breeding	239	1.8068	1.6162	2.0896		
1986/87	Breeding	15	1.7742	1.6889	1.9178	4.37	0.037
	Non-breeding	111	1.9286	1.7284	2.2353		
1987/88	Breeding	24	1.7475	1.5084	1.9216	4.26	0.039
	Non-breeding	105	1.8987	1.6667	2.0857		

Significant variation in the index occurred over the study period (Kruskal-Wallis $\chi^2_{39} = 225.48$, $p < 0.0001$). The index generally increased prior to the breeding period, was high at the onset of breeding and then decreased (Figure 3.8). The index also varied significantly between years ($\chi^2_2 = 35.73$, $p < 0.0001$), increasing from a median of 9.95 in the 1985/86 cycle to 13.21 in the 1987/88 cycle.

Significant numbers of juveniles first entered the trappable population in February (1985/86), May (1986/87) and April (1987/88), three to four months after the onset of breeding and within one month of maximum breeding intensity (Figure 3.6). Maximum trap success of juveniles occurred one to two months following maximum trap success of pregnant females.

An index of recruitment was defined as the number of juveniles per mature female present during the breeding season. The recruitment index was similar in 1986/87 and 1987/88 at 0.47 (46/97) and 0.45 (49/108) respectively. In 1985/86 a recruitment index of 0.37 (103/279) coincided with the disruption of the breeding period by Cyclone Winifred (see Figure 3.6).

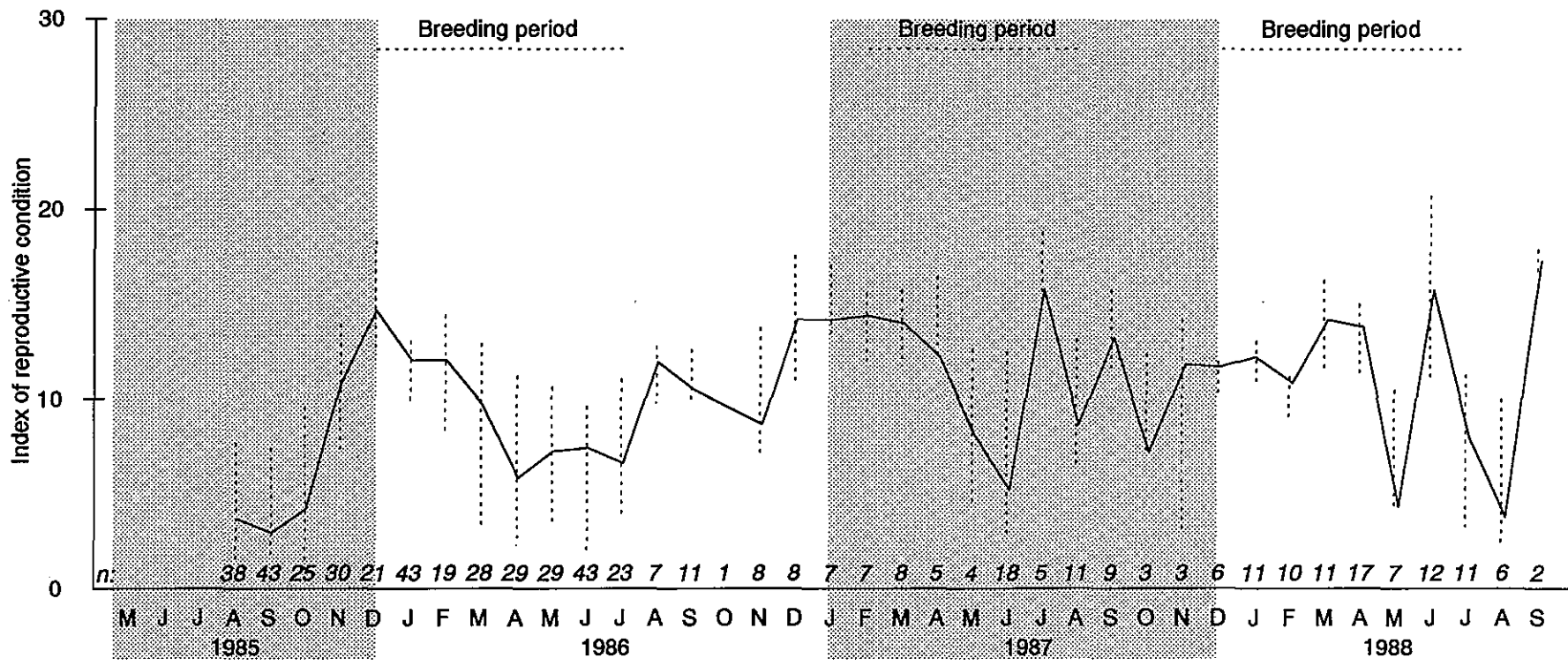


Figure 3.8 Median index of reproductive condition of male *R. sordidus* over the study period

Upper quartile
 Median
 Lower quartile
n: Sample size

In each year of the study, maximum population size occurred *during* the breeding period just prior to the beginning of the harvest period (July 1985, June 1986, June 1987, April 1988) (Figure 3.6). During harvest periods, grasslands were utilised more than crop habitats (Figure 3.5).

Due to staggered harvesting throughout the district, individual crops were present for differing times throughout the harvest period. In all three population cycles, trap success in most of the individual crops that were present for two months during the harvest period declined in a similar fashion to the district pattern. An increase in trap success occurred in only 3/14, 3/16 and 5/24 individual crops in 1986, 1987 and 1988 respectively. The decline in trap success within individual crops that existed during the harvest period shows that the removal of sugarcane habitat via harvesting is not responsible for the general decline in trap success throughout the district over the breeding period.

Diet

Throughout the study, seed, sugarcane and non-cane vegetation were the major components ($\geq 50\%$ by volume) of stomach contents. Unidentified matter was the major component in only 14% of stomachs.

The frequency of sugarcane as the major component ($\geq 50\%$) of stomach contents varied significantly during each year of the study (1985, $\chi^2_5 = 32.1$, $p < 0.05$; 1986, $\chi^2_{11} = 26.6$, $p < 0.05$; 1987, $\chi^2_{11} = 66.0$, $p < 0.05$; 1988, $\chi^2_{11} = 31.3$, $p < 0.05$). Sugarcane as the major component of stomach contents was least frequent over the January - March (1986), February to April 1987 and December to March 1988 periods (Figure 3.9). In each year, these periods corresponded to the first 3 - 4 months of the breeding period. In 1986, sugarcane was the major component of stomach contents in over 50% of individuals throughout the year.

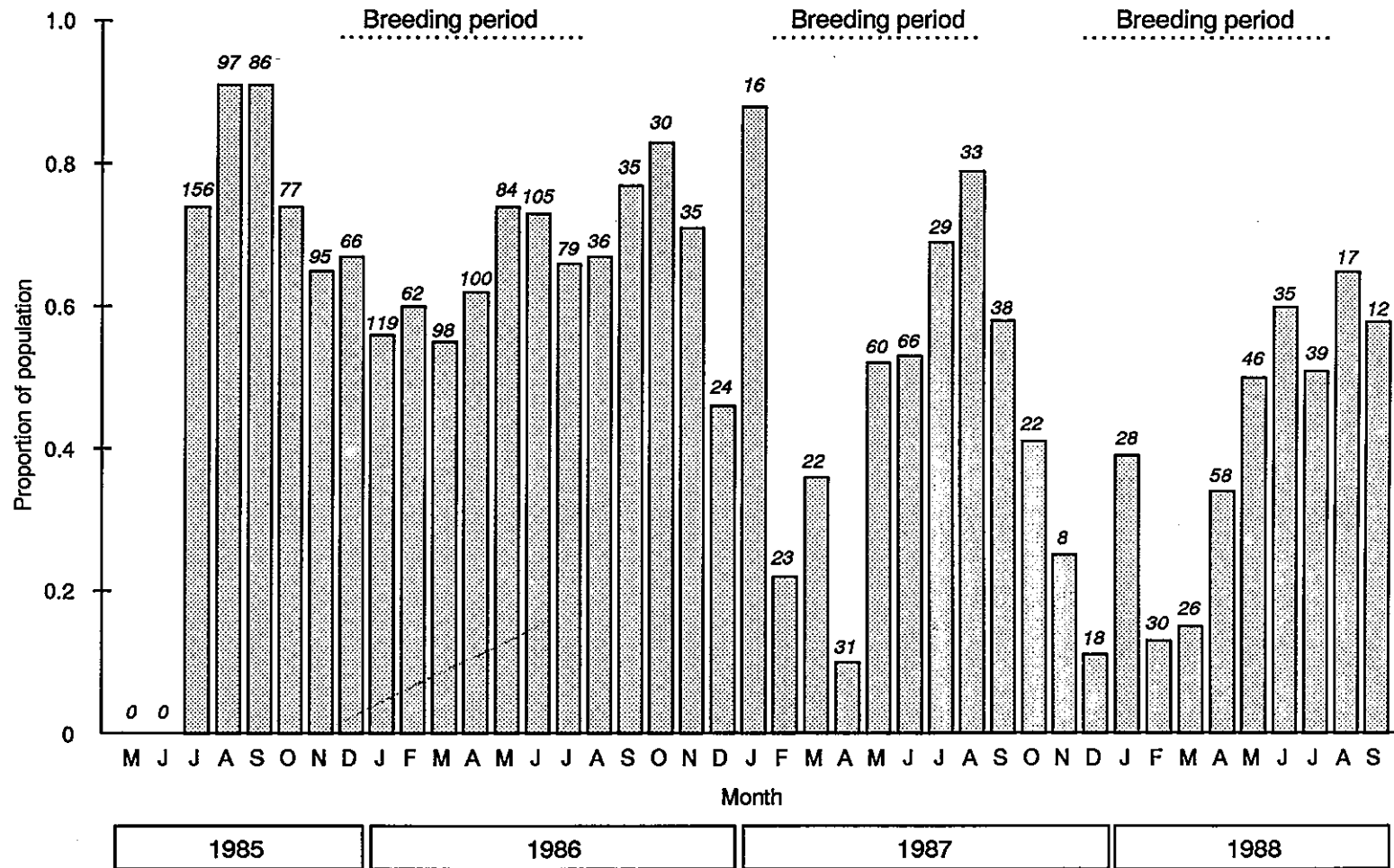


Figure 3.9 Proportion of the total population with stomachs containing significant amounts (>50%) of sugarcane. (Numbers above bars indicate the total sample size)

The frequency of sugarcane as the major component of stomach contents (all individuals) was significantly lower in crop margin and non-crop habitat populations than in crop populations in all years except 1986 (Table 3.14).

Table 3.14

Proportion of *R. sordidus* in crop and non-crop habitats with stomachs containing significant amounts ($\geq 50\%$) of sugarcane

Location	Proportion of stomachs containing $\geq 50\%$ sugarcane in each year of the study			
	1985	1986	1987	1988
Non-crop habitat	0.41 (239)	0.59 (222)	0.33 (118)	0.12 (34)
Crop margin	0.46 (194)	0.66 (174)	0.42 (62)	0.37 (65)
Crop interior	0.66 (407)	0.67 (432)	0.59 (204)	0.47 (196)
Difference in frequency with location (χ^2_2)	44.85 ($p < 0.05$)	4.49 ($p > 0.05$)	21.04 ($p < 0.05$)	15.83 ($p < 0.05$)

() Sample size

A difference in stomach contents between mature male and female individuals only occurred in 1986 when sugarcane was more frequently present in significant quantities in stomachs of mature males (Table 3.15).

Table 3.15

Proportion of mature male and female individuals with sugarcane predominating in stomach contents ($\geq 50\%$ of stomach contents)

Year	Proportion of each strata with significant amounts ($\geq 50\%$) of sugarcane in stomach contents		Difference between strata (χ^2_1)
	Mature females	Mature males	
1985	0.82 (185)	0.83 (168)	0.075 ($p > 0.05$)
1986	0.63 (297)	0.78 (206)	12.13 ($p < 0.05$)
1987	0.53 (125)	0.62 (94)	1.73 ($p > 0.05$)
1988	0.38 (131)	0.46 (97)	1.55 ($p > 0.05$)

() Total number in stratum

3.1.3 Discussion

The influence of landscape factors on survival and population success of a species has long been recognised (Hansson 1977; Stenseth 1977; Hasting 1982; Kincaid and Cameron 1985). Hansson (1977) suggested that as suitable habitats are often separated by large uninhabitable areas, many suitable areas may be underpopulated (or even unpopulated) at population peaks. Thus the relative distribution of habitat types in a landscape regulates the total production of the species. It therefore follows that an understanding of the spatial dynamics of a species in a heterogeneous landscape is necessary for a comprehensive model of population dynamics (Hansson 1977; Merriam *et al* 1988).

Spatial heterogeneity is a characteristic of sugarcane growing areas both in Australia and overseas. Expanses of crop monoculture are frequently interspersed with areas of natural vegetation which may act as "donor" habitats to rodent pest populations. In Hawaii, gulches provide a stable habitat to Polynesian rats (*R. exulans*). Populations commonly reside in gulches and individuals forage into neighbouring fields (Lindsey *et al* 1973; Fellows and Sugihara 1977). As the cane matures and provides more shelter to rodents, populations then establish in the crop.

R. sordidus comprised 91% of captures while *Melomys spp.* comprised only 7.5% of captures throughout the study period. This result is in accordance with previous research which reports *Melomys spp.* to be a relatively minor pest in the Herbert River District (McDougall 1946; Hitchcock 1973; Redhead 1973). Consequently, only the population dynamics of *R. sordidus* will be considered.

The study period encompassed three different year types. In 1986, a cyclone in February caused major flooding throughout the district; at the beginning of 1987 conditions were extremely dry with significant rainfall only

occurring after March; and in 1988 rainfall was higher than in 1987 but still below average over the December - March period. Although *R. sordidus* population levels varied according to the prevailing environmental conditions, population processes were similar each year. A general population cycle may therefore be described.

An annual phase of crop colonisation has been observed in Hawaiian sugarcane growing areas (Lindsey *et al* 1973; Fellows and Sugihara 1977). Factors such as rainfall, soil fertility and cane variety, all of which affect the time when the crop provides sufficient shelter and food resources, have an influence on the timing of colonisation of sugarcane crops by Polynesian rats (*R. exulans*) and black rats (*R. rattus*) (Lindsey *et al* 1973).

Low trap success of *R. sordidus* in crops which had recently been harvested, indicates that young crops (1 to 2 months old) are not favourable habitat for this species. As the crop canopy closes, and the soil environment becomes more stable as cultivation ceases, the environment becomes more favourable to *R. sordidus*. This is reflected in an increase in trap success of *R. sordidus* with crop age. Due to staggered harvesting of crops over the June - December, the crop colonisation phase extends from July to January. Although crops may provide suitable habitat to *R. sordidus* two months after harvest and ratoon growth or planting of a new crop, mature crops are preferred. The level of colonisation is therefore dependent on the availability of mature crops. Most crops are colonised over the November - January period when the proportion of the district supporting mature crops is extremely low. This was evident during the harvest period of the 1986/7 and 1987/8 crops when sites which were harvested early in the season were not colonised until November/December. As colonisation of crops occurs on an annual basis, the population dynamics of *R. sordidus* during the study period can be divided into three complete population cycles from colonisation of new crops to dispersal from harvested fields.

Following colonisation of the study sites and an increase in population levels, breeding occurred. Although the first oestrus occurs at about two months of age, McDougall (1946a) reported that female *R. sordidus* do not produce young until they are approximately five months of age. Pregnancy in individuals less than five months old has been observed (Gard 1935; Taylor and Horner 1973) but records are infrequent. In this study, females were aged by the relationship between head-body length and age reported by McDougall (1946). No pregnancies were recorded in individuals less than 10 weeks of age. Although young individuals between 10 weeks and one year (head-body length class 125-149mm) were observed to be pregnant, records of pregnancy were most common for individuals over one year old (head-body length >150mm). During each cycle, the female population was characterised by a high proportion of individuals in the oldest age class. It is significant that these individuals were most frequent during the breeding period of the 1985/6 cycle, when population growth was highest; and least frequent during the breeding period of the 1986/7 cycle, when population growth was lowest.

Differential breeding intensity between age classes may be considered as either a result of physiological and/or social factors. In microtine populations, female spacing behaviour as a result of increased densities leads to females preventing immigration, therefore limiting the number of potential breeders in the population (Boyce and Boyce 1988). Jamon (1986) observed similar regulation of reproduction in *Apodemus sylvaticus* populations with reproducing females becoming territorial and excluding younger females from breeding.

Variability in the month of breeding onset occurred between cycles with breeding commencing in December of the 1985/6 and 1987/8 cycles, but not until February of the 1986/7 cycle. Breeding ceased in July/August of each cycle.

Historically, seasonal reproduction in field populations of *R. sordidus* has been attributed to rainfall which regulates food supply (Gard 1935; McDougall 1946; Redhead (1973, 1980). However, the nature of the food sources and how they may effect seasonal breeding have not been defined. Fellows and Sugihara (1977) reported fruit and cane borer grubs to be favoured food sources of Norway rats (*R. norvegicus*) and Polynesian rats (*R. exulans*) in Hawaiian sugarcane fields. As sugarcane crops are generally protein deficient environments; crude protein only represents 1.2% and 2.2% of the pith and rind of cane respectively (Garrison and Breidenstein 1970); it was suggested that fruit and cane borer grubs provide a major source of carbohydrate, protein and fat to rodents. Bates (1960), observing most damage in immature and mature crops to be confined to the apical growing point suggested that this tissue is chosen for its higher amino acids and/or trace elements content. Considering the low nutritional quality of sugarcane together with evidence suggesting that rodents only begin to attack cane when it is approaching maturity and sucrose is being stored (Fellows and Sugihara 1977; Garrison and Breidenstein 1970) it is apparent that sugarcane is mainly utilised by rodents as a source of moisture or due to its high palatability (Garrison and Breidenstein 1970; Hood *et al* 1970; Azizi and Sund 1971).

Woods (1966) observed stomachs of *R. sordidus* to contain a high volume (greater than 50 percent of volume) of grasses and other non-cane vegetation in December and from February to April (no sample for January). Analysis of stomach contents in this study also indicate variability in diet throughout the year. Although sugarcane is utilised as a food source throughout the year, an increase in non-cane vegetation and seed in the diet occurs over the December - April period, corresponding to the period over which summergrasses are available in crops. As breeding is coincidental with summergrass availability, it may be inferred that summergrasses, which contain relatively higher levels of protein compared

to sugarcane (Butler and Barley 1973), provide *R. sordidus* with the high level of nutrition required for reproduction. This is further denoted by peak breeding intensity occurring immediately following peak biomass of summergrasses in crops.

The stimulatory effects of small amounts of dietary supplements on reproduction has suggested that the constituents of plant food rather than the biomass, may be the important factor in regulation of reproductive effort (Negus and Pinter 1966; Negus et al 1977; Alhibai 1985). From this study it is not possible to determine whether reproduction of *R. sordidus* was triggered by some plant chemical compound or an increase in condition of individuals associated with the availability of a more nutritious food source. Whatever the factor responsible, it is evident that the availability of summergrasses contributes to the variability of reproductive effort throughout a district and possibly between years.

This conclusion, in part, supports the mechanism proposed by Redhead (1973, 1980). Rainfall may have an effect on the overall potential for reproduction through its effect on growth of summergrasses. In this study, rainfall during the November - January period determined when summergrasses became available. Onset of breeding was delayed until February in the 1986/7 cycle when rainfall over the November - January period was low. In other years, rainfall was average during this period and breeding commenced in December.

A direct cause for cessation of breeding in July/August is not evident from this study but may be attributed to a decrease in condition due to poor food supply; temperature effects; social factors; or a combination of these factors.

The decline in breeding intensity of *R. sordidus* each year coincided with a decline in the availability and possibly nutritional quality of summergrasses in crops. The decline in availability of summergrasses was reflected by an increase in utilisation of sugarcane as a food source by *R. sordidus*. Warneke (1971) observed that reproductive rate of bush rats (*R. fuscipes*) varied with changing availability of the preferred food sources. Reproduction only occurred during the period when seeds and arthropods (providing a source of carbohydrate, fat and protein) were abundant. Cessation of reproduction was attributed to rats being in poor condition during other periods when pine bark (a low quality food source) was utilised. The decrease in breeding intensity of *R. sordidus* may therefore be due to a decline in condition of animals with a low nutritive diet.

The end of the breeding period also coincided with a decrease in temperature. Maintenance of reproductive condition by male *R. sordidus* in field populations throughout the year (McDougall 1946a) suggests that reproductive potential is dependent on the female, an occurrence which has been reported for other species (Warneke 1971; Cockburn 1981). As a faster metabolic rate is generally the consequence of lowered temperatures (Barnett and Coleman 1959; Sadleir *et al* 1973), it is likely that female *R. sordidus* needs to expend more energy on maintaining body temperature rather than reproductive effort, hence the cessation of breeding during winter months. Lower temperatures may also indirectly affect breeding by affecting food resource quality, as observed for populations of house mice in cereal farms of New South Wales (Bomford 1987b).

Cessation of breeding may also be considered as a consequence of increased population densities leading to increased stress in *R. sordidus* populations. The end of each breeding season coincided with a peak in population density. It is therefore possible that increased population density,

at a time when the preferred food supply is limiting, leads to increased stress, a decrease in condition and therefore cessation of breeding.

McDougall (1946b) suggested that juvenile mortality was a reason why *R. sordidus* populations never reached their full potential. In this study, trap success of juveniles increased soon after breeding onset, and increased to a peak one to two months following peak breeding intensity. However, trap success of juveniles did not appear to be related to breeding intensity, being lowest in the 1987/8 cycle and similar in 1985/6 and 1986/7 despite pronounced differences in breeding activity. McDougall (1946a) considered several factors which may contribute to variable recruitment of juveniles throughout the year, given the potential for continued breeding. From direct observations in the laboratory, it was ascertained that immediately following birth, up to one sixth of the litter was killed and eaten by either the male or female. Embryo absorption due to below optimal conditions was also considered as an important variable, and was indicated as being the first sign of a population crash. In this study, trappability of juveniles may have varied between cycles, depending on the density of the mature population. Alternatively, juvenile mortality may be lower when there are fewer mature individuals competing for resources.

The presence of juvenile individuals in all months of the study suggests that breeding continues throughout the year. Taylor and Horner (1973) reported births to occur in all months except September and October. McDougall (1944), Gard (1935) and Sawers (1938) also suggested that breeding may occur throughout the year providing sufficient nutritional food sources are available. Such a strategy may be extremely important for survival of populations during years of unfavourable conditions when quality or quantity of food resources are low.

After the June/July period, population levels decrease due to mortality and/or dispersal of animals prior to harvest of the crop. McDougall (1946b), suggested that the sharp decrease in population levels from late June to August, was due to increased mortality as a result of unfavourable conditions during a period of high population movement. As condition of the animal has probably decreased due to a non-nutritional diet, and additional stresses are placed on *R. sordidus* due to a decrease in the cropped area, it is likely that this decrease is due to mortality rather than dispersal.

Spatial heterogeneity is a characteristic of most agricultural systems. Expanses of crop monoculture are frequently interspersed with areas of natural vegetation which act as 'donor' habitats to rodent pest populations (Hansson 1977). The significance of permanent non-crop habitats for survival of rodent pest species in agricultural systems has been reported (Bykovsky 1986; Hood *et al* 1970; Lindsey *et al* 1973; Newsome 1969; Singleton 1985; Singleton 1989; Williams *et al* 1978).

Non-crop habitats are extremely important to Polynesian rats (*R. exulans*) in Hawaiian sugarcane growing areas (Hood *et al* 1970; Lindsey *et al* 1973; Fellows and Sugihara 1977). Hood *et al* (1970) reported that only 10 percent of rodents in Hawaiian sugarcane fields survive harvest. Colonists for new crops are therefore derived from populations which reside in gulches (Lindsey *et al* 1973; Fellows and Sugihara 1977). In North Queensland, the spatial nature of the sugarcane landscape ensures that permanent non-crop habitats are available to rodents during the harvest period, when the area of crop available to *R. sordidus* is reduced. These areas may therefore have some significance for survival of *R. sordidus* between crop cycles.

Higher population densities and a higher level of damage to sugarcane crops in close proximity to non-crop habitats (Redhead 1973; Redhead and

Saunders 1980), indicate that *R. sordidus* utilise non-crop areas, although the significance of these areas for survival of populations during the harvest period and the proportion of *R. sordidus* surviving from one season to the next have not been documented.

McDougall (1947), observing extensive areas of suitable non-crop habitat to occur without the presence of *R. sordidus*, considered that survival, productivity and distribution of *R. sordidus* populations in Queensland cane-growing areas were not influenced to any great extent by the presence of non-cane harbourage (eg. grassland, swamp or open forest habitat). It was suggested that as sugarcane fields comprise a significantly greater proportion of the district compared to non-cane areas, they provide a more important harbourage. During the harvest period, unharvested crops provide a more important 'refuge' for dispersing animals and a 'source' of colonists to new crops than non-crop habitats.

The disturbances associated with its cultivation ensure, however, that sugarcane crops can only be considered as a temporary habitat in comparison to the permanent nature of non-crop areas (Redhead 1973). The relative importance of wasteland (undisturbed grassland) and sugarcane fields as harbourage, and thus reservoirs for reinvasion, was demonstrated by Redhead (1973) in a study of rodents in the Babinda district. Damage was significantly higher in fields adjacent to wastelands of dense Para grass, than fields adjacent to other habitat types. It was suggested that weed infested drains may also provide harbourage to *R. sordidus* following observations of high damage in canefields with these areas adjacent.

The suitability of grasslands as habitat for *R. sordidus* was highlighted in this study. Population levels in this habitat type were consistently higher than in the adjacent crop during all stages of the population cycle.

Woodlands and the grassy fringes of drainage channels and swamps also supported substantial populations of *R. sordidus* though not at the same densities as grassland habitats. Low light penetration and sparse ground cover in the closed forests may have resulted in low utilisation of this habitat by *R. sordidus*. Grazing paddocks were also poorly utilised, with low grass heights and the compaction of the soil by cattle making burrowing and the colonisation of such areas difficult. It is apparent that the physical structure and vegetational composition of non-crop habitats are therefore critical to the level of utilisation by rodents. The blady grass of woodlands and para grass of drainage channels and swamps provide suitable cover for colony establishment whereas the wide variety of herbs and grasses available as a food source in the grassland areas result in heavy colonisation and utilisation.

Redhead and Saunders (1980) suggested that crops in close proximity to areas of wasteland (suitable non-crop refuges) may be colonised earlier. Rodents would therefore be present in crops and cause damage over a longer time period. In the present study, the level of utilisation of the non-crop habitat was not reflected by population levels in the adjacent crop. For example, the population in a crop adjacent to a grazing paddock (a poorly utilised habitat) was higher than the population in a crop adjacent to a grassland (a highly utilised habitat). This indicates that incrop factors such as soil type (suitability for burrowing) and weed cover (food sources) have a greater influence in determining population size than adjacent non-crop habitat type, and therefore has important implications for management. Although the presence of favourable non-crop habitats in an area may contribute to high survival rates during the harvest period and therefore the potential for higher population densities and damage within an area, effective incrop management may reduce damage potential on a local scale.

3.2 THE MACKAY DISTRICT

The major population processes that regulate *R. sordidus* populations in the Herbert River District have been documented in section 3.1. If control strategies based on an understanding of these mechanisms are to be useful to the sugar industry, it is important to determine if populations in other districts are regulated by similar mechanisms. A two phase approach of (a) determining the processes responsible for damage and then (b) providing validation of the importance of these processes in regulating populations in a geographically isolated area was taken to ensure that the results of the study do not simply relate to a particular district but that they are applicable to populations throughout the major sugarcane growing areas. The Mackay district was chosen for phase (b) as it includes most of the non-cane habitats that occur throughout the sugarcane growing areas of Queensland and is geographically isolated from the Herbert River District.

3.2.1 The study area

The Mackay canegrowing district, located on the central coast of Queensland, covers an area of approximately 290 000 hectare (Figure 3.10). It encompasses all cane land for the sugar mills of Cattle Creek, Marian, Pleystowe, Racecourse and Farleigh.

Monthly rainfall for the period January 1988 to December 1991 and long term averages for six stations throughout the district are shown in Figure 3.11. Rainfall is variable throughout the district, decreasing westward from Mackay and then increasing in the Cattle Creek area (Finch Hatton area). Rainfall along the coast is relatively uniform. Approximately 70% of the yearly rainfall occurs over the December - March period. Tropical cyclones may occur from December to April.

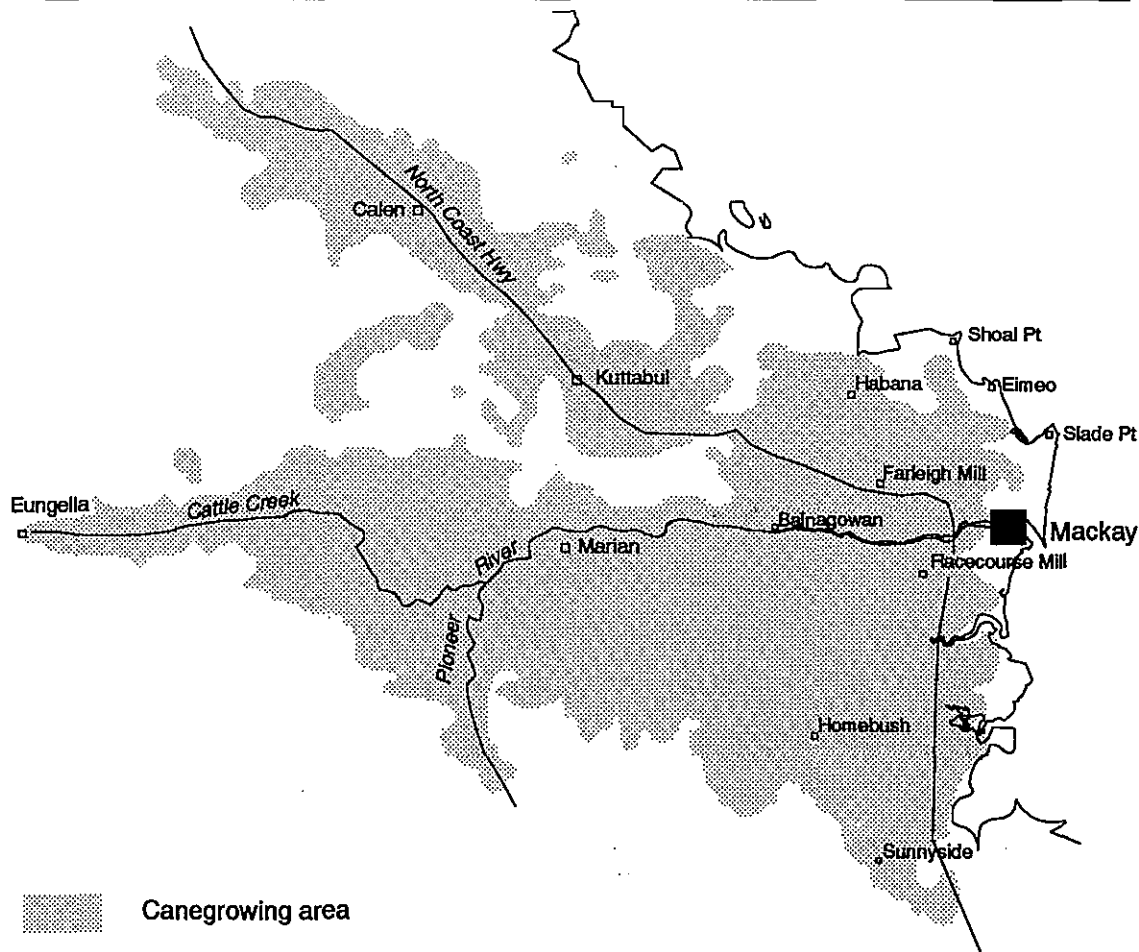


Figure 3.10 Sugarcane growing area of the Mackay District

Cyclones in April 1989 and December 1990/January 1991 resulted in moderate to severe flooding in many parts of the district. Unseasonably low rainfall occurred in January 1988, January 1989, December 1989, February 1990 and January to March 1991.

Much of the land within the district has been cleared for sugarcane. In general, natural vegetation is now restricted to isolated hills, mountains and the banks of watercourses. Major non-cane habitats include open *Eucalypt* woodlands, forests, grasslands (mainly grazing land), freshwater swamps and mangrove communities. Closed forests are restricted to stream terraces or sheltered gullies.

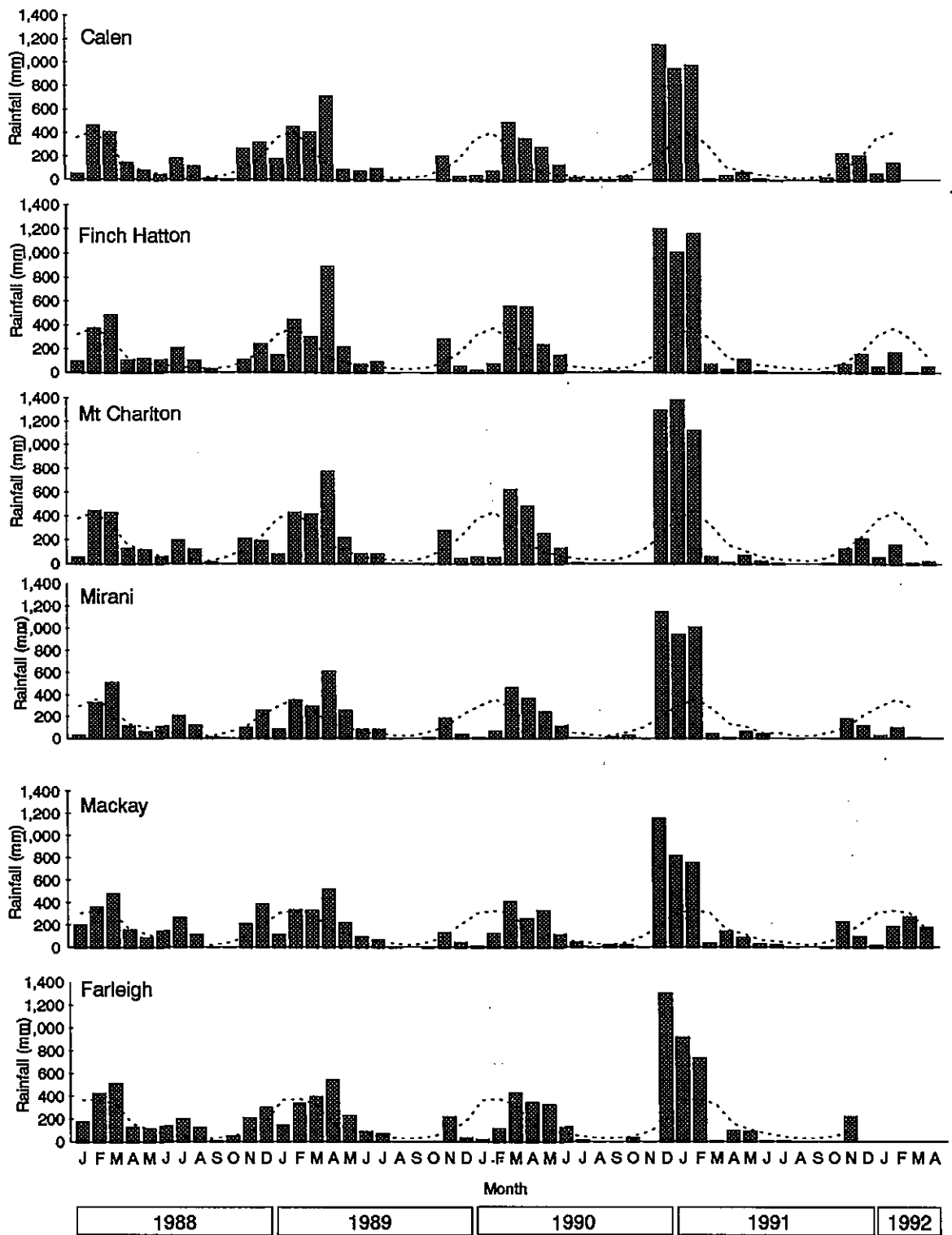


Figure 3.11 Monthly rainfall and long term averages for six stations in the Mackay canegrowing district

3.2.2 Methods

The district was divided into 42 zones on the basis of:

- . geographic isolation
- . topography
- . soil type
- . frequency and type of non-crop habitats.

A description of each zone is given in Appendix 1.

The rodent population and habitat attributes were monitored monthly at one site (sugarcane crop) selected at random within each zone from December 1988 to September 1990 (Figure 3.12). In September 1990, it became apparent that the diversity and spatial distribution of non-crop habitats in the north coast district was more complex than originally considered and so the 42 original zones were revised to cater for this complexity. Zones were redefined (Figure 3.13) resulting in a reduction in the number of zones in the more homogeneous southern area and an increased number of zones in the north coast area (Table 3.16). Sampling commenced at these new sites in December 1990.

On one night per month for the duration of the study, one line of twenty snap traps baited with paper soaked in linseed oil were set in the canefield at each site. Traps were laid at ten metre intervals within each trapline.

All animals were autopsied and the following data collected:

- . Location
- . Sex and reproductive condition:
 - Males: testes abdominal - immature
 - testes scrotal - mature

- Females
- immature - Vaginal perforation occurs at an age of approximately 37 days although first oestrus does not occur until an age of approximately 70 days, corresponding to a head-body length of 125mm (McDougall 1946b). A head-body length of 125mm was therefore assumed as the upper limit of the immature female stratum.
 - pregnant - Determined by dissection. The number of embryo were also recorded.

- . Head-body length (mm)
- . Weight (g)
- . Stomach contents: The amount of sugarcane, seed, non-cane vegetation and other material was estimated as a volume percentage of the total stomach contents (to the nearest 10%).

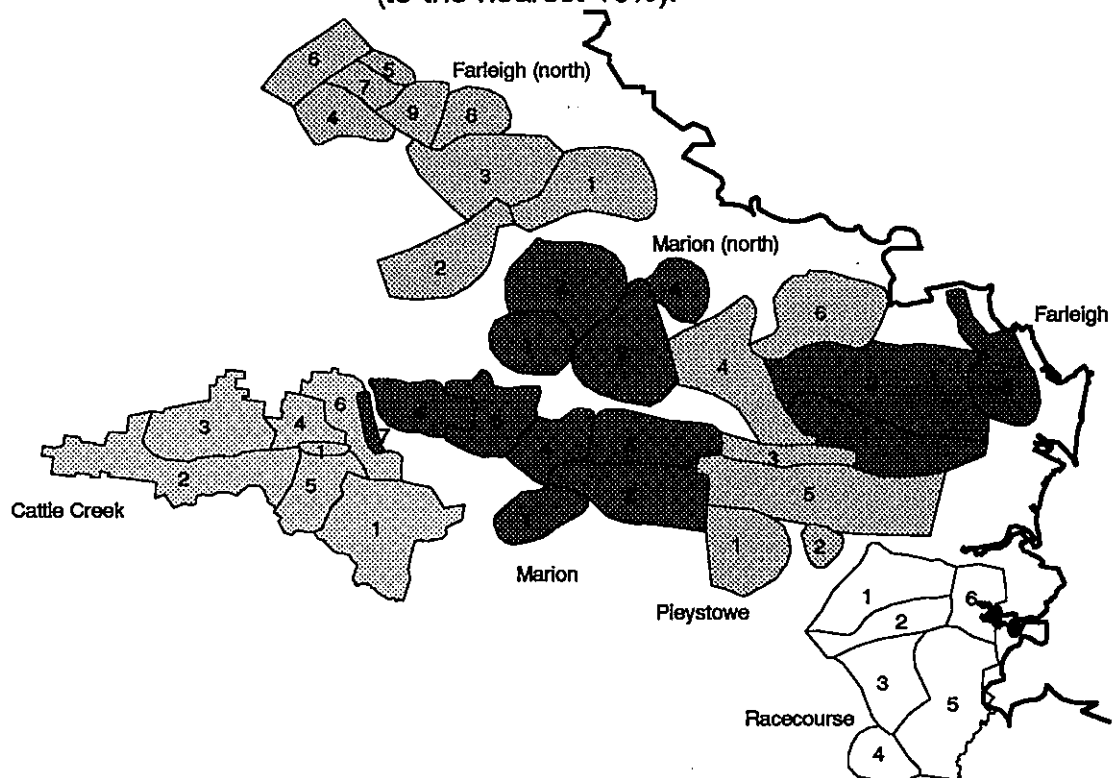


Figure 3.12 Study zones within mill regions of the Mackay canegrowing district
Zones are numbered within each mill region

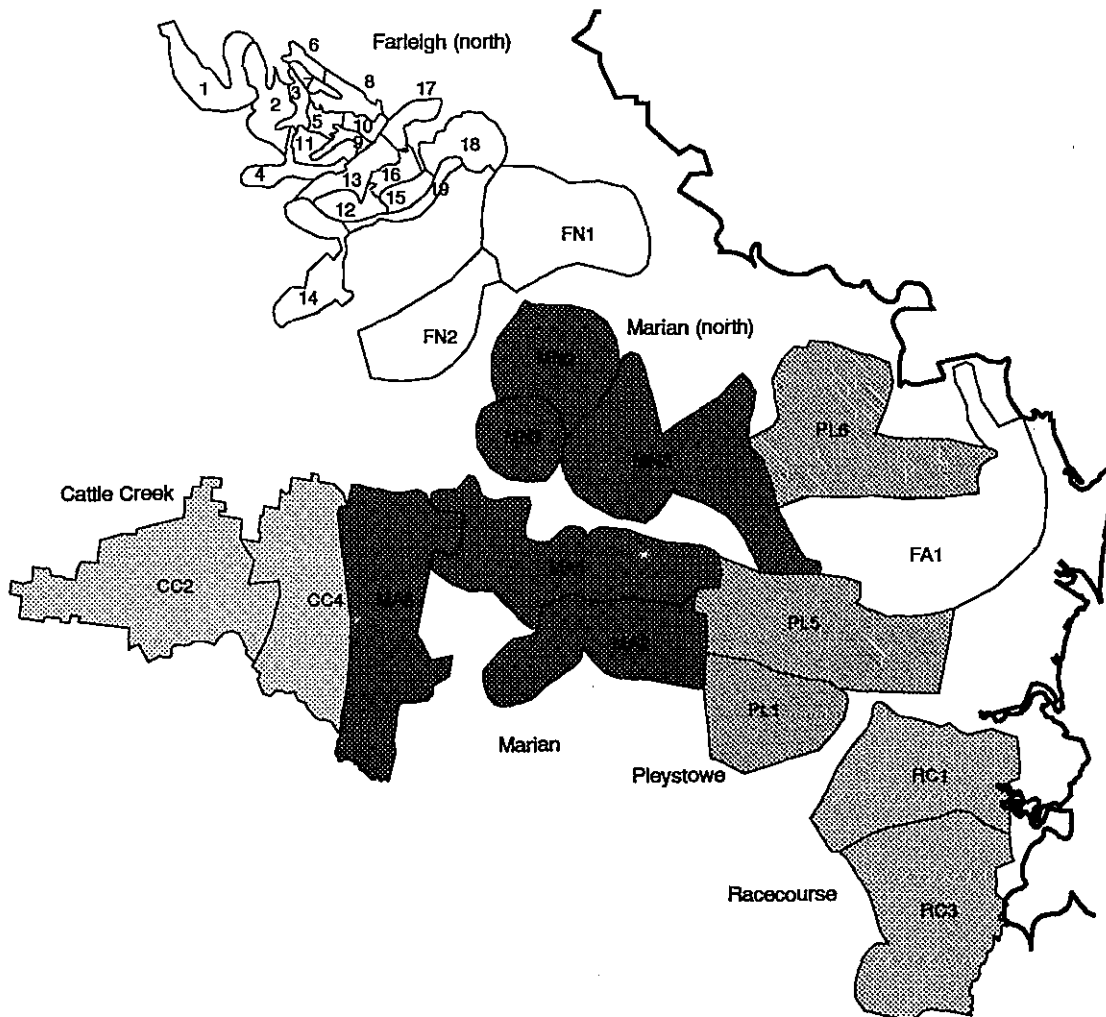


Figure 3.13 Study zones (October 1990 to December 1991)
Zones are coded within each mill region

Non-cane vegetation in each of the crops was subjectively assessed as light, moderate, heavy or very heavy in accordance with experiences in the Herbert River District. Weed species were recorded in order of dominance (ground cover). Any major perturbations or farm management practices occurring since the previous trapping session were also recorded.

Damage was also subjectively assessed as absent, light, moderate or severe in accordance with experiences in the Herbert River District.

Table 3.16

Original and revised distribution of sites throughout the Mackay District

Area	Number of defined areas	
	Original	Revised
Cattle Creek	6	2
North Eton	1	0
Marian	7	3
Pleystowe	6	3
Racecourse	6	2
Farleigh	3	3
Marian (north)	4	3
Farleigh (north)	9	21
Total	42	37

3.2.3 Results

In-crop weeds

The percentage of crops with incrop weed cover varied throughout each crop cycle, increasing from less than 20% of sites during the September - November period to more than 60% of sites from January to July.

Four weed species predominated in crops over the study period, although there was seasonality in their occurrence. Nut grass (*Cyperus rotundus*) was the dominant species in a small percentage of crops during the early half of the crop cycle (September 1989 to May 1990; December 1990 to April 1991). Barnyard grass species (*Echinochloa spp.*) and summer grass (*Digitaria ciliaris*) predominated in crops over the December - June period each year. The percentage of crops where *Ageratum spp.* was the predominant species increased from April to June when it was dominant in more than 50% of crops.

The level of cover of summergrasses varied between years. Heavy cover was only recorded in more than 15% of crops in April 1989 and February 1991. A higher percentage of crops supported moderate to heavy levels of summergrass cover in 1991 than any other year. The diversity and successional cycle of in-crop weeds followed the same pattern as in the Herbert River District.

Crop populations

Over the period of the study, December 1988 to December 1990, a total of 538 *R. sordidus* and 104 *M. burtoni* were captured. Incidental captures were made of *R. rattus* (black rat), *Mus domesticus* (house mouse) and *Hydromys chrysogaster* (water rat). *R. sordidus* and *M. burtoni* represented 89.1% and 8.9% of total captures respectively.

Population trends over the study period are shown in Figure 3.14. Overall trap success varied significantly between the 1988/89 and 1989/90 cycles with an overall trap success of 3.82% and 4.62% respectively ($\chi^2_1 = 6.16$, $p < 0.05$). Due to the relocation of sites in October 1990, it was not valid to compare trap success in the 1990/91 cycle with that of previous cycles.

Fallow and recently harvested sites (crop age=0) were not sampled. Percentage trap success was always low in new crops (Table 3.17) and pregnancies were only recorded in crops greater than two months of age indicating that crops are colonised annually by *R. sordidus*.

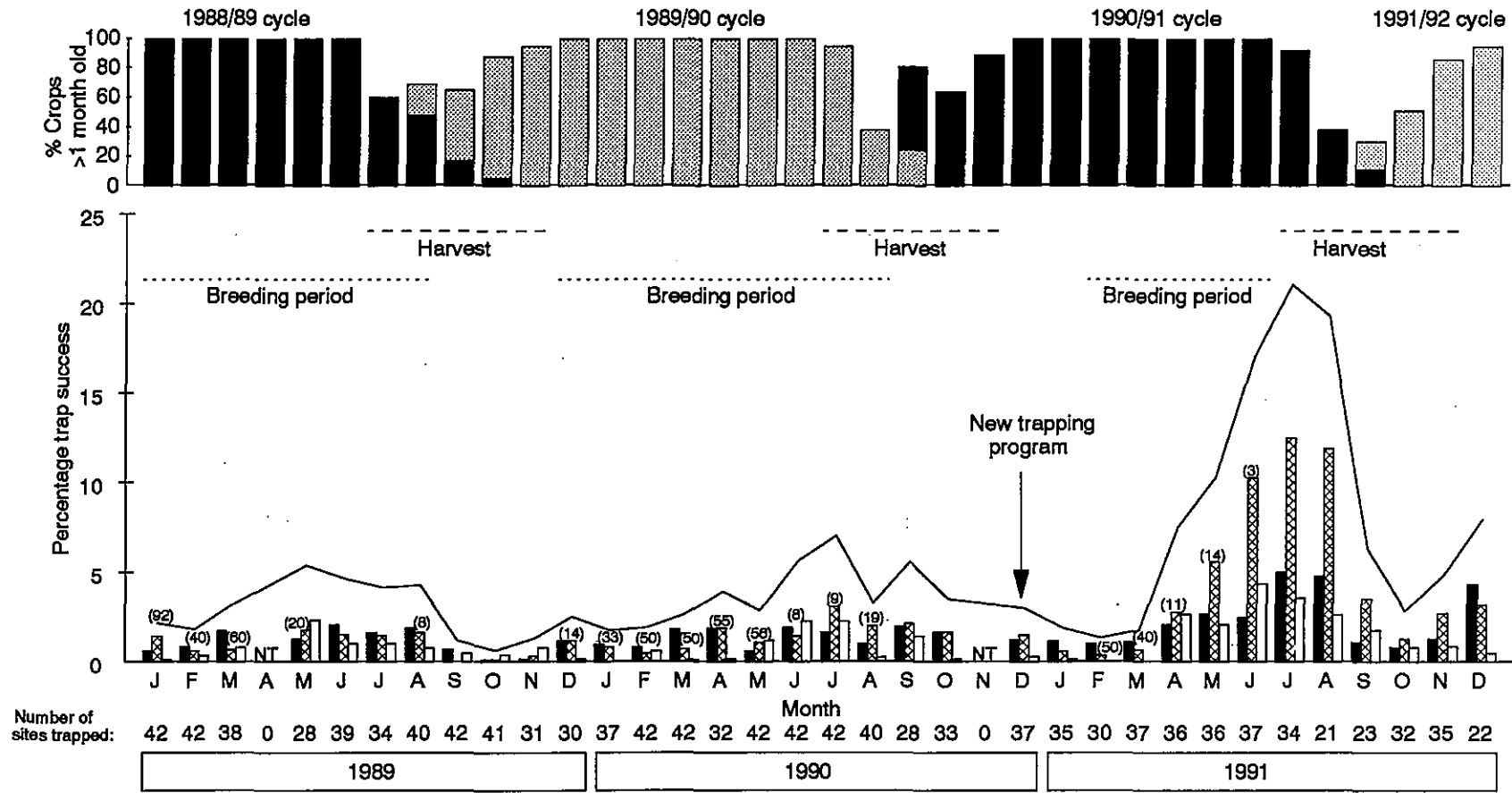


Figure 3.14 Population characteristics of *R. sordidus* in crops of the Mackay District
(No trapping was undertaken in fallow fields)

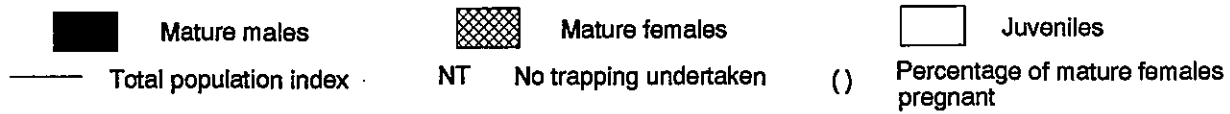


Table 3.17Trap success of *R. sordidus* in crops of each age class

Crop age (months)	1989	1990	1991
1	0.83 (840)	0.19 (520)	1.32 (680)
2	0.50 (800)	2.50 (480)	4.46 (740)
3 - 4	1.98 (1060)	1.85* (920)	4.57* (920)
>4	5.22* (5100)	5.45* (5960)	10.86* (5140)

() Number of trap nights per year

* Pregnancies recorded in sample

Table 3.18 shows that the majority of crops were not colonised until at least two months following harvest and/or planting. In the 1989/90 and 1990/91 cycles, 45% and 55% of sites had been colonised by the time crops were four months old. During the 1991/92 cycle, 92% of sites had been colonised when crops were four months old. Sites were relocated following the 1990/91 colonisation phase.

In all years of the study, both mature crops awaiting harvest and newly planted crops were present over the July - December period due to staggered harvesting throughout the district (Figure 3.14). Consequently, there was overlap between the three population cycles documented in this study (January to September 1989; July 1989 to September 1990; July 1990 to August 1991).

Table 3.18

The percentage of crops where *R. sordidus* were trapped and crop age during each crop cycle

Crop age (months)	Percentage of crops in which <i>R. sordidus</i> were trapped ¹		
	1989/90	1990/91	1991/92*
1	0	9	5
2	0	13	19
3	5	13	24
4	5	17	
5	10	22	
6	17	22	
>6	33	61	
Total number of crops	42	42	37

¹ Greater than one capture of *R. sordidus* was required to avoid including incidental captures

* Crops were less than four months of age when trapping ceased

The two month period following harvest for a ratoon crop or planting of a new crop was defined as the colonisation phase (Tables 3.17 and 3.18). The period during which sites were being colonised extended from August 1989 to January 1990 (1989/90 cycle); July to December 1990 (1990/91 cycle) and August to November 1991 (1991/92 cycle). Sites had already been colonised at the commencement of the study in January 1989.

Colonists were defined as those animals trapped during the two months following harvest (for a ratoon crop) or planting (for a new crop). Conversely, established populations were from mature crops awaiting harvest. A comparison of the structure of established and colonising populations over the entire study period (Table 3.19) showed that there was no significant difference in either the adult sex ratio ($\chi^2_1 = 0.11$, $p > 0.05$) or the proportion of juveniles ($\chi^2_1 = 0.14$, $p > 0.05$). No pregnancies were

recorded from either the colonising or established populations during the colonisation period of each cycle.

Table 3.19

The structure of colonising and established populations over the period of the study

Stratum	Number of captures			
	Colonising population		Established population	
Mature males	30	(0.33)	34	(0.35)
Mature females	42	(0.47)	44	(0.46)
Juveniles	18	(0.20)	18	(0.19)

() Proportion of population

The pattern of colonisation shown in Tables 3.17, 3.18 and 3.19 is identical to the pattern that occurred in the Herbert River district in all respects except that the colonising populations in the Herbert River District were biased towards mature males.

Over the study period 58 pregnancies were recorded. A well defined breeding period occurred during each crop cycle with greater than 95% of pregnancies being recorded during January to May 1989 (1988/89 cycle), December 1989 to August 1990, and February to June 1991 (1990/91 cycle).

Total reproductive effort over the December - August period varied significantly between cycles due to the extremely low pregnancy rate during the 1990/91 crop cycle ($\chi^2_2 = 49.12, p < 0.05$). Overall reproductive effort during the three cycles were 29%, 27% and 4% of mature females pregnant in the 1988/89, 1989/90 and 1990/91 cycles respectively (Table 3.20). The trend in breeding intensity within each crop cycle was not as

consistent as in the Herbert River District where maximum breeding intensity always occurred in the third month of the breeding season. In the Mackay District, maximum breeding intensity occurred in the fifth and first months of the 1989/90 and 1990/91 cycles respectively.

The interpretation of the data on reproductive effort and the timing of maximum reproduction in the Mackay District must be treated with extreme caution due to the abnormal rainfall conditions that existed over the breeding periods. Both the 1989/91 and 1990/91 breeding periods coincided with environmental catastrophes - an extremely severe drought in 1989/90 and extensive flooding in 1990/91 (Figure 3.11).

As in the Herbert River District, there was a strong relationship between breeding and the presence of summergrasses in crops. In the Mackay District, there was a strong correlation between the proportion of crops containing summergrasses and the proportion of mature females pregnant two months later ($r_s=0.765$, $n=18$, $p=0.0012$).

The number of embryos per pregnant female did not vary significantly during the breeding period ($F_{6,33} = 0.827$, $p=0.56$) or between cycles ($F_{2,54} = 1.02$, $p=0.36$). The number of embryos ranged from 3 to 13 with a mean of 6.95 ± 0.35 over the study period. The number of embryos was not correlated with head-body length ($r_s = -0.0648$, $n=45$, $p=0.67$) or weight ($r_s = 0.0534$, $n=45$, $p=0.73$) of pregnant females.

Pregnancies were only recorded for females having a head-body length exceeding 125mm (Table 3.21). Pregnancies were most frequently recorded for individuals having a head-body length greater than 150mm.

Table 3.20

Reproductive effort of *R. sordidus* over the study period

Cycle	Month of breeding period	Number of mature females	Percentage of mature females pregnant (number of pregnancies)	Number of embryos	
				Mean	Range
1988/89	(Dec)				
	1 (Jan)	12	92 (11)	7.4	4 - 13
	2 (Feb)	5	40 (2)	7.5	7 - 8
	3 (Mar)	5	60 (3)	8.7	6 - 10
	4 (Apr)	0	- (0)		
	5 (May)	10	20 (2)	6.0	5 - 7
	6 (Jun)	12	0 (0)	0	
	7 (Jul)	9	0 (0)	0	
8 (Aug)	13	8 (1)	3.0	3 - 3	
1989/90	1 (Dec)	7	14 (1)	8.0	8 - 8
	2 (Jan)	6	33 (2)	5.0	5 - 5
	3 (Feb)	4	50 (2)	6.0	3 - 9
	4 (Mar)	6	50 (3)	10.3	8 - 13
	5 (Apr)	11	55 (6)	8.5	6 - 11
	6 (May)	9	56 (5)	6.2	3 - 8
	7 (Jun)	12	8 (1)	12.0	12 - 12
	8 (Jul)	23	9 (2)	4.5	4 - 5
	9 (Aug)	16	19 (3)	3.3	3 - 4
1990/91	(Dec)	10	0 (0)	0	
	(Jan)	4	0 (0)	0	
	1 (Feb)	2	50 (1)	12.0	12 - 12
	2 (Mar)	5	40 (2)	7.0	7 - 7
	3 (Apr)	19	11 (2)	7.0	5 - 9
	4 (May)	35	14 (5)	6.2	3 - 8
	5 (Jun)	71	3 (2)	4.5	3 - 6
	(Jul)	83	0 (0)	0	
(Aug)	49	0 (0)	0		
Total	1	21	62 (13)	7.8	4 - 13
	2	16	38 (6)	5.7	5 - 8
	3	28	25 (7)	7.4	3 - 10
	4	41	20 (8)	7.8	3 - 13
	5	92	11 (10)	7.2	3 - 11
	6	21	24 (5)	6.2	3 - 8
	7	21	5 (1)	12.0	-
	8	36	8 (3)	4.0	3 - 5
	9	16	19 (3)	3.3	3 - 4

- No sample

Table 3.21

Number of females and percentage pregnant
within each head-body length class

Population cycle	Head-body length class (mm)					
	≤125		126 - 149		≥150	
	Percentage pregnant	Total females*	Percentage pregnant	Total females*	Percentage pregnant	Total females*
1988/89	0	10	45	11	71	21
1989/90	0	20	24	50	33	39
1990/91	0	58	7.5	67	9	78

* Total number trapped during the breeding period of each cycle.

Significant numbers of juveniles first entered the trappable population in February (1989), May (1990) and April (1991). As in the Herbert River District, the appearance of juveniles occurred three to four months after the onset of breeding and within one month of maximum breeding intensity (Figure 3.14). Maximum trap success of juveniles occurred one to two months following maximum trap success of pregnant females.

Trap success of juveniles varied significantly between cycles ($\chi^2_2 = 27.77$, $p < 0.05$). An index of recruitment was defined as the number of juveniles per mature female present during the breeding season. The recruitment index was similar in 1988/1989 and 1989/1990 at 0.42 (28/66) and 0.38 (36/92) respectively. The 1990/1991 index was higher at 0.5 (66/132). Juveniles were most abundant during the 1990/91 cycle with a mean trap success of 1.56% during the cycle. In contrast, mean trap success of juveniles was only 0.98% and 0.73% during the 1988/89 and 1989/90 cycles respectively.

In 1989 and 1990, maximum population size occurred *during* the breeding period (March 1989, July 1990). In all three years, maximum population size occurred at the beginning of the harvest period.

Diet

Throughout the study, seed, sugarcane and non-cane vegetation predominated in stomach contents. Unidentified matter was the major component ($\geq 50\%$) of stomach contents in only 4% of cases.

The frequency of sugarcane as the major component of stomach contents varied significantly during each year of the study (1989, $\chi^2_8 = 48.64$, $p < 0.05$; 1990, $\chi^2_{10} = 106.85$, $p < 0.05$; 1991, $\chi^2_{10} = 107.14$, $p < 0.05$). Sugarcane was most frequently the major component of stomach contents during the periods August to July 1989, August to December 1990 and June to December 1991.

There was no significant difference in the proportion of mature males or mature females with sugarcane as the major component of stomach contents during any cycle (Table 3.22).

Table 3.22

Proportion of mature male and female individuals with sugarcane predominating in stomach contents ($\geq 50\%$ of stomach contents)

Population cycle	Proportion of each strata with significant amounts ($\geq 50\%$) of sugarcane in stomach contents.		Difference between strata (χ^2_1)
	Mature females	Mature males	
1988/89	0.44	0.55	1.71 ($p > 0.05$)
1989/90	0.35	0.40	0.44 ($p > 0.05$)
1990/91	0.67	0.69	0.21 ($p > 0.05$)

3.3 DEVELOPMENT OF A PREDICTIVE MODEL

The studies in the Herbert River and Mackay Districts encompassed a range of environmental conditions (year types) from severe drought to cyclonic activity and widespread flooding. Environmental conditions

determined the degree to which population processes such as breeding intensity and juvenile recruitment were expressed in terms of maximum population size and damage.

It has been shown (sections 3.1.2 and 3.2.3) that the occurrence, timing and sequence of the population processes and organism/environment interactions that govern the operation of the populations are independent of environmental conditions and are consistent across the two geographically isolated areas (Table 3.23). This consistency between areas strongly suggests that a predictive model based on the data from this study will be applicable to all major sugarcane growing areas in North Queensland.

R. sordidus population dynamics followed a predictable cycle each year despite variable environmental conditions. It is apparent that the potential for population growth in any year is determined by the initial level of crop colonisation, rainfall during the November - January period and the availability of summergrasses. The influence of each of these factors on population levels in the Herbert River District is shown in Table 3.24.

In the 1985/86 cycle, relatively high population levels in June were the result of a high level of colonisation and good rainfall over the November - January period which contributed to good summergrass growth. Consequently there was a large breeding population present during the December - August period and a high rate of population growth. Population growth and crop damage was probably reduced as a result of severe flooding of the district associated with Cyclone Winifred (February 1986). Relatively low population levels in June of the 1986/87 and 1987/88 population cycles may be attributed to a low level of crop colonisation (as a result of population levels in the preceding year) and low rainfall during the November - January period resulting in low availability of summergrasses.

Table 3.23

Population processes in the Herbert River District (1985/88) and the Mackay District (1989/91)

Attribute	Herbert River District	Mackay District
Species composition	<i>R. sordidus</i> approximately 90%, <i>M. burtoni</i> less than 10%	
Habitat utilisation	Grasslands>sugarcane=open forest>closed forest=grazing	Not determined
Colonisation	Annual. Crops over two months of age are preferred.	
Colonising population	Mature, non-breeding. Dominated by mature males.	Mature, non-breeding. Equal representation of male and female.
Onset of breeding	Variable in time but correlates with the first appearance of summergrasses.	
Breeding intensity	Variable depending on environmental conditions. Occurs one month after the peak biomass of summergrasses (both areas) and three months after onset (Herbert River District).	
Pregnancies	No pregnancies in animals < 125 mm. Most frequent in animals > 150mm.	
Number of embryos	Constant regardless of environmental conditions. No strong correlation with physiological condition.	
Cessation of breeding	July/August regardless of environmental conditions. Coincides with the beginning of harvest.	
Juveniles	Enter population 3-4 months after onset of breeding and within one month of maximum breeding intensity. Maximum trap success within 1-2 months of maximum breeding intensity.	
Maximum population size	Variable in time but always occurs during the breeding season and coincides with the beginning of harvest.	
Diet	Sugarcane is predominant during the non-breeding period. Weeds predominate during the breeding season.	
Damage	Minimal during the breeding period. Increases from the end of the breeding season to harvest.	Not determined

Table 3.24

Population and environmental attributes of each cycle leading to a prediction of damage level

Attribute	Population cycle		
	1985/6	1986/7	1987/8
Level of colonisation (Percent trap success during colonisation)	1.5%	0.6%	0.9%
Rainfall* :			
November	High	Average	Average
December	Low	Low	Low
January	Average	Low	Low
Summergrass availability			
%crops with heavy grass cover in January	43%	10%	11%
Biomass in January (g.m ⁻²)	832	224	272
Month of peak biomass	January	March	Feb./Mar.
Breeding			
Onset	December 1985	February 1987	December 1987
Month of peak intensity	February 1986	April 1987	indeterminate
Percent pregnant at peak	50%	55%	-
Trap success at peak	1.94%	0.88%	0.59%
Percent mature females with HB \geq 150mm	73.3%	61.9%	65.8%
Population levels in June (i.e. percent trap success in month prior to commencement of harvest)	9.65%	5.15%	3.89%
Environmental catastrophes	Cyclone Winifred (February 1986)	-	-
Damage			
% damaged stalks	4.0%	2.5%	3.0%
tonnes sugar lost	1720	1160	1370

* Relative to long-term monthly averages

The data from both the Herbert River and Mackay Districts have been used to develop a model to predict damage levels within a district (Figure 3.15). The model allows a prediction of crop damage at harvest to be made in January of the same year.

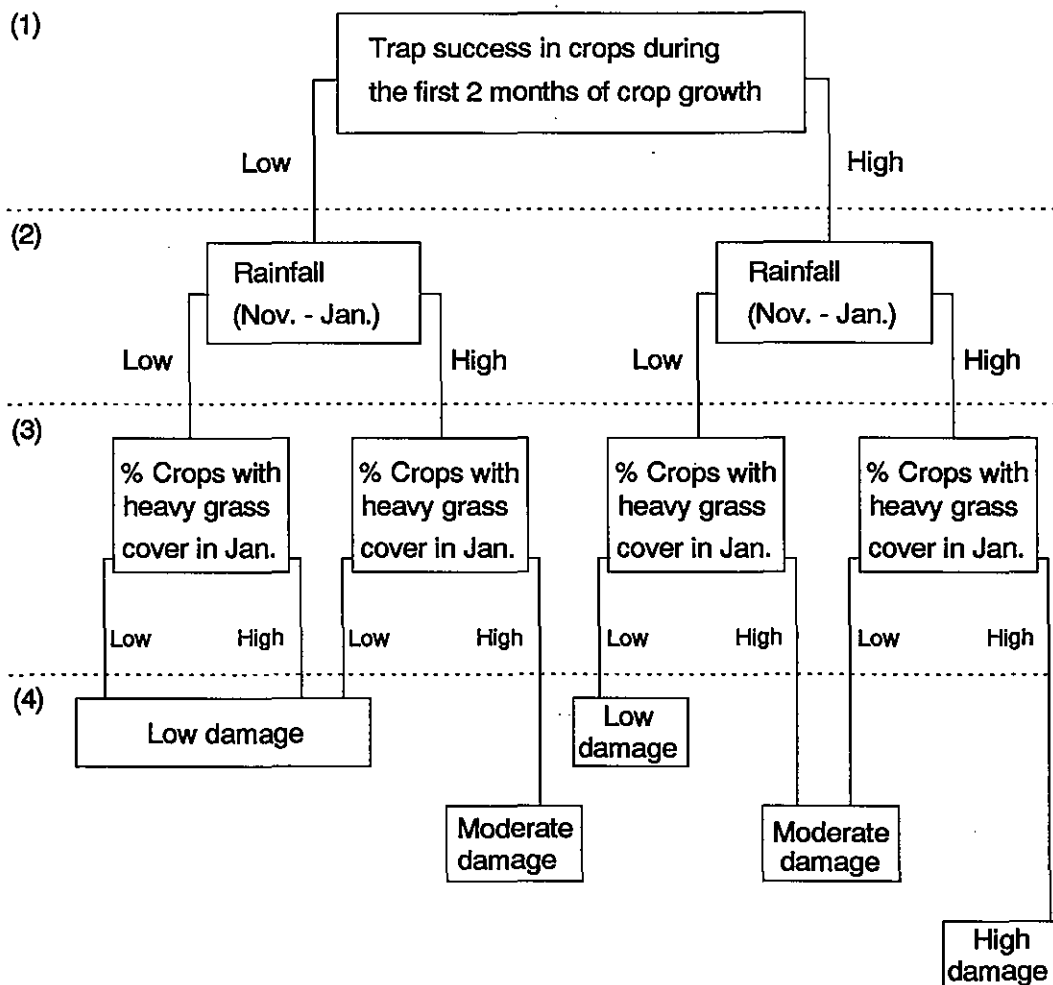


Figure 3.15 Model for the prediction of rodent populations in sugarcane growing areas of North Queensland

(1) *Level of colonising population*

Trap success of *R. sordidus* in young crops (crops <2 months old) during the colonisation phase (August - January) is an indication of survival during the harvest period. If trap success is high relative to previous years, it

follows that the potential for rapid population increase following colonisation will also be high. If trap success during this period is relatively low, the potential for large populations to develop is also low.

(2) Rainfall

Summergrasses are a favoured food source of breeding *R. sordidus* populations. The timing and intensity of the breeding period each year is determined by when these grasses become available both in and around crops. Rainfall directly affects summergrass growth both in and around crops. Average and above average rainfall (referred to as "High" in Figure 3.19) during the November - January period ensures optimal grass growth conditions. Rainfall must be consistent over this period to provide a constant supply of summergrasses in crops. In some instances, November rainfall may cause initial summergrass growth, but if rainfall in December and January is below average (referred to as "Low" in Figure 3.19), growth will be suppressed, breeding will be delayed and the potential for large populations will be reduced.

(3) Summergrass availability

Although directly linked to rainfall, in-crop summergrass availability may also be affected by cultural practices. Herbicide applications or heavy trash-blankets which suppress in-crop grass growth may result in a high percentage of the cropped area being relatively free of grasses. A reduction of the favoured food source is likely to result in reduced breeding effort and therefore a reduced potential for population growth. The effect of these agricultural practices on a local scale are discussed in more detail in Chapters 5 and 6.

(4) Crop damage at harvest

If information pertaining to the level of the colonising population, rainfall and summergrass availability are known, then a prediction of low, moderate or

high population and damage potential for the district may be made in January. This prediction may need to be modified during the ensuing months to account for environmental catastrophes such as severe drought or cyclonic activity.

Effect of environmental catastrophes

Cyclone Winifred (February 1986) caused severe flooding of the District in February 1986. Consequently, population levels were reduced and although breeding continued, populations did not achieve the potential level had the cyclone not occurred. Severe rodent damage was therefore avoided.

The occurrence of a cyclone causing severe flooding of a district will reduce the potential for population growth. However, in the instance where only a small proportion of the district is affected by flooding, rainfall may contribute to an increase in population growth potential due to increase in grass growth both in and around crops. As herbicide applications and slashing are not possible under extremely wet conditions the situation is exacerbated.

This system is designed to produce an indication of the relative level of damage that can be expected within a region. Division of a region into damage potential zones on the basis of landscape characteristics will allow control costs to be related to the level of damage (see chapter 6).

THE ROLE OF WEEDS IN THE DAMAGE PROCESS

4.1 INTRODUCTION

Most rodent control programs rely on the use of toxic baits to reduce population size. The control of *R. sordidus* in Australian sugarcane growing areas is no exception in that it currently relies on the widespread aerial application of packeted thallium-treated wheat baits. Trials in the Herbert River and Babinda districts have shown that although this procedure can significantly reduce the incidence of damage, results are extremely variable with success depending on the severity of the rodent infestation and the timing of the control procedure (Hitchcock and Kerkwyk 1975; Hitchcock 1973; Redhead 1973).

Many alternative approaches to rodent control, whilst theoretically attractive, are either impractical or uneconomic. Taylor (1972) suggested synchronous harvesting as a means of preventing rodents taking refuge in neighbouring crops coupled with an amalgamation of fields into a large monoculture in order to reduce the number of crop margins available for colonisation whilst Redhead (1980) advocated the destruction of adjacent non-crop habitat together with perimeter baiting as a control procedure. McDougall (1946a,b), Taylor (1972) and Roach and Evans (1979) examined the possibility of breeding "rat resistant" varieties of sugarcane with a thick, hard rind.

The most practical and environmentally acceptable alternative to baiting is habitat manipulation - the manipulation of habitats that are critical to the development or maintenance of high reproductive rates within the rodent population. Habitat manipulation has been used successfully in the management of a variety of small mammal pests, for example populations of snowshoe hare have been suppressed by removing deciduous shrubs that provided ground cover (Sullivan and Moses 1986). Vole and pocket

gopher populations in orchards were controlled by eliminating ground cover with herbicides (Godfrey 1985) and the removal of weeds from ricefields resulted in a reduction of damage due to *R. argiventer* (Drost and Moody 1982).

Habitat manipulation has also proved successful in reducing rodent damage to sugarcane. Dopenmeyer (1936) showed that *R. rattus* invaded several Hawaiian canefields from adjacent scrubland. The removal of isolated patches of this refuge resulted in a lower level of damage to sugarcane. More recent methods of controlling rodents in Hawaiian canefields include the removal of cycads (in particular *Cycas revoluta*) from crop margins where they were providing a primary food source for rodents during part of the year (Yabe and Wada 1983) and the reduction of in-crop weeds (Fellows and Sugihara 1977).

The regional trapping program of this study showed that the diet of *R. sordidus* in sugarcane paddocks consisted predominantly of non-cane vegetation during the breeding season although sugarcane was available at this time (Chapter 3). The switch to a diet of predominantly sugarcane coincided with the end of the breeding season in all years of the study. In addition, the onset of breeding coincided with the first appearance of summergrasses (*Digitaria ciliaris*, *Brachiaria subquadriflora*, *Echinochloa crus-galli*, *Echinochloa colona* and *Eleusine indica*) in and around crops.

In its native habitat the diet of *R. sordidus* consists mainly of grasses together with a small quantity of seeds and insects (Taylor and Horner 1973; Watts 1977). In canegrowing areas the diet has been extended to include sugarcane (Harrison 1962; Woods 1966).

Woods (1966) observed that the proportion of sugarcane in the diet varied throughout the year. From November to March only a small percentage of

R. sordidus stomachs contained sugarcane and then only in small amounts. There was a dramatic change in diet over the March/April period when over 60% of *R. sordidus* stomachs contained significant quantities of sugarcane. Over the April/October period, sugarcane was the major food source.

Seasonal dietary preferences and the timing of the damage process were recognised by Fellows and Sugihara (1977) and Garrison and Breidensen (1979) where it was shown that rodents only attacked Hawaiian sugarcane once it had matured and sucrose had been stored. These and other studies (Hood *et al* 1970; Azizi and Sund 1971) suggested that rodents utilise sugarcane as either a palatable luxury item or as a source of moisture.

In Australia, Redhead (1973) observed higher damage in sugarcane crops adjacent to drainage channels and wastelands supporting large stands of para grass (*Brachiaria mutica*) and suggested that the reduction of weed biomass around and within crops may result in a reduction of damage. This suggestion was based only on observation and no mechanism linking weeds and damage was proposed.

This study was implemented to assess the effect of in-crop weeds on the population dynamics of *R. sordidus*. A better understanding of the relationships between the dynamics of this pest species and the agricultural system may provide the basis for an alternative control strategy.

4.2 METHODS

The study was undertaken in the Herbert River District. The site consisted of a 16ha field of plant cane surrounded on three sides by a road. The fourth side was bounded by a cleared drainage channel. The field was divided into two treatment areas (Figure 4.1):

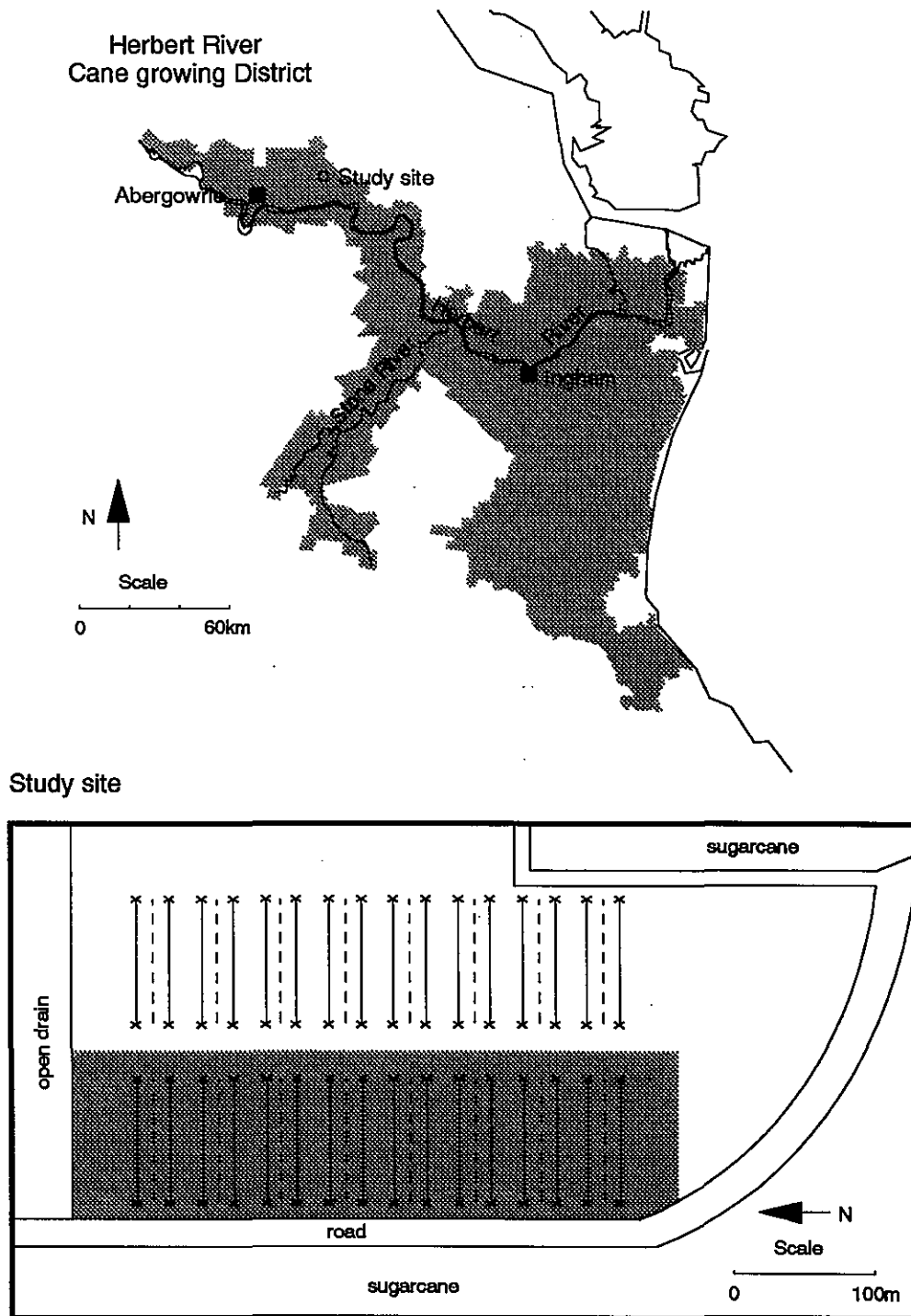

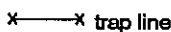




Figure 4.1 Location and design of the study site

- | | | | |
|---|-------------------------|--|------------------------------|
|  | Weeded treatment area |  | x---x trap line |
|  | Unweeded treatment area |  | ----- damage sample transect |

1. Weeded area: weeds and grasses were controlled by spraying with Atrazine (6 l.ha^{-1}) and Shirquat (1.4 l.ha^{-1}) in January.
2. Untreated area: no herbicide was applied.

The physical layout of the treated and untreated areas was dictated by the grower hence a Latin Square design was not possible.

The study site was aerially baited with thallium sulphate as part of a regional baiting campaign in early April.

On one night per month from December to July, 160 snap traps baited with paper soaked in linseed oil were set in each treatment area as indicated in Figure 4.1. Ten traps were laid at ten metre intervals in each trapline. A 50 metre buffer zone separated the traplines in the two treatment areas.

All animals were autopsied and the following data collected:

Treatment area

Sex and reproductive condition:

Males: testes abdominal - immature

testes scrotal - mature

Females perforate - Vaginal perforation occurs at an age of approximately 37 days although first oestrus does not occur until an age of approximately 70 days (McDougall 1946b) therefore an immature stratum was not defined.

pregnant - Determined by dissection.

- . Head-body length (mm)
- . Weight (g)
- . Stomach contents: The amount of sugarcane, seed, non-cane vegetation and other material was estimated as a volume percentage of the total stomach contents.

Non-cane vegetation in each of the treatment areas was sampled monthly. Forty 0.5m x 0.5m (0.25m²) quadrats were placed at random within each treatment area and the above-ground vegetation harvested. Total wet weight (g) and dominant species were recorded.

Rodent damage in each treatment area was determined each month as the number of bitten stalks in a row of 500 consecutive stalks (eight rows per treatment area). The same stalks were examined each month to provide an estimate of cumulative damage (Figure 4.1).

4.3 RESULTS

Over the period of the study, 269 individual *R. sordidus* were captured (Table 4.1) together with incidental captures of *Uromys caudimaculatus* (white-tailed rat) and *R. rattus* (black rat).

The site was colonised in October/November and by December a mature, breeding population of *R. sordidus* was established throughout the site (Figure 4.2).

The mature population remained stable at a relatively low density from December to February before increasing towards the end of the breeding season. Further population growth was temporarily halted when the district was aerially baited with thallium sulphate in April. The rapid increase in population size after May corresponded to the harvesting of adjacent fields.

Table 4.1

Captures of *Rattus sordidus* throughout the study period.

Date	Unweeded section				Weeded section			
	Males		Females		Males		Females	
	Immature	Mature	Perforate	Pregnant	Immature	Mature	Perforate	Pregnant
December	0	4	0	3	0	7	1	3
January	0	5	2	4	0	3	0	2
February	1	3	3	1	1	0	2	3
March	6	8	11	4	1	4	1	3
April	6	2	12	2	0	0	1	0
Total	13	22	28	14	2	14	5	11
May	9	3	11	0	3	2	2	0
June	10	2	16	0	8	5	18	1
July	14	15	14	0	7	2	17	1
Total	33	20	41	0	18	9	37	2
Total period	46	42	69	14	20	23	42	13

Shaded box: Breeding period

Clear box: Non-breeding period

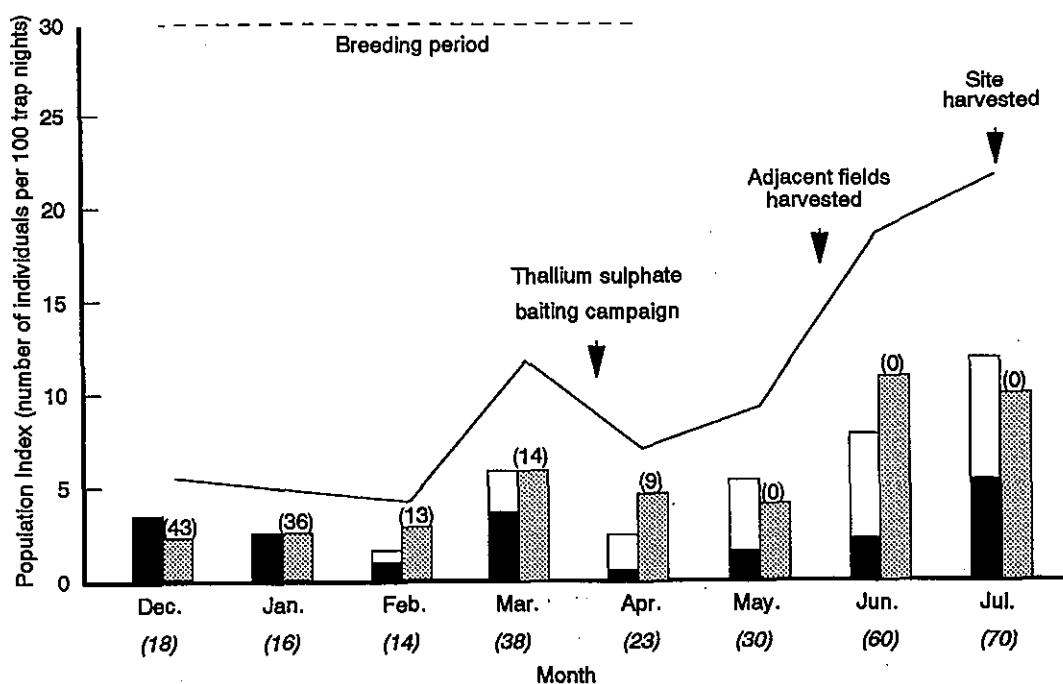


Figure 4.2 Population characteristics of *R. sordidus* in the study site

■ Mature males ▨ Females — Total population index
 □ Juvenile males () Percentage of females pregnant
 () Number of animals trapped

Pregnancies were recorded over the December/April period. The highest breeding intensity was recorded in December with 43% of the female stratum pregnant.

Juveniles entered the trappable population in February as shown in Figure 4.2 and resulted in a decrease in both the mean head-body length and weight of the male and female strata from January to March (Figure 4.3).

Part of the study site was weeded in January (Figure 4.1). Weed biomass in the weeded area never exceeded 10 g.m^{-2} . In the unweeded area, weed biomass was greater than 250 g.m^{-2} in February and decreased over the March - July period. Species composition changed from predominantly *Digitaria spp.* during the early growth stages of the sugarcane to more shade tolerant species as canopy cover developed (Figure 4.4).

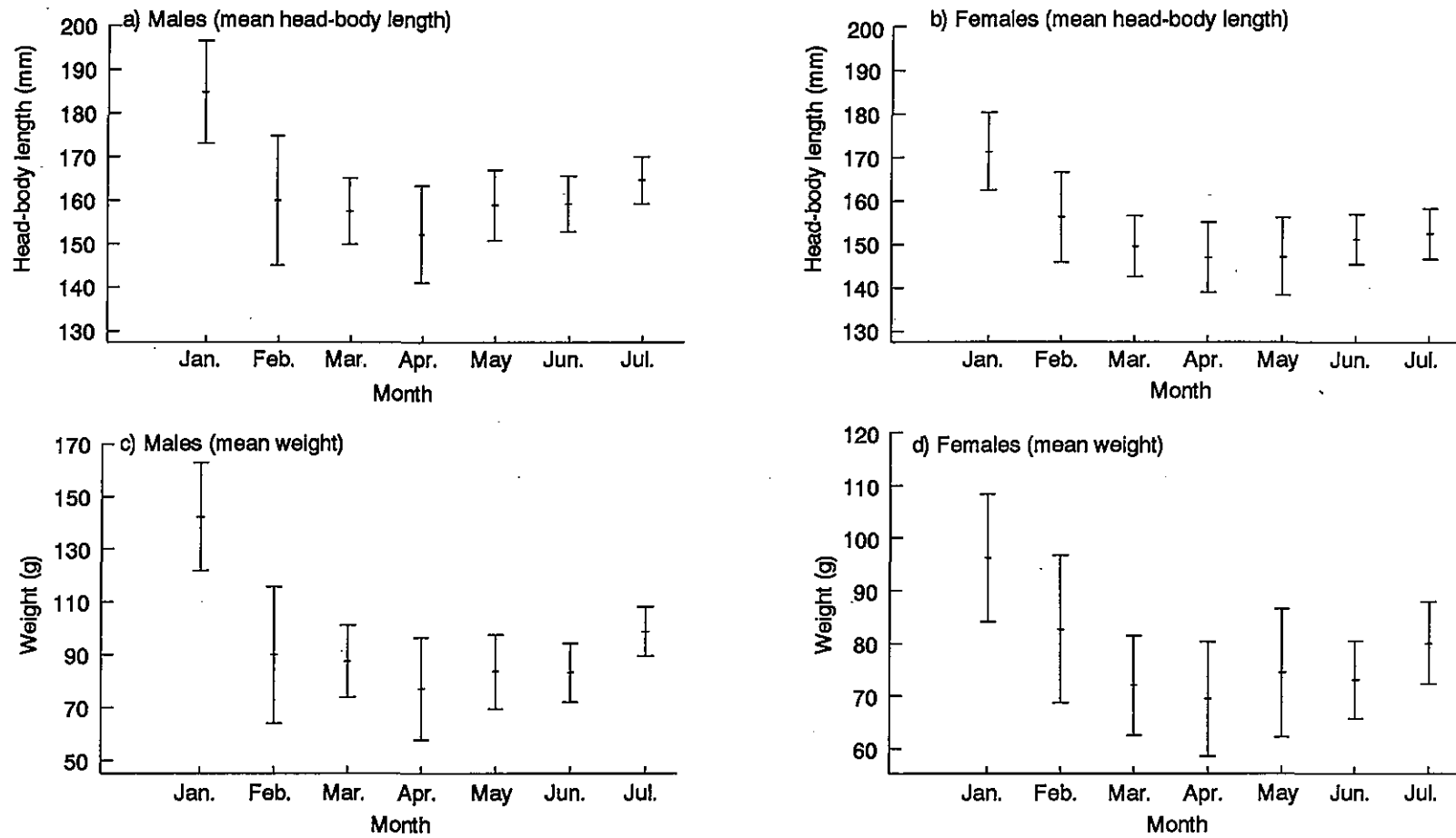


Figure 4.3 Mean head-body length and weight (with 95% c.i.) of male and female *R. sordidus* over the period of the study.

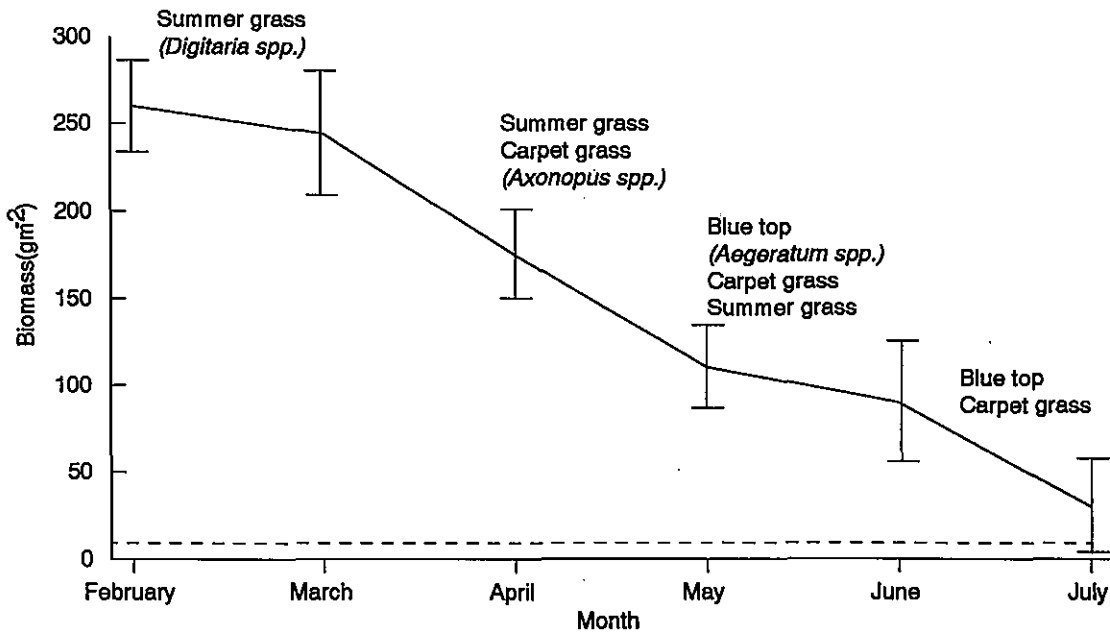


Figure 4.4 Mean biomass (with 95% c.i.) of non-cane vegetation in the study site. Dominant species are indicated.

— Unweeded area - - - Weeded area

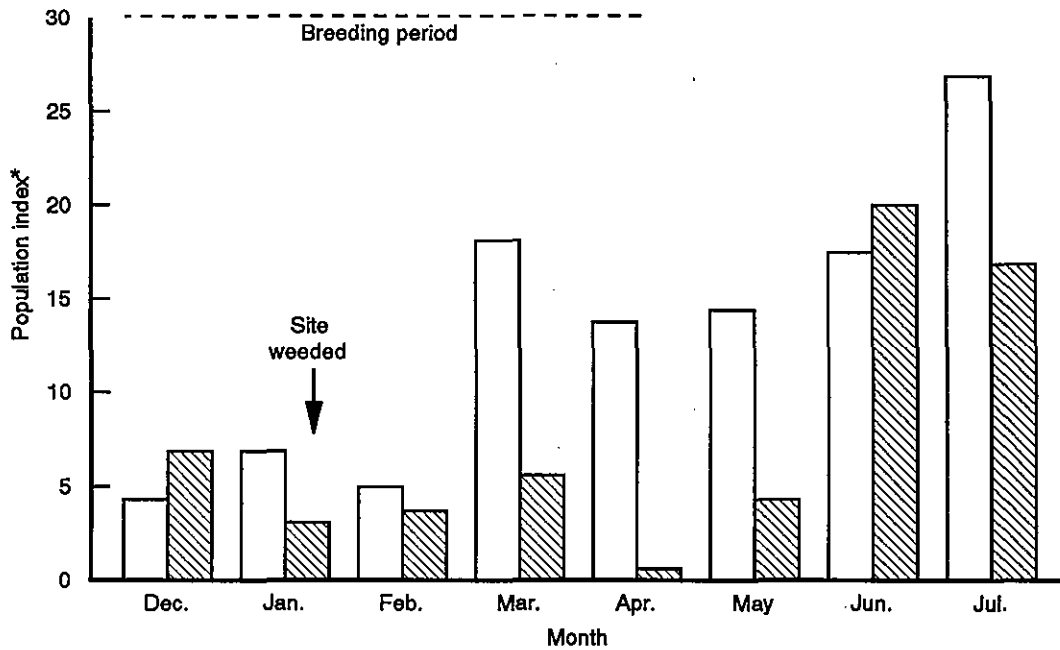


Figure 4.5 Distribution of *R. sordidus* between weeded and unweeded areas.

□ Unweeded area ▨ Weeded area

* Number of individuals per 100 traps

The groups of animals utilising the unweeded and weeded areas possessed similar structures with respect to the proportion of mature females that were pregnant during the breeding period ($\chi^2=0.022$, $p>0.05$), sex ratio during both the breeding ($\chi^2=0.19$, $p>0.05$) and non-breeding ($\chi^2=3.71$, $p>0.05$) periods and the ratio of juvenile to adult males during both the breeding ($\chi^2=3.21$, $p>0.05$) and non-breeding ($\chi^2=0.15$, $p>0.05$) periods (Table 4.1). The low number of captures in the weeded section precluded a monthly comparison of population structure.

Prior to weeding (December and January), a similar number of animals were captured in both areas of the study site ($\chi^2=0.12$, $p>0.05$). After weeding (February to July), 82 animals were captured in the weeded area compared to 153 in the unweeded area ($\chi^2=21.45$, $p<0.001$) (Figure 4.5). The lower utilisation of the weeded area persisted through both the breeding period (66 compared to 94) ($\chi^2=24.65$, $p<0.001$) and the non-breeding period (16 compared to 59) ($\chi^2=4.9$, $p<0.05$). Only in June were the two areas utilised to a similar extent and this period corresponded to the harvesting of adjacent crops (Figure 4.5).

Table 4.2 shows the prevalence of sugarcane in the stomach contents of animals trapped during the study. The percentage of animals with stomach contents containing $\geq 50\%$ sugarcane was similar between the weeded and unweeded areas (total period: $\chi^2=2.69$, $p>0.05$; breeding period: $\chi^2=0.96$, $p>0.05$; non-breeding period: $\chi^2=3.43$, $p>0.05$).

The frequency of occurrence of sugarcane as the major component ($\geq 50\%$) of stomach contents varied significantly between the breeding and non-breeding periods in both the weeded and unweeded areas (unweeded area: $\chi^2=21.77$, $p<0.001$; weeded area: $\chi^2=30.99$, $p<0.001$).

Over the December to March period, seed and non-cane vegetation formed the major component of the diet, with only 28% of animals having stomachs

containing $\geq 50\%$ of sugarcane. Once breeding ceased in April, sugarcane became the major dietary component with 73% of animals having stomachs containing $\geq 50\%$ sugarcane.

Table 4.2

Percentage of animals with sugarcane as the major component ($\geq 50\%$) of stomach contents.

	Unweeded area	Weeded area	Total area
Breeding period	31 (24/77)	22 (7/32)	28 (31/109)
Non-breeding period	67 (63/94)	80 (53/66)	73 (116/160)
Total period	51 (87/171)	61 (60/98)	55 (147/269)

The dietary change accompanying cessation of breeding was even more pronounced within the mature female stratum of the population where, over the breeding period, less than 10% of this stratum had stomachs containing over 50% sugarcane compared to over 70% of the stratum during the non-breeding period (Figure 4.6).

Damage to sugarcane was low until April and then increased through to July when the crop was harvested (Figure 4.7). Most damage was confined to the unweeded area where, at harvest, an average of 9.1% of stalks were damaged compared to an average of only 3.5% in the weeded area.

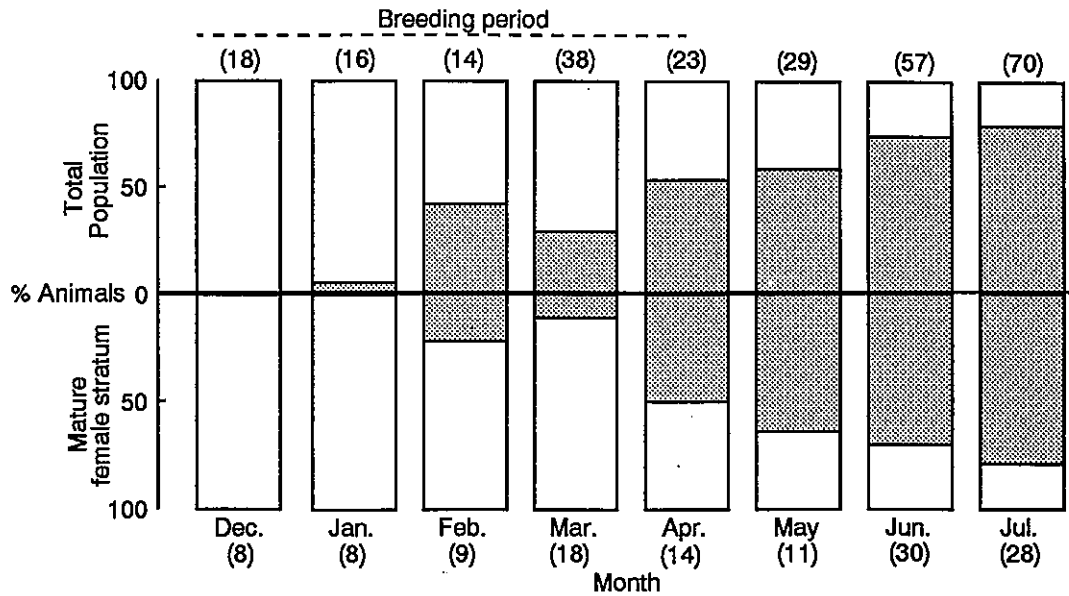


Figure 4.6 The frequency of occurrence of sugarcane in stomach contents.

Animals with stomachs containing >50% seed and non-cane vegetation.
 Animals with stomachs containing >50% sugarcane.
 () Sample size

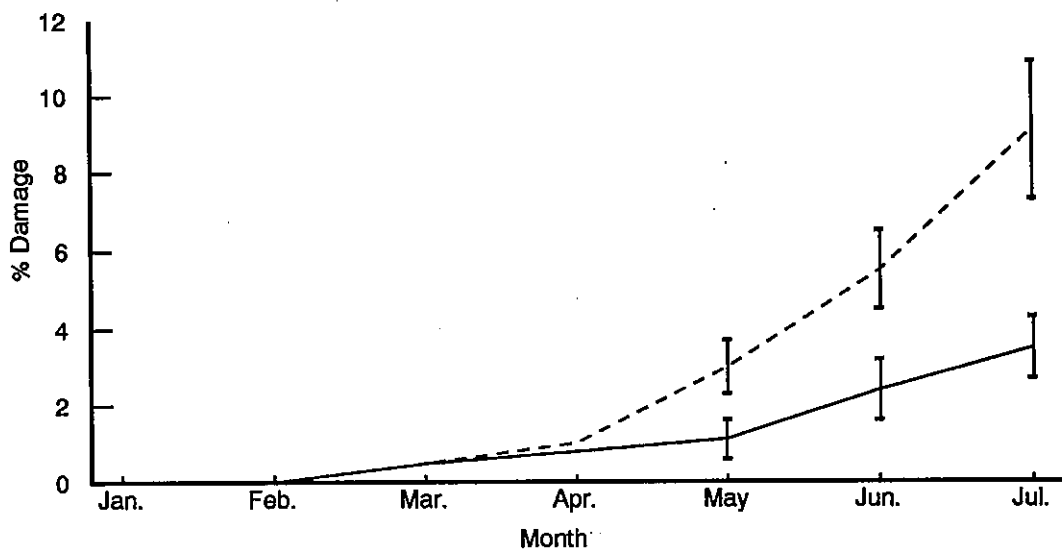


Figure 4.7 Cumulative percent damaged stalks in the weeded and unweeded areas.

Weeded area Unweeded area

4.4 DISCUSSION

This study documented a complete population cycle from the colonisation of the crop by rodents to dispersal at harvest (rodents do not persist in crops after harvest - see Chapter 3).

Onset of breeding occurred in November/December and breeding continued to April. Although the exact timing of onset cannot be determined, the absence of juveniles in the December and January trapping sessions suggests that breeding intensity was low prior to December and that the site was colonised by mature, breeding individuals.

The variation in the time period from crop colonisation to onset of breeding in different years has also been documented in Chapter 3 and suggests that *R. sordidus* populations commence breeding in response to some factor external to the crop cycle.

The seasonal nature of reproduction in *R. sordidus* has been well documented (Gard 1935; McDougall 1946a; Taylor and Horner 1973) however factors affecting the timing of reproduction in this species have not been thoroughly investigated. To date, only rainfall has been considered as a determinant of the timing and intensity of breeding, however there is considerable uncertainty about the mechanism by which rainfall regulates reproduction.

Gard (1935) observed *R. sordidus* to breed soon after the onset of a wet period and suggested that breeding was in response to the availability of young, green plant food after rain. Following observations of low breeding intensity during periods when lush food sources were abundant or in years of early, long or heavy wet seasons, McDougall (1946a) concluded that the major determinant of reproductive effort was spring rainfall. It was suggested that spring rains not only allow spring breeding to occur but also

"conditions" the population for future optimum breeding. McDougall (1946a) also proposed that although an increase in breeding intensity may follow rain, the breeding intensity observed by Gard (1935) was influenced by a "carry-over of conditioning for breeding" from the previous spring. This assertion was never explained in terms of population processes and data related to this "conditioning" were not presented.

Redhead (1973) attempted to quantify the effect of rainfall on population levels in order to provide predictions of expected damage throughout a district. It was suggested that good rainfall during the normally dry autumn/spring period may result in increased population levels by increasing survival between seasons and by allowing extended reproduction to occur. The proposed mechanism was that spring rains allow advanced young cane to be present before the completion of the current harvest. This would result in an increase in survival as *R. sordidus* would not need to take refuge in occupied non-crop habitats. This mechanism also suggested that the breeding season may be extended as favoured food sources would be available over an extended period. It was further suggested that unseasonal rain would result in drains and headlands being overgrown at a time when they would normally be burnt or mown thus extending the availability of favoured non-crop habitats and food resources.

The relationship between the onset of breeding and the appearance of summergrasses (*Digitaria spp.* and *Brachiaria spp.*) described in Chapter 3 show that breeding is dependent on the availability of in-crop weeds.

Prior to weeding, both the weeded and unweeded areas were utilised to the same extent, however the utilisation of the weeded area was depressed immediately after weeding and remained depressed throughout the study. The breeding period corresponded to the time when summergrasses were abundant and non-cane vegetation predominated in stomach contents. Non-cane vegetation was also predominant in the stomachs of breeding females

trapped in the weeded area and it is tempting to suggest that they were foraging over a much larger area than their counterparts in the unweeded area. More data are needed to confirm if this is the case.

Nutritionally, sugarcane is a poor food source for rodents as digestibility is extremely low (Garrison and Breidenstein 1970). The pith of sugarcane contains approximately 70% free water and 30% dry matter consisting almost entirely of sucrose (Barnes 1974). Crude protein represents only 1.2% and 2.2% of the pith and rind respectively (Garrison and Breidenstein 1970). Conversely, the dominant weeds of the area can contain 10% to 20% crude protein depending on the conditions under which they are grown (Butler and Barley 1973).

The high utilisation of summergrasses by *R. sordidus* over the breeding season suggests that these grasses are a major source of nutrition and that they play a significant role in determining both the onset and success of the reproductive season. Alternatively, the onset of breeding may be triggered by some compound present in these grasses (Negus and Pinter 1966; Negus *et al* 1977; Alhibai 1985) whilst overall breeding success may depend on the nutrition provided by this food source. The latter view is most probably the case as both the weeded and unweeded areas were utilised by groups of animals with similar age/sex structures throughout the study. The effect of weeding was simply to depress the overall level of utilisation of the weeded area. Whatever the mechanism, it is evident that the availability of summergrasses plays an extremely important role in the regulation of populations of *R. sordidus*.

The conclusions from this study support, in part, the mechanism proposed by Redhead (1973, 1980). Rainfall may have an effect on the overall potential for reproduction through its effect on the growth of summergrass. Sufficient rainfall early in the crop season may result in summergrasses being available to *R. sordidus* at an earlier date and therefore result in an

earlier onset of breeding. Rainfall however is not the direct determinant of breeding success and so it is not surprising that the model of Redhead (1973, 1980) does not adequately predict damage levels throughout a district.

A direct cause for cessation of breeding is not evident from this study. As the breeding season progressed, the nutritional quality of available food decreased as grasses were shaded out by the cane canopy, temperatures decreased and population density increased. One or all of these factors may contribute to cessation of breeding.

Analysis of stomach contents, together with an increase in damage to sugarcane and a decrease in the biomass of summergrasses indicate that *R. sordidus* were utilising increasing amounts of sugarcane as the crop cycle progressed. One possibility is, therefore, that cessation of breeding was due to a decline in condition of animals that were forced to exploit a diet low in protein.

Temperature also decreased throughout the breeding season with the mean monthly minimum temperature dropping from 21.5°C in December to 16.9°C in May. It is difficult to isolate the effect of temperature on the reproductive effort of field populations except when extreme temperatures are encountered. For example Bomford (1987a) suggested that low temperatures may inhibit breeding in field populations of house mice. In a subsequent study (Bomford 1987b) it was found that reduced breeding intensity in winter months could not be directly attributed to low temperatures but rather to a decrease in the quality of food resources.

McDougall (1946a) in a parallel laboratory and field study of *R. sordidus* observed that testes ascended in the cooler months and then descended with the occurrence of warmer weather in September. No loss of fertility was associated with these changes. It was concluded that the reproductive

potential of *R. sordidus* populations was dependent on females and that males retain reproductive condition throughout the year, a mechanism that has been shown to operate in other species (Warneke 1971; Cockburn 1981). A major deficiency of McDougall's study was that the effects of temperature and food supply on the reproductive potential of female *R. sordidus* could not be isolated.

During this study, cessation of breeding occurred simultaneously in both the weeded and unweeded areas and therefore it is unlikely that the limitation of a food resources was solely responsible for cessation of breeding.

This study clearly illustrates the relationship between in-crop weeds and rodent damage. The marked reduction in damage to sugarcane was a direct consequence of decreased utilisation of the weeded area by rodents. At harvest, an average of 9.1% of stalks were damaged in the unweeded area compared to only 3.5% in the weeded area - a reduction in damage of 60%.

The cost of the herbicides required to control summergrasses is approximately \$50/ha (1992 prices, BSES *pers comm*) whilst application costs are approximately \$30/ha (McMahon *et al* (1989). Reduced competition from in-crop weeds due to the application of herbicides can result in increased cane yields of 5 tonne/ha, currently valued at approximately \$100 (McMahon *et al* 1989). The nett gain in product value due to in-crop weed control (without any consideration of its effect on the reduction of damage due to rodents) is therefore of the order of \$20/ha.

Thallium sulphate bait applied at a rate of 0.84kg/ha represent a cost to the grower of \$7/ha (1992 prices, BSES *pers comm*). Hitchcock (1973) and Hitchcock and Kerkwyk (1975) showed that the maximum reduction in rodent damage that can be expected from the current baiting strategy is 52% in years of low damage and 35% in years of high damage. Assuming that the current baiting strategy reduced rodent damage by 60% (as did in-

crop weed control in this study), the nett benefit of herbicide application over baiting is of the order of \$27/ha.

Over the 1980 - 1988 period, thallium sulphate baits were applied annually to approximately 35,000ha of the Herbert River District. If rodents had been managed by in-crop weed control, the district would have achieved a productivity gain of almost \$1 million annually.

Weed control is a more efficient and acceptable method of rodent control than baiting. It has none of the environmental and public health risks that are associated with baiting and whilst the cost of herbicides exceeds that of thallium sulphate baits, increased sugarcane yields associated with the use of herbicides make the application cost-effective in its own right. The significant reduction in damage due to rodents is a side effect that is achieved at no additional cost to the grower.



THE EFFECT OF AGRICULTURAL TECHNIQUES ON THE POPULATION DYNAMICS OF *R. SORDIDUS*

5.1 INTRODUCTION

Populations of *R. sordidus* in the Herbert River District are influenced by temporal changes in resources and cycle accordingly (Chapter 3). Landscape factors also influence the success of *R. sordidus* in sugarcane growing regions due to the spatial distribution of soil types and the availability of permanent refugia.

The existence of two agricultural practices; trash-blanketing (minimum tillage) and conventional cultivation, contributes additional variability to the landscape of sugarcane growing regions. Agronomic advantages have led to the implementation of green cane harvest and trash-blanketing on a large scale, especially in northern mill areas (Dick and Hurney 1986). In 1987, in the Herbert River District, 72% and 64% of the Victoria and Macknade mills' crops respectively were harvested green. This represents a significant increase since 1982 when only 1.2% and 3.6% of crops in each mill area respectively were harvested green (Churchward and Poulsen 1988).

As the population dynamics of *R. sordidus* are closely related to the cropping system (Chapter 3) and in-crop weeds (Chapter 4), it is possible that these two agricultural practices may contribute to the success of *R. sordidus* populations.

The conventional cultivation practice involves intensive cultivation of the field prior to and following emergence of the new crop (July to December). During this period, crop habitats are highly unstable and therefore unfavourable to *R. sordidus*. This is reflected by low trap success of *R. sordidus* in these habitats relative to mature, unharvested crops (Chapter

3). With trash-blanketing, crops are not burnt prior to harvest and following harvest, the trash, comprising the green "tops" and dry leaf material (15 to 20 t.ha⁻¹ (Sallaway 1979)), is left as a "trash-blanket" on the ground and minimum or zero tillage techniques employed. As a result, a trash-blanketed crop is a more stable habitat and provides substantial ground cover prior to crop emergence. This practice may therefore result in an increased area of suitable habitat during harvest periods thereby increasing survival of *R. sordidus*.

Additionally, trash-blanketing may also favour *R. sordidus* by producing a favourable change in the structure of soils which, in turn, may alter burrowing characteristics. A higher organic matter content in the soil of trash-blanketed fields improves surface friability and soil drainage.

Trash-blanketing may also have a detrimental effect on *R. sordidus* populations. The relationship between the onset of breeding and the first appearance of summergrasses, coupled with a dietary switch between the breeding and non-breeding season indicates that breeding is dependent on the availability of a non-cane food source. Consequently, in-crop weeds play an important role in determining the potential for crop damage. Summergrasses predominate in conventional crops during the December - April period and therefore provide *R. sordidus* with a favoured food source. In contrast, a heavy trash-blanket effectively suppresses weed growth during the crop cycle (Capelin and Prove 1983; Wood 1986; Page *et al* 1986). Breeding and growth of populations occupying trash-blanketed crops may therefore be restricted.

The objective of this study was to determine the effects of green cane harvest and trash-blanketing as opposed to conventional harvest and cultivation techniques on the population dynamics of *R. sordidus*. The effects of these agricultural practices on *R. sordidus* populations were

investigated by an intensive live-trapping study at four sites in the district over the period November 1987 to September 1988.

5.2 METHODS

In selecting sites, consideration was given to variables which may affect rodent population levels including distance from, type and extent of non-crop habitats, and cane variety. The four sites used in this study consisted of common sugarcane varieties and covered a range of crop locations from a crop surrounded by extensive non-crop habitat (Site 1) to one which was remote from non-crop habitats (Site 2). As far as possible, variables other than crop treatment were constant within each site (Table 5.1). Sites comprised a conventionally harvested and cultivated area (conventional) and a green cane harvested and trash-blanketed area (trash-blanketed) (Figure 5.1). As size and location of treatment areas were determined by the grower and logistics of agricultural practices, a traditional Latin Square design was not possible.

A district-wide aerial baiting program occurred in May, immediately prior to the May trapping session. The sites monitored in this study were **NOT** baited.

A pilot trapping survey was undertaken in November 1987 to determine if sites had already been colonised by *R. sordidus*. Sampling was undertaken in the conventional and trash-blanketed areas using 'Elliot' brand live traps. Forty traps (five rows of eight trap positions at 10m intervals), baited with a piece of cardboard soaked in linseed oil, were set for five consecutive nights in each treatment area of Sites 2, 3 and 4. Farm management activities prevented access to Site 1.

Table 5.1

A summary of the major characteristics of each site

Site	Agricultural practice	Ratoon	Planted/ Harvested (1987)	Non-crop habitats
1	Conventional	2	October (last cultivation - November)	Bordered by extensive open forest
	Trash-blanket	2	October	
2	Conventional	1	October	Approximately 750m to extensive open forest
	Trash-blanket	1	September	
3	Conventional	Plant cane	August (last cultivation - November)	Bordered on three sides by a drainage channel Approximately 1.5km to extensive open forest
	Trash-blanket	1	October	
4	Conventional	Plant cane	August (last cultivation - November)	Drainage channel approximately 100m from trapping grids Approximately 1.5km to extensive open forest
	Trash-blanket	2	August	

The sex and head-body length of each *R. sordidus* trapped was recorded. Each individual was marked uniquely using a system of toe clipping (Davis 1956).

Trapping grids (0.3 ha), consisting of five rows of eight trap positions at 10m intervals, were located in each treatment area (Figure 5.1). Each month over the period of the study (December 1987 to September 1988) an 'Elliot' brand live trap baited with a piece of cardboard soaked in linseed oil was set at each position. In each treatment area of each site, trapping continued for five nights resulting in a total of 200 trap nights per month in each treatment area.

The recapture status, reproductive condition and head-body length of each animal trapped was assessed using external characteristics (Chapter 3).

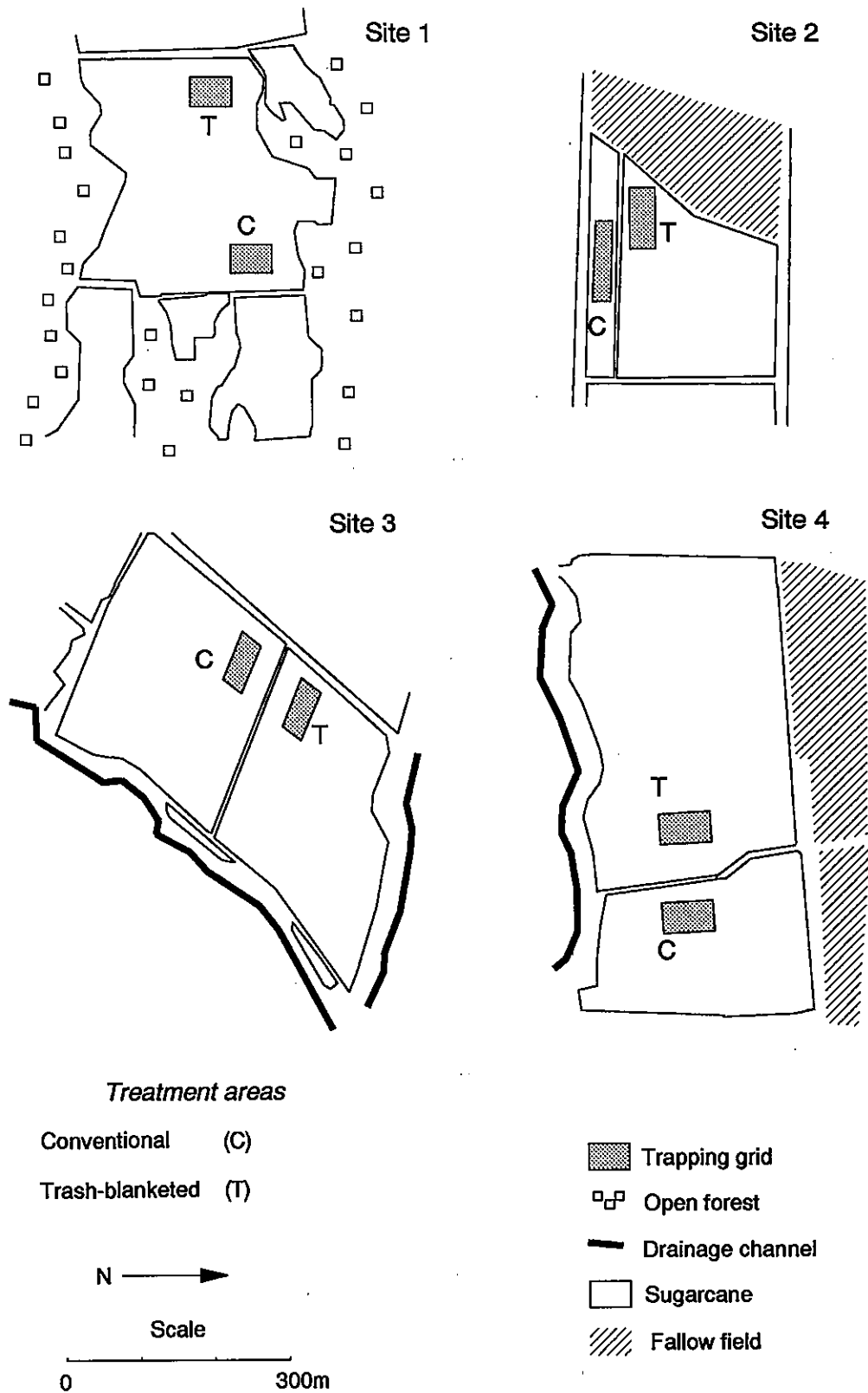


Figure 5.1 Maps of the four study sites showing location of trash-blanketed and conventional treatment areas.

Pregnancies were identified by palpation. Each individual was marked uniquely using a system of toe clipping (Davis 1956).

Three age classes were defined for male and female strata using the relationship between head-body length and age observed by McDougall (1944):

- i) juvenile less than 10 weeks old
 head-body length $\leq 125\text{mm}$

- ii) 'adult' 10 weeks to one year old
 head-body length male: 126mm to 174mm
 female: 126mm to 149mm

- iii) 'old adult' over one year old
 head-body length male: >174mm
 female: >149mm

On one night during each trapping session, the populations in the conventional and trash-blanketed areas of each site were sampled using snap traps baited with paper soaked in linseed oil. One line of forty snap traps at 10m intervals were set in each treatment area approximately 50m from trapping grids. The sex and stomach contents of each *R. sordidus* trapped were recorded (Chapter 3).

Each month, rodent damage and a qualitative estimate of ground cover of non-cane vegetation were recorded for each treatment area of the four sites.

Ground cover of non-cane vegetation was assessed every month in each treatment area of the four sites on a four point ranked scale:

- 1 = zero cover
- 2 = light (1 - 25% cover)
- 3 = moderate (26 - 50% cover)
- 4 = heavy (>50% cover)

A relative estimate of damage due to *R. sordidus* was calculated as the

number of bitten stalks in a row of 500 consecutive stalks in the centre of the trapping grid of each treatment area. The same stalks were used in this estimate each month to provide an estimate of cumulative damage over the study period.

5.3 RESULTS

In conventional areas summer grass¹ (*Digitaria ciliaris*), green summer grass¹ (*Brachiaria subquadrifera*), awnless barnyard grass¹ (*Echinochloa colona*) and crowsfoot grass¹ (*Eleusine indica*) were present over the December - May period (Figure 5.2). Blue top (*Ageratum spp.*) predominated from May to September. Percentage ground cover of weeds in these areas peaked in February/March.

In trash-blanketed areas, weed growth was suppressed so that the percentage ground cover of weeds was never higher than 25% in these areas. Summergrasses were present until March after which blue top predominated.

In November 1987, a total of 37 individual *R. sordidus* were trapped in a pilot study undertaken at each site. Of these, 93% were trapped in trash-blanketed areas (Table 5.2).

From 14 200 trap nights, there were 2287 captures (743 individuals) of *R. sordidus* and 46 captures (30 individuals) of *Melomys spp.* Incidental captures were made of *R. rattus* (Black rat), *R. fuscipes* (Bush rat), *Uromys caudimaculatus* (White-tailed rat), *Isodon macrourus* (Northern brown bandicoot) and *Antechinus flavipes* (Yellow-footed Antechinus).

¹ These species will subsequently be referred to collectively as "summergrasses"

Table 5.2

Percentage trap success of *R. sordidus* in conventional and trash-blanketed areas in November 1987

Site	Conventional		Trash-blanketed	
1	-		-	
2	1	(2)	6	(12)
3	0.25	(1)	7.5	(15)
4	0	(0)	3.5	(7)

() Number of individuals trapped

- No trapping undertaken

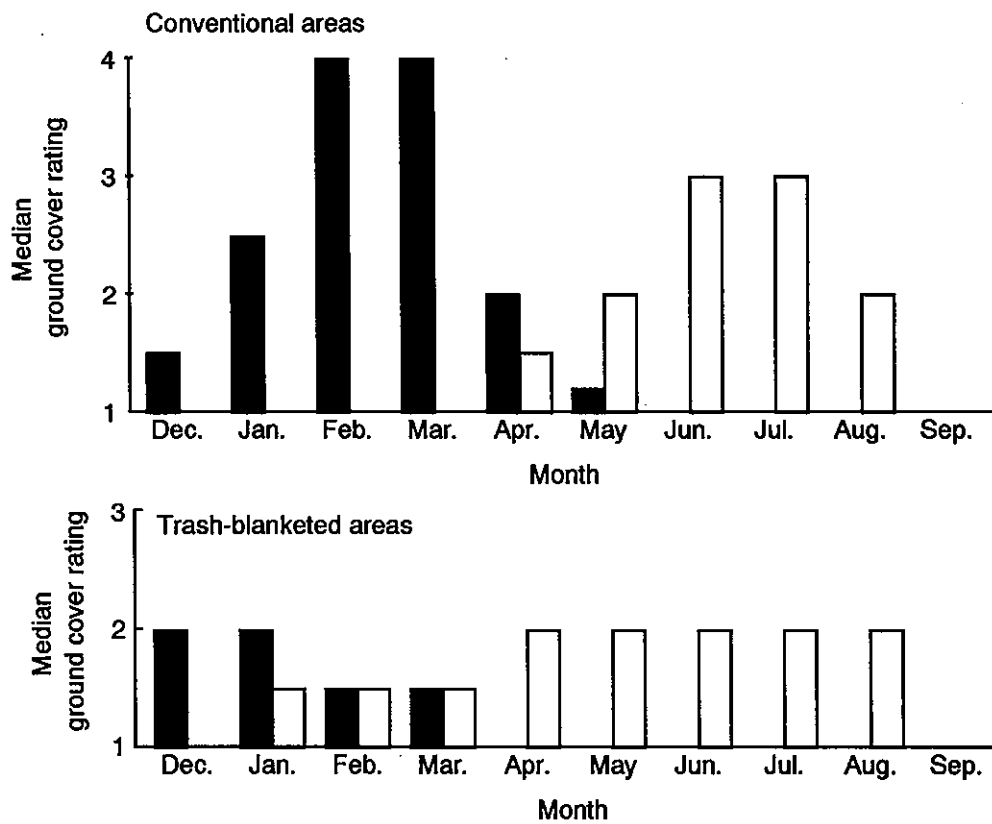


Figure 5.2 Median ground cover of summergrasses and bluetop in conventional and trash-blanketed areas over the study period.

 Summergrasses	<i>Ground cover rating</i>
 Blue top	1 = zero cover
	2 = light cover
	3 = Moderate cover
	4 = Heavy cover

The proportion of traps filled on each trapping night was low, with greater than 50% of the traps being filled at one site on only one of 50 trapping nights at that site. On most nights (82%), less than 20% of traps were filled. This low trap usage resulted in a large number of traps still available to rodents, indicating that the number of traps was not limiting the catch (Caughley 1977).

In 61 of a total of 71 trapping sessions, the number of new individuals trapped on the last night was less than 1% of the total number of individuals trapped during the trapping session (Appendix 2). A low proportion of new individuals captured on the last trapping night, coupled with the low proportion of traps filled, suggests that on these occasions, a high proportion of the trappable population was trapped.

On only five occasions was the percentage of the total number of individuals captured on the last night greater than 15%. Sex ratio and age structure did not vary significantly from day 1 to day 5 of the trapping sessions (Appendix 3) suggesting that the only consequence of incomplete trapping out was an underestimate of population size.

Due to relatively low capture rates within treatment areas at each site per month, data for the four sites were pooled for analysis (Figure 5.3). The characteristics of populations within conventional and trash-blanketed areas are summarised in Appendix 4. The number of *R. sordidus* trapped and trap nights in each treatment area each month are given in Appendix 5.

Cultivation of conventional areas planted in July/August continued until November. In November and December, percentage trap success in conventional areas was low (November: 0.38%, 3 individuals; December: 2%, 20 individuals). In January, trap success increased to 5.9% (59 individuals).

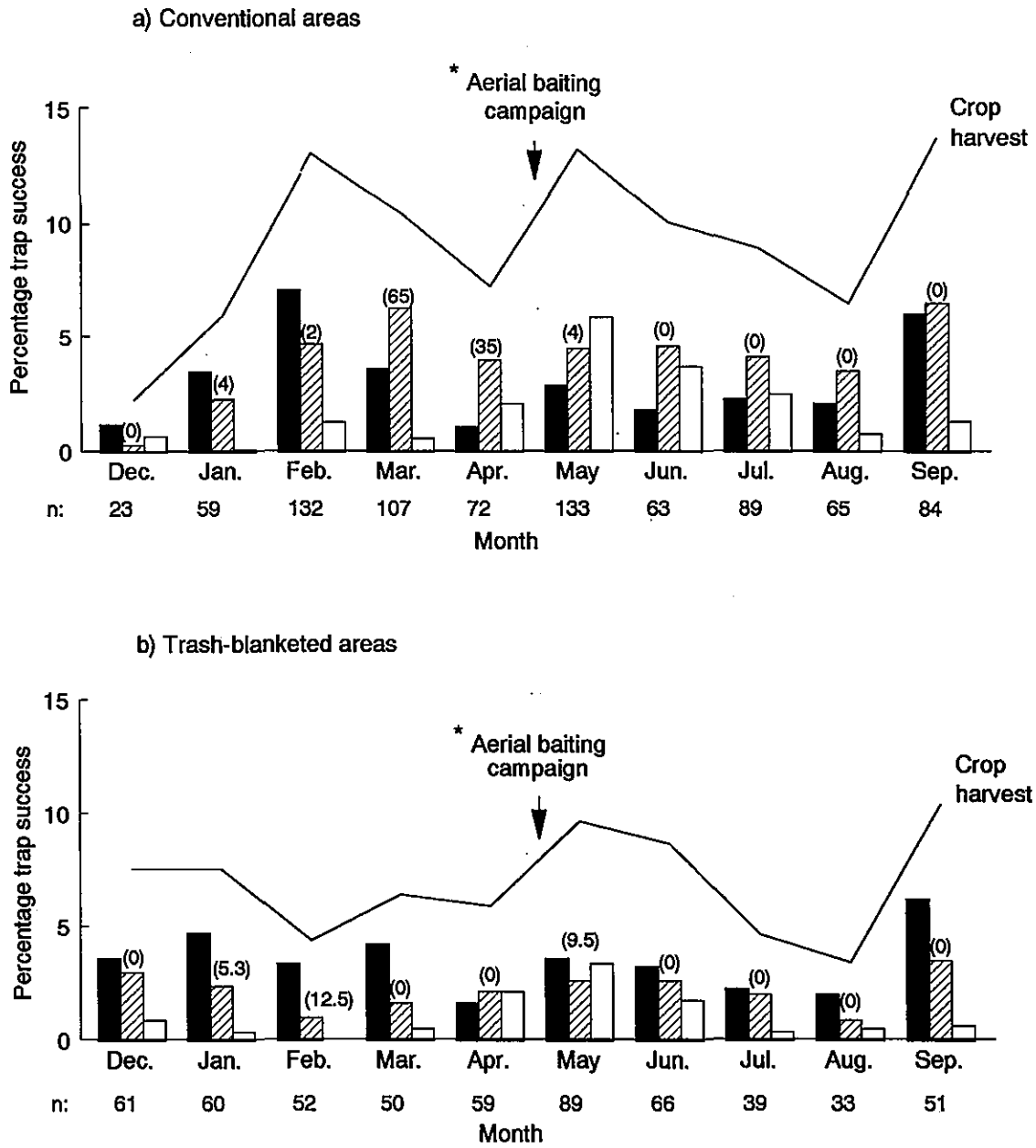


Figure 5.3 Population characteristics of *R. sordidus* in the conventional and trash-blanketed treatment areas (based on pooled data from the four sites)

- Mature males
- ▨ Mature females
- Juveniles
- Total population

- n: Total number of individuals trapped
- () Percentage of the mature female stratum pregnant.

* Sites used in this study were NOT baited

In contrast, percentage trap success in trash-blanketed areas which were harvested in late September/early October, was relatively high prior to January. In November percentage trap success of *R. sordidus* in trash-blanketed areas was 6.5% (39 individuals). In December, 7.6% (61 individuals) trap success was recorded in these areas.

R. sordidus were distributed uniformly between trash-blanketed and conventional areas in all but four months of the study (December $\chi^2_1 = 19.51$, $p=0.00001$, February $\chi^2_1 = 36.0$, $p<0.00001$, March $\chi^2_1 = 8.5$, $p=0.0036$ and May $\chi^2_1 = 6.68$, $p=0.0098$). In December, population levels were highest in the trash-blanketed areas. In February, March and May population levels were highest in the conventional areas (Figure 5.4).

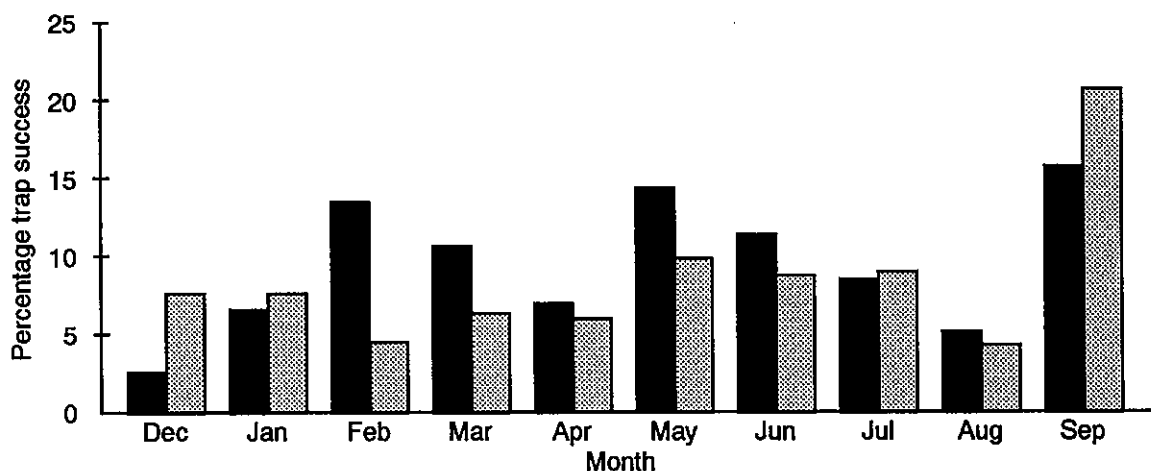


Figure 5.4 Percentage trap success in conventional and trash-blanketed areas over the period December 1987 to September 1988

■ Conventional areas ▨ Trash-blanketed areas

Pregnancies were recorded over the period January to May although intensity of breeding varied during this period and between treatment areas. Breeding was most intense in conventional areas where 45.2% (47/104) of the mature females present during the January - May period were pregnant on at least one occasion and 10.6% (11/104) were pregnant on two occasions.

In these areas, peak breeding intensity was recorded in March when 65% (40/62) of mature females were pregnant. Breeding intensity in trash-blanketed areas was low during the January - May period with pregnancies only being recorded for seven (9.2%) of the 76 mature females present in these areas during that period.

In both treatment areas pregnancies were only recorded for females having a head-body length greater than 125mm. Records of pregnancy were most frequent for individuals having a head-body length greater than 150mm (Table 5.3).

Table 5.3

Percentage of females pregnant in each head-body length class

Period	Month	Percentage of females pregnant		
		head-body length 126 - 149mm	head-body length \geq 150mm	head-body length unknown
	Dec	0 (6)	0 (11)	0 (12)
Breeding	Jan	0 (14)	4 (28)	0 (10)
	Feb	0 (12)	5 (43)	0 (2)
	Mar	21 (24)	89 (45)	0 (5)
	Apr	14 (14)	49 (37)	0 (1)
	May	5 (21)	7 (45)	0 (0)
Non-breeding	Jun	0 (29)	0 (33)	0 (8)
	Jul	0 (15)	0 (29)	0 (12)
	Aug	0 (9)	0 (32)	0 (7)
	Sep	0 (10)	3 (50)	0 (1)

In conventional areas, the proportion of females in the mature population varied significantly over the study period ($\chi^2_9 = 49.64$, $p < 0.005$) (Table 5.4).

In these areas sex ratio deviated significantly from unity in December and February when males were predominant, and over the March - August period due to a high proportion of females in the population. In trash-blanketed areas, the proportion of females in the mature population did not vary significantly over the study period ($\chi^2_9 = 12.23$, $p > 0.05$). In these areas sex ratio only deviated significantly from unity in February when there was a high proportion of males in the population.

Table 5.4

Proportion of females in the mature population of conventional and trash-blanketed areas

Month	Conventional areas			Trash-blanketed areas			χ^2_1 Difference between areas
	Proportion	n	χ^2_1	Proportion	n	χ^2_1	
Dec	0.20	(15)	5.40*	0.51	(51)	0.02	4.52*
Jan	0.40	(58)	2.48	0.49	(59)	0.02	1.07
Feb	0.40	(118)	4.88*	0.26	(42)	9.52*	2.49
Mar	0.65	(102)	8.82*	0.36	(42)	3.43	10.16*
Apr	0.78	(51)	16.49*	0.42	(36)	1.0	12.27*
May	0.65	(82)	7.02*	0.50	(56)	0	2.94*
Jun	0.69	(42)	6.10*	0.54	(54)	0.30	2.33
Jul	0.65	(66)	6.06*	0.48	(33)	0.03	2.54
Aug	0.64	(58)	4.41*	0.43	(30)	0.53	3.37
Sep	0.53	(76)	0.21	0.54	(39)	0.23	0.02

χ^2_1 H_0 : Proportion of females is 0.5
Significant statistic ($p < 0.05$)

The sex ratio varied between conventional and trash-blanketed areas in December, March and April. In December, there was a higher proportion of males in the population of conventional areas. In March and April there was a higher proportion of females in the population of conventional areas.

Of the juveniles marked throughout the study period, 78% (109/139) and 74% (83/112) in conventional and trash-blanketed areas respectively, were marked over the February - June period. The number of juveniles in both treatment areas peaked in May, two months following the peak in breeding intensity. In May, juveniles comprised 38% (51/133) of the total population in conventional areas and 37% (33/89) of the total population in trash-blanketed areas.

A two month lag between the peak in breeding intensity and peak in the number of juveniles in the populations suggests that juveniles first became trappable eight weeks following the trapping session when the female was recorded as pregnant. An index (I) of juvenile recruitment (DeLong 1967):

$$I = \frac{\text{Number of juveniles present}}{\text{Number of pregnant females 8 weeks previous}}$$

was used to compare major differences in recruitment between populations over the total study period. This index equalled 2.72 (158/58) in conventional areas and 15.71 (110/7) in trash-blanketed areas.

An index of less than six, the average litter size of *R. sordidus* (Chapter 3) in conventional areas suggests that juveniles in these areas may have dispersed or died prior to becoming trappable. A high index for trash-blanketed areas suggests that these areas were being invaded by juveniles during the study period.

Significant differences in age structure between treatment areas occurred during the January - March period ($\chi^2_2 = 12.62$, $p < 0.05$) but not in the April - June ($\chi^2_2 = 5.89$, $p > 0.05$) or the July - September periods ($\chi^2_2 = 1.62$, $p > 0.05$) (Table 5.5).

"Old adults" dominated the population of conventional areas from January to March. In trash-blanketed areas, the population comprised a low proportion of these individuals over the same period.

Percentage trap success of "adult" females was relatively constant in both treatment areas over the study period. There was no increase in the number (and proportion) of these individuals in the population after the April - June period despite a decrease in the number of juveniles in all areas.

Table 5.5

Proportion of females in each age class during the periods January to March (early breeding period), April to June (late breeding period) and July to September (non-breeding period) of the study*

Period	Treatment area	≤ 125	126 - 149	≥ 150
Jan - Mar	Conventional [unweeded]	0.12 (17)	0.21 (29)	0.67 (93)
	Trash-blanketed [unweeded]	0.21 (12)	0.39 (22)	0.39 (22)
Apr - Jun	Conventional [unweeded]	0.36 (61)	0.18 (31)	0.46 (77)
	Trash-blanketed [unweeded]	0.47 (54)	0.22 (25)	0.31 (36)
Jul - Sep	Conventional [unweeded]	0.09 (11)	0.20 (25)	0.71 (88)
	Trash-blanketed [unweeded]	0.09 (5)	0.27 (15)	0.64 (35)

* Data were pooled for these periods due to low monthly sample sizes in some treatment areas

() Number of individuals in sample

Significant differences in age structure between treatment areas occurred during the January - March ($\chi^2_2 = 13.40$, $p < 0.05$) and April - June periods ($\chi^2_2 = 10.61$, $p < 0.05$), but not during the July - September period ($\chi^2_2 = 1.01$, $p > 0.05$) (Table 5.6).

The populations of both treatment areas were dominated by "old adult" individuals throughout the study period. Over the January - March period, the proportion of these individuals in the population was highest in conventional areas. There was a large decrease in the size of the "old adult" age class in conventional areas between the January - March and April - June periods. A similar decrease did not occur in trash-blanketed areas.

The proportion of "juveniles" and "adults" in the populations was highest over the April - June period. An increase in the number (and proportion) of "adults" in the population did not correspond to the decrease in the number of juveniles in each area after the April - June period.

Table 5.6

Proportion of males in each age class during the periods January to March (early breeding period), April to June (late breeding period) and July to September (non-breeding period) of the study*

Period	Treatment area	≤ 125	126 - 149	≥ 150
Jan - Mar	Conventional [unweeded]	0.04 (5)	0.10 (13)	0.86 (113)
	Trash-blanketed [unweeded]	0.17 (14)	0.16 (13)	0.67 (56)
Apr - Jun	Conventional [unweeded]	0.35 (33)	0.22 (21)	0.43 (40)
	Trash-blanketed [unweeded]	0.16 (15)	0.20 (18)	0.64 (59)
Jul - Sep	Conventional [unweeded]	0.10 (11)	0.15 (16)	0.75 (81)
	Trash-blanketed [unweeded]	0.15 (10)	0.12 (8)	0.74 (50)

* Data were pooled for these periods due to low monthly sample sizes in some treatment areas

() Number of individuals in sample

Change in the proportion of "recaptures" in the population during a trapping session was considered after February once populations had become established and a large number of animals had been marked (Table 5.7).

The proportion of "recaptures" in the male and female populations of conventional areas did not vary significantly over the March - September period (females: $\chi^2_6 = 7.59$, $p > 0.05$; males $\chi^2_6 = 10.45$, $p > 0.05$). In these areas the proportion of "recaptures" in the female population (0.51) was significantly higher than that of the male population (0.36) over the March - September period ($\chi^2_1 = 13.2$, $p < 0.05$). The proportion of "recaptures" in the male and female populations of trash-blanketed areas did not differ significantly over the March - September period (0.25 females: $\chi^2_6 = 11.99$,

$p > 0.05$; and 0.38 males: $\chi^2_6 = 10.38$, $p > 0.05$). In these areas there was a significantly higher proportion of "recaptures" in the male than female population over this period ($\chi^2_1 = 6.90$, $p < 0.05$).

Table 5.7

The "recaptured" proportion of the male and female populations of conventional and trash-blanketed areas

Month	Conventional areas			Trash-blanketed areas		
	Females	Males	χ^2_1	Females	Males	χ^2_1
Jan	0.12 (3/24)	0.11 (4/35)	0.02	0.52 (15/29)	0.29 (9/31)	3.21
Feb	0.12 (7/59)	0.19 (14/73)	1.30	0.28 (5/18)	0.24 (8/34)	0.11
Mar	0.46 (31/68)	0.46 (18/38)	0.03	0.21 (4/19)	0.17 (5/31)	0.15
Apr	0.55 (29/53)	0.37 (7/19)	1.79	0.12 (4/33)	0.38 (10/26)	5.57*
May	0.43 (34/79)	0.22 (12/54)	6.14*	0.27 (14/52)	0.30 (11/37)	0.08
Jun	0.55 (22/40)	0.30 (7/23)	3.55	0.32 (11/34)	0.47 (15/32)	1.46
Jul	0.65 (30/46)	0.42 (18/43)	4.88*	0.56 (9/16)	0.48 (11/23)	0.27
Aug	0.56 (22/39)	0.52 (13/25)	0.12	0.38 (5/13)	0.45 (9/20)	0.14
Sep	0.49 (21/43)	0.33 (13/40)	2.29	0.27 (7/26)	0.48 (12/25)	2.42
Mean Mar - Sep	0.51	0.36	13.2 4	0.25	0.38	6.90

Significant statistic ($p < 0.05$)

() Number of recaptures/total

The proportion of "recaptures" in the female population varied significantly between treatment areas over the March - September period with a higher proportion of "recaptures" in conventional areas. There was no significant difference in the proportion of "recaptures" in the male population between treatment areas over this period.

A high proportion of "recaptures" in the female population of conventional areas compared to trash-blanketed areas indicates a lower rate of turnover of these individuals. Turnover of the male population does not vary according to treatment area. In conventional areas, the difference in proportion of "recaptures" in the male and female populations indicates that turnover of males is higher than that of females. In the trash-blanketed areas, turnover is higher in the female population than the male population.

The frequency of occurrence of sugarcane as the major component ($\geq 50\%$) of stomach contents varied significantly over the study period ($\chi^2_{10} = 33.08$, $p < 0.005$). From November to March, non-cane vegetation was the major component of stomach contents of ≥ 50 percent of the population. In March, non-cane vegetation was the major component of stomach contents of all *R. sordidus* trapped. From April to September, sugarcane was the major component of stomach contents of ≥ 50 percent of the population (Figure 5.5).

The change in diet from non-cane vegetation to sugarcane was more pronounced within the mature female stratum (Table 5.8). Over the breeding period, only 25% and 42% of stomachs from this stratum in conventional and trash-blanketed areas respectively, contained more than 50% sugarcane. A significantly higher percentage of stomachs of mature male *R. sordidus* contained more than 50% sugarcane over the same period ($\chi^2_1 = 6.2$, $p < 0.05$).

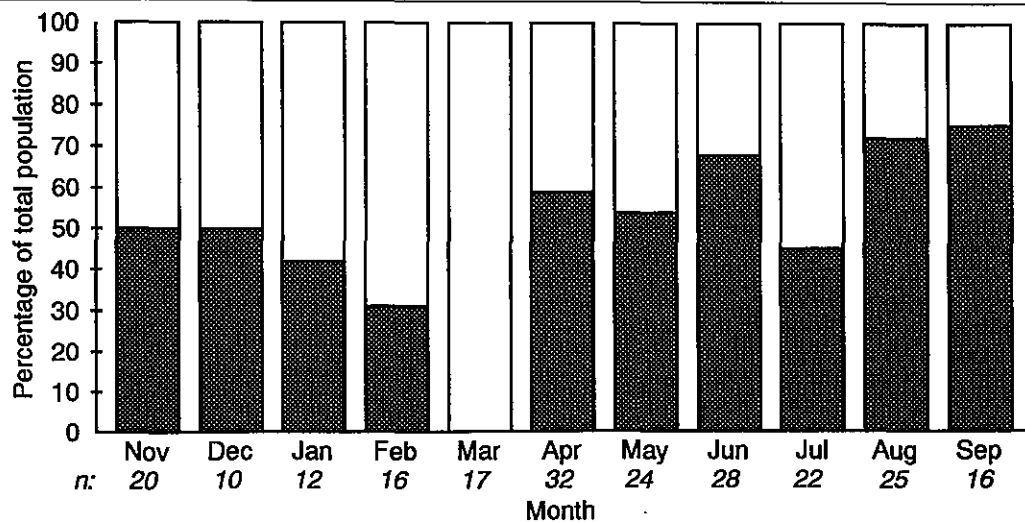


Figure 5.5 Percentage of *R. sordidus* with significant amounts of sugarcane in stomach contents over the period November 1987 to September 1988

■ Percentage of the population with >50% sugarcane in stomach contents.
 n: Number of individuals in sample

Table 5.8

Proportion of mature male, mature female and juvenile *R. sordidus* in conventional and trash-blanketed treatment areas with stomachs containing significant amounts ($\geq 50\%$) of sugarcane during the breeding (Jan - May) and non-breeding (Jun - Sep) periods

Stratum	Period	Conventional	Trash-blanketed	Comparison of treatments χ^2_1
Juvenile	Breeding	0.36 (11)	* (4)	-
	Non-breeding	0.83 (12)	* (7)	-
	χ^2_1	5.3		
Mature female	Breeding	0.25 (40)	0.42 (10)	1.25
	Non-breeding	0.52 (21)	* (9)	-
	χ^2_1	6.35	1.7	
Mature male	Breeding	0.36 (17)	0.59 (17)	1.35
	Non-breeding	0.59 (22)	0.75 (12)	3.53
	χ^2_1	2.4	4.2	

* Sample size less than 10

There was no significant difference in diet of individuals between conventional and trash-blanketed areas.

Severe lodging of cane prevented the continuation of damage estimation in all or part of each site after June.

Damage was low in both conventional and trash-blanketed areas until March, after which damage rapidly increased (Figure 5.6). There was no significant difference in the proportion of stalks damaged between treatment areas in any month of the study.

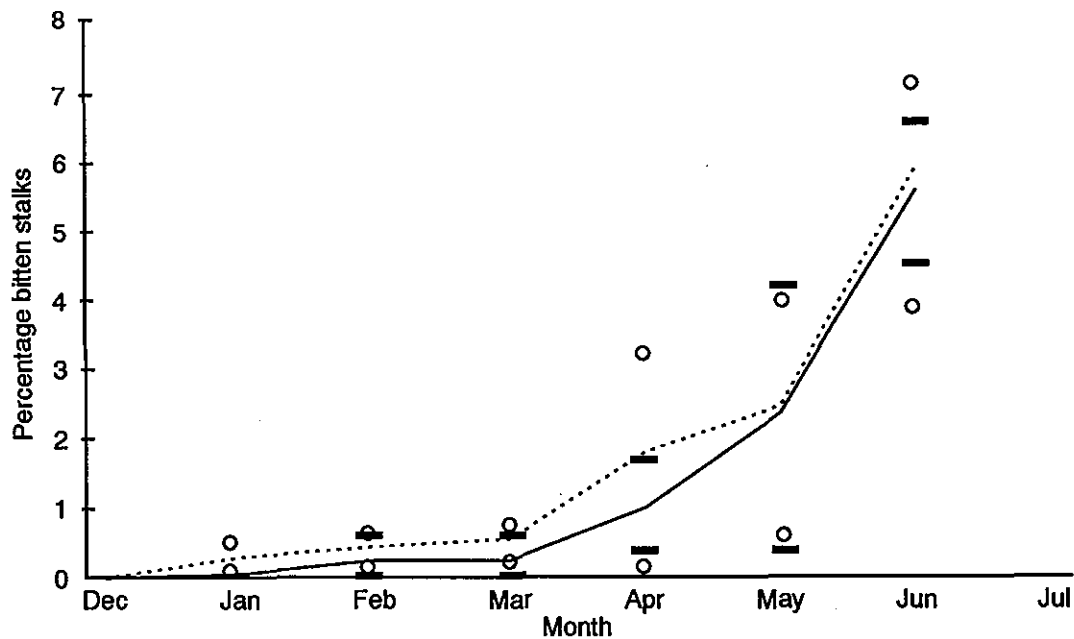


Figure 5.6 Cumulative percent bitten stalks in conventional and trash-blanketed areas over the study period.

— Conventional areas (with 95% ci) ···· Trash-blanketed areas (with 95% ci)

5.4 DISCUSSION

The general population cycle described in this study reflected that described for the general Herbert River and Mackay Districts (Chapter 3). Consequently, any conclusions as to the effect of agricultural practice on *R. sordidus* populations may be extended to these districts. The dynamics of *R. sordidus* populations as determined by the two agricultural practices are summarised in Figure 5.7 and a summary of the population processes occurring in each treatment area are shown in Table 5.9.

Significant modification of population processes of *R. sordidus* resulted from the implementation of trash-blanketing. The cover and minimal disturbance of the ground associated with trash-blanketing and minimum tillage enabled *R. sordidus* to establish populations in these areas in November/December, two months following harvest of the previous season's crop. Continual cultivation of conventional areas during the July - November period precluded population establishment in these areas until December/January. As a trash-blanketed crop provides shelter for animals during harvest, it is likely that implementation of this practice on a regional scale will increase the probability of survival of *R. sordidus* during the harvest period when the area of suitable shelter is reduced.

At crop harvest *R. sordidus* must disperse into favourable habitat or face a high probability of mortality. In areas where permanent habitats are infrequent, and the area of crop is reduced through harvest, the distance between harvested crops and suitable habitat may be large, thereby reducing the probability of survival of dispersing *R. sordidus*. Higher survival rates should result when the distance between the harvested crop and other suitable habitat is reduced (Redhead 1980). Redhead (1980) suggested that this may occur in years when rainfall during the harvest period accelerates crop growth so that a suitable amount of crop cover is

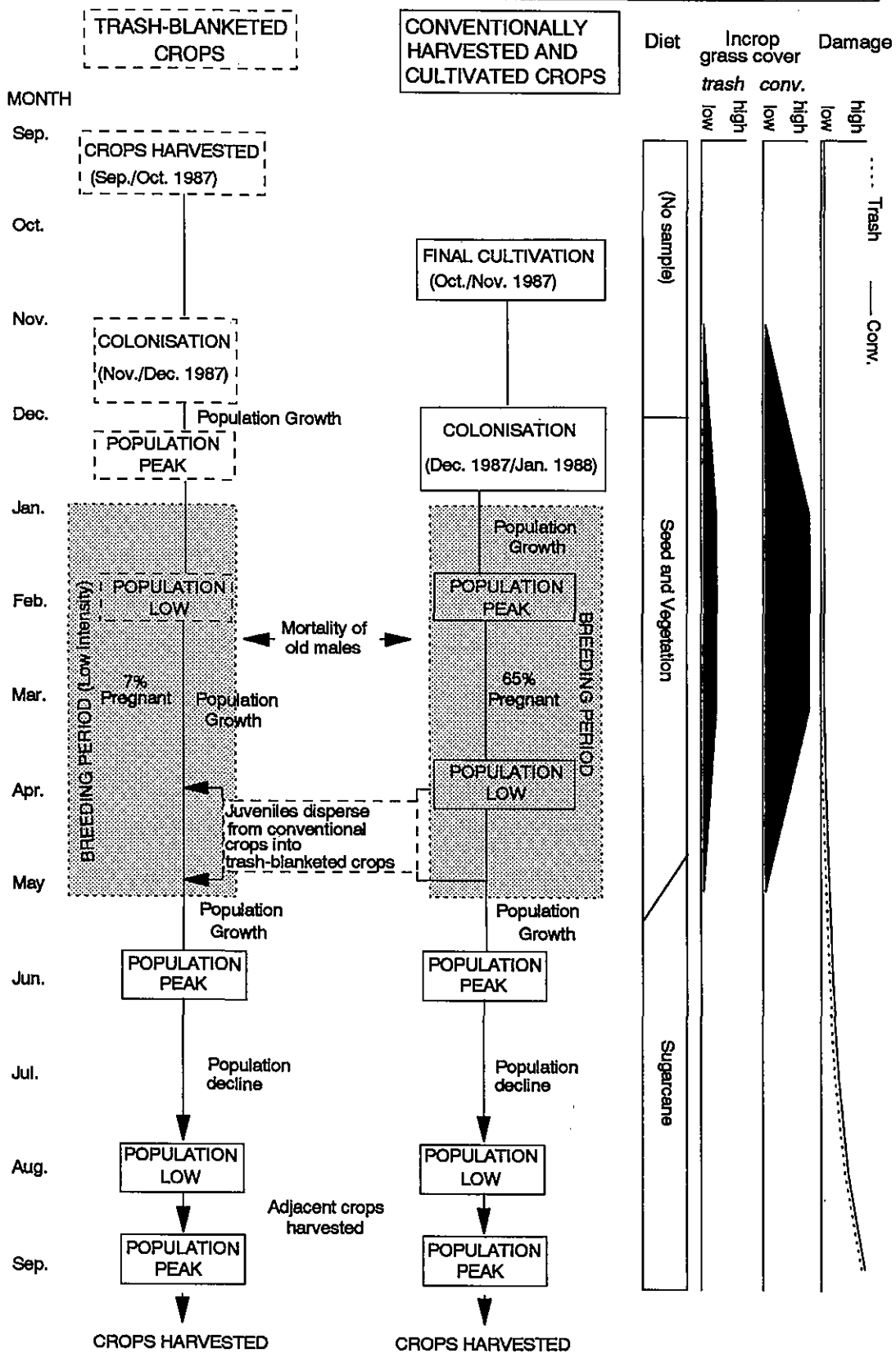


Figure 5.7 Population dynamics of *R. sordidus* in conventional and trash-blanketed crops.

Table 5.9

Summary of the major effects of agricultural treatment on the characteristics of *R. sordidus* populations

Characteristic	Summary of results
Breeding	Breeding intensity was high in the weeded conventional area and low in trash-blanketed areas.
Sex ratio	The sex ratio of the mature population in the unweeded conventional areas was female-biased in most months. In contrast, sex ratio of the mature population in trash-blanketed areas was close to unity in most months.
Juvenile recruitment	Juvenile recruitment was low in unweeded conventional areas and high in trash-blanketed areas relative to breeding rates in each area. This suggests that juveniles disperse from areas of high breeding intensity into trash-blanket areas.
Age structure	There was a high proportion of "old adults" in the female and male population of unweeded conventional areas compared to trash-blanketed areas during the early months of the breeding period (January - March). In the female population, this difference continued until the end of the breeding period in June.
Population turnover	The female population was more stable in unweeded conventional areas than in other treatment areas. Turnover of the male population was more rapid than that of the female population but did not vary according to treatment area. Juveniles had a similar rate of turnover to mature males.
Population levels	Populations established 1 to 2 months earlier in trash-blanketed than conventional areas. Population levels rapidly increased in the unweeded conventional areas so that population levels were significantly higher in these treatment areas during the breeding period. Once breeding had ceased, population levels were similar between treatment areas due to dispersal. Low population levels were characteristic of the weeded conventional areas.

provided earlier than normal. The practice of trash-blanketing by providing an increased area of suitable habitat may similarly increase survival of *R. sordidus* during the harvest period.

Following population establishment in conventional areas in December/January, population levels increased in these areas to reach a peak level in February. A similar increase did not occur in trash-blanketed areas so that in February and March, population levels were significantly lower in these areas. The difference in population levels between the two treatment areas corresponded to a difference in the percentage ground cover of summergrasses. Summergrass growth was rapid in conventional areas from December to February/March when the ground cover of grasses peaked. In contrast, the heavy trash-blanket effectively suppressed weed growth (less than 25% ground cover) from January to April.

The predominance of seed and non-cane vegetation in stomach contents during the December - April period indicates that summergrasses are a preferred food source of *R. sordidus*. Availability of the favoured food source therefore determined the distribution of *R. sordidus* between treatment areas, with significantly higher population levels in conventional areas in February and March. *R. sordidus* may have also benefited from the additional cover provided by summergrasses in conventional areas. In addition to the difference in population levels, breeding intensity, sex ratio of the mature population, age structure and population turnover were also affected by agricultural practice.

Breeding occurred over the January - May period, with the highest percentage of mature females pregnant in March. Despite pregnancies not being recorded outside this period, the presence of juvenile individuals in all months of the study suggests that low level breeding does occur during unfavourable periods. Such a strategy may be extremely important for

survival of populations during years of unfavourable conditions when quality or quantity of food resources are low.

Breeding was most intensive in the conventional areas where 45.2% of mature females were pregnant during the January - May period. At the peak of the breeding period 65% of mature females in this area were pregnant. In contrast, only 9.2% of mature females were pregnant during the same period in trash-blanketed areas, with 7% of mature females pregnant at the peak of the breeding period. Higher breeding intensity in areas of high summergrass abundance and during the period when seed and non-cane vegetation was available and the preferred food source, suggests that summergrasses provide the essential nutritional requirements and/or a chemical cue for breeding. The link between summergrasses and breeding is highlighted by peak breeding intensity occurring in March, one month later than the peak in cover of summergrasses.

The presence of non-cane vegetation in the stomachs of female *R. sordidus* in the trash-blanketed areas, together with the observation of low damage to sugarcane over the January - April period indicates that these animals had been foraging in conventional areas for the preferred food source. At all but one site, this would have entailed *R. sordidus* travelling in excess of fifty metres before reaching the conventional area with high summergrass cover.

High thermoregulatory costs as a consequence of small body size, and high energetic costs of the female's reproductive cycle relative to her ability to obtain food, make small mammals extremely susceptible to reproductive inhibition (Bronson and Perrigo 1987). Energy must first be directed to cellular maintenance, thermoregulation and locomotor costs before reproduction can be supported (Bronson and Perrigo 1987). Decreased food availability results in increased locomotor costs and time spent foraging and therefore reduced reproductive effort (Perrigo and Bronson

1985). An increased risk of predation may also be associated with individuals foraging over larger areas (Ostfield *et al* 1988). Reduced breeding in females of trash-blanketed areas may therefore have been due to these individuals having higher locomotor costs than females living in areas of high summergrass availability.

Sex ratio varied significantly from unity in both treatment areas during the study period. Sex ratio of the mature population was male-biased in both conventional and trash-blanketed areas in February, the beginning of the breeding period. A decrease in the number of males from February to March lead to a female-biased sex ratio in conventional areas from March to August. In contrast, the population of trash-blanketed areas was characterised by a male-biased sex ratio in March and a sex ratio of unity over the remainder of the study period.

Seasonal variation in the secondary sex ratio of small mammal populations has been recognised (eg. Kikkawa 1964; Clark 1980; Cockburn 1981). However, it is often difficult to determine whether a sex bias is real or simply a consequence of differential trappability of males and females (Kikkawa 1964; Clark 1980). McDougall (1946a) suggested that sex ratio of *R. sordidus* populations does not deviate significantly from unity throughout the year, if the population is completely trapped out. Redhead (1973) observed a greater number of males from the first night of trapping and suggested that this may be due to males making longer movements or by increased trappability of these individuals. Any deviation from a sex ratio of unity was therefore attributed to changes in trappability. During most trapping sessions of this study, a low proportion of new captures from each trapping grid on the last night of each trapping session indicates that the greatest possible proportion of each population was trapped (ie "trapped out"). As sex ratio did not vary significantly throughout a trapping session, it

may also be inferred that sex ratio was not affected on those occasions when the population was not "trapped out".

A high proportion of males in the adult population prior to an increase in reproductive effort has been observed in house mouse populations (Crowcroft and Rowe 1957; DeLong 1967). DeLong (1978) suggested that a high proportion of adult male mice is necessary for stimulating oestrus in parous females. However, once population density increases, the high proportion of males is not tolerated and dispersal or death of males leads to a female biased sex ratio. In the present study, the decrease in number of males in the conventional areas was due to loss of individuals in the oldest age class (head-body length $\geq 175\text{mm}$). A decrease in the number of old males also occurred in trash-blanketed areas. This indicates a high mortality rate within this age class immediately after breeding onset.

Lidicker (1975) suggested that mortality schedules may be affected by sexual biases in dispersal. If males disperse more frequently or to a greater distance than females, males would be more often at a greater risk. Aggression and territoriality of "old" males at the onset of the breeding period may have increased dispersal and therefore mortality of males within the oldest age class. The result is a high proportion of females in the population of conventional areas where food is most abundant, during the period of most intensive breeding. In trash-blanketed areas, low availability of the necessary food source results in a low number of adult females present during the breeding period. Sex ratio is therefore close to unity in these areas in most months of the breeding period.

Higher utilisation of sugarcane throughout the year by male *R. sordidus* and the relatively uniform distribution of adult males between conventional and trash-blanketed areas indicates that males do not need to satisfy such high nutritional demands as females.

This distribution of males and females between optimal and less preferred habitat ensures that the environment is efficiently exploited and guarantees maximum reproduction during favourable periods. Differences in sex ratio of *R. sordidus* populations due to variations in local food supply suggests that sex ratios of unity throughout the year, documented in previous studies may simply be a reflection of the prevailing local conditions.

Despite the first oestrus occurring at about two months of age, records of pregnancy of *R. sordidus* which are less than five months old are infrequent (Gard 1935; McDougall 1946a; Taylor and Horner 1973). In the present study, no pregnancies were recorded for individuals less than 10 weeks of age. Although young individuals between 10 weeks and one year (head-body length class 125-149mm) were observed to be pregnant, records of pregnancy were most common for individuals over one year old (head-body length >150mm).

Drickamer (1981, 1988) investigated the consequences of accelerated or delayed sexual maturation in house mice. It was suggested that earlier puberty for some females is a means of successfully passing on genes more rapidly to subsequent generations and a way of ensuring at least some reproduction in a species with a short lifespan and low probability of surviving to produce more than a few litters. Alternatively, selection may favour females which delay the onset of their reproduction, when as a consequence of that delay, those females will produce more young. The potential productivity of the oldest females may also be increased due to their higher social position in the population (DeLong 1978).

The distribution of females between age classes in trash-blanketed and conventional areas of sites where breeding was intensive suggests that social factors may regulate the number of younger, breeding individuals within a population of *R. sordidus*. The population of conventional areas

was characterised by a high proportion of older individuals during the breeding period. In contrast, the number of older female *R. sordidus* decreased from January to February in trash-blanketed areas. Higher frequency of pregnancy in older female *R. sordidus*, suggests that these individuals dominate the population and younger animals are forced to utilise other habitats where preferred food resources are limiting. This may be effected by changes in female spacing behaviour with increased densities leading to females preventing immigration. The number of potential breeders in the population would therefore be limited, as observed in microtine (Boyce and Boyce 1988) and wood mice (*Apodemus sylvaticus*) populations (Jamon 1986). Alternatively, if physiological factors preclude younger females from breeding, these individuals may not need to satisfy the same high nutritional demands as older, breeding individuals and therefore establish in areas where competition as well as availability of food resources is lower.

Male *R. sordidus* were less specific in their selection of habitat type, as reflected by their relatively uniform distribution, and the absence of a consistent difference in age structure between conventional and trash-blanketed areas during the breeding period. It is therefore evident that the lower energetic constraints on these individuals during the breeding period allows them to exploit a range of habitat types with varying resource levels.

Juveniles were present in greatest numbers over the period February to June. A peak level of juveniles in both conventional and trash-blanketed areas occurred in May, two months following peak breeding intensity. Despite low level establishment of populations and the low intensity of breeding in trash-blanketed areas, population levels increased rapidly after May due to a level of juvenile recruitment similar to that in conventional areas.

Using capture-mark-release techniques, it is not possible to obtain an estimate of the number of juveniles surviving from birth until trappable age in field populations. That is, unmarked juveniles dispersing from one area cannot be distinguished from those juveniles born elsewhere. DeLong (1967) used an index of the number of young produced per lactating female to investigate juvenile recruitment into a population of house mice. It was suggested that inaccuracy in the index could be caused by changes in trappability of either adults or juveniles. Therefore the index was only considered adequate for comparing major differences in recruitment between populations or throughout a breeding season within a population.

Estimation of this index for conventional and trash-blanketed areas, revealed a low level of juvenile recruitment in conventional areas and a high level of juvenile recruitment in trash-blanketed areas, relative to average litter size. This suggests that juveniles were dispersing from conventional areas where breeding intensity was high into trash-blanketed areas.

Dispersal of juveniles from conventional areas to trash-blanketed areas occurs during the period when summergrass cover is declining in conventional areas. Juvenile survival may therefore be enhanced by their dispersal into trash-blanketed areas where competition due to lower population levels is reduced. Consequently, population levels are similar in conventional and trash-blanketed areas from April to September.

In the present study, trapping did not continue after September so that individuals trapped over the July - September period had a reduced probability of recapture. This therefore precluded an investigation of population turnover after June. Over the February - June period, population turnover (indicated by the proportion of "recaptures" present in the population) was consistent from both conventional and trash-blanketed areas. Constant turnover of populations in crops during periods when

habitats are relatively stable and food availability is high, is characteristic of a pre-saturation dispersal strategy (Lidicker 1975). Where pre-saturation dispersal occurs, migrants are normally in good condition and are not necessarily socially subordinate as there is still a surplus of resources in their environment (Lidicker 1975). Consequently, these individuals have a high probability of surviving migration.

Sugarcane growing regions are characterised by three major factors which are conducive to the development of a pre-saturation dispersal strategy (Fleming 1979):

- 1) there is a high impending probability of the area currently inhabited undergoing a catastrophic change;
- 2) there is a high probability of a dispersing individual locating a favourable habitat type within a short travelling distance;
- 3) vacant, favourable habitat patches periodically become available.

McDougall (1946b) also described steady turnover rates of *R. sordidus* in North Queensland sugarcane growing regions throughout the year characteristic of a pre-saturation dispersal strategy. High survival of migrants was indicated by increases in population density in favourable habitats. An increase in population turnover during periods of peak population density (McDougall 1946b) suggests saturation dispersal also occurs. At these times, migrants are generally socially subordinate animals in poor condition due to a shortage of resources. As a result these individuals have a low probability of surviving migration (Lidicker 1975). McDougall (1946b) suggested that environmental conditions at times when saturation dispersal is occurring, are important in determining survival of *R. sordidus* during these periods. "Mild" conditions may lead to increased survival of migrants, resulting in an increase in population density to "plague" proportions.

The differential proportion of recaptures in populations of conventional and trash-blanketed areas may be considered as a reflection of differences in habitat quality. Higher food availability in conventional areas results in greater population stability, indicated by a high proportion of recaptured individuals present during trapping sessions. In conventional areas, the female population was more stable than the male population with "recaptures" comprising a mean 51% of these individuals compared to only 36% of males individuals over the March - September period. Such a sex bias in dispersal rates is characteristic of many small mammal populations. Lower energy constraints on males means that these individuals are not disadvantaged by a highly mobile lifestyle. In contrast, the high energy demands of breeding on females confers some stability within this stratum during breeding periods.

Dispersal of juveniles from conventional areas to trash-blanketed areas suggests that saturation dispersal is also characteristic of *R. sordidus* populations following breeding. Entry of juveniles into the trappable population of both treatment areas was reflected by significantly lower head-body lengths of "new captures" compared to "recaptures" in both areas. In trash-blanketed areas, head-body lengths of "new captures" were significantly lower than those of "recaptures" from February to September. In conventional areas head-body lengths of "new captures" were lower from April to July.

Destruction of large areas of suitable habitat during the crop harvest period (June to December) results in increased movement of *R. sordidus* populations throughout the district (McDougall 1946b). As dispersing *R. sordidus* must cross large areas of inhospitable habitat created by crop harvest, higher mortality rates due to increased energy expenditure and increased risk of predation, are likely during this period. The decline in population levels in both conventional and trash-blanketed areas from May

to August observed in the present study may therefore be attributed to decreased survival of dispersing individuals. The area of suitable habitat type continues to decrease until September when new crops emerge and become suitable for colonisation. Crops which remain unharvested in September when availability of suitable cover is lowest, are therefore highly exploited by surviving *R. sordidus*, as indicated by the sharp increase in population levels from August to September.

Despite differences in the way in which *R. sordidus* utilises conventional and trash-blanketed areas, damage to cane at crop harvest was similar between treatment areas. In both treatment areas damage was low until March/April, and then increased until crop harvest. The increase in damage to cane after March reflected the change in diet of *R. sordidus* from seed and non-cane vegetation to sugarcane. At this time population levels were similar in conventional and trash-blanketed areas due to dispersal.

5.5 SUMMARY

Continual cultivation of new crops during the June - December period prevented colonisation of these areas by *R. sordidus* until December/January. As a trash-blanketed crop is not subject to conventional tillage practices, it is a more stable environment and may be colonised by *R. sordidus* two months after harvest of the previous season's crop. The practice of trash-blanketing may therefore increase survival of *R. sordidus* during the harvest period by increasing the area of suitable habitat.

Summergrasses were a preferred food source of *R. sordidus* over the January - May period. A trash-blanket suppressed summergrass growth during the breeding period, resulting in lower population levels and reduced breeding intensity in trash-blanketed areas. Populations in conventional

areas were characterised by a female-biased sex ratio and lower turnover rates than in trash-blanketed areas.

Following breeding, animals dispersed from conventional crops into trash-blanketed areas. As *R. sordidus* had begun to exploit sugarcane as a food source during this period, damage to cane increased in both trash-blanketed and conventional areas. No differences in damage between trash-blanketed areas and conventional areas were observed.

THE SPATIAL DISTRIBUTION OF CROP DAMAGE

6.1 INTRODUCTION

The concept of a population as a local assemblage of interbreeding individuals has resulted in a multitude of studies that describe a population in terms of temporal variations in population size and structure. Operational definitions such as "(a population is)...a biological unit at the level of ecological integration where it is meaningful to speak of a birth rate, a death rate, a sex ratio and an age structure in describing the properties of the unit" (Cole 1957) have reinforced the view that temporal variations in reproduction and mortality are the major population processes affecting the long-term viability of the population. In many studies, immigration and emigration are assumed to be equal and are not considered important (Odum 1971).

This simplistic approach assumes that the boundaries of the population are known and that there is a discontinuity that isolates the population under study from adjacent populations. This situation is rare at the level of scale at which most small mammal studies are undertaken. More common is a situation where animals are distributed such that natural groupings are evident but no group can be considered entirely discrete (Caughley 1977). In the latter situation, dispersal (especially density dependent dispersal) must be considered a significant population process as it has been shown to influence mortality, growth rate, age and sex structure and social structure (Lidicker 1975; Gaines and McClenaghan 1980; Stenseth 1983).

At the regional level of scale, interaction between localised populations can be a major determinant of population success. The extinction of localised populations can be considered a normal component of the regional dynamics of many species (Hanski and Gilpin 1991) especially when

suitable habitats are separated by large, uninhabitable areas (Hansson 1977). It follows that a full understanding of the processes regulating populations in a heterogeneous landscape must include both spatial and temporal factors.

Interaction between localised populations is particularly important in agricultural systems where the regional mosaic of crop and non-crop habitats and the regular cycle of cultivation, planting and harvesting result in a large number of temporally unstable habitats and a high degree of spatial variability (Levins 1969).

Spatial dynamics as a set of interactions between localised populations was first proposed by Levins (1969). The importance of the "metapopulation" concept in that it may limit the success of populations in heterogeneous environments has only recently received attention (Gilpin and Hanski 1991 for review). Although Levins' original concepts were developed to assist in the control of agricultural pests on a regional scale, very few studies have investigated factors affecting the spatial distribution of rodents in agricultural systems. Most studies concentrate on temporal changes in population size and structure and consider interaction between only two compartments of the system - crop habitats and non-crop habitats (refuges).

The concept of refuges as areas of temporal stability in an otherwise temporally unstable system is well established. In agricultural systems these refuges are usually permanent non-crop habitats and their importance to the success of rodent pest species in agricultural systems is well documented (Bykovsky 1986; Hood *et al* 1970; Lindsey 1973; Newsome 1969a,b; Singleton 1985, 1989; Williams *et al* 1978). With the exception of Singleton (1989), these studies did not consider non-crop habitats as a component of a regional landscape and concentrated on their use as a refuge during times when crop habitats were absent or unable to provide sufficient food

and/or shelter.

Several studies have shown that rodent damage to sugarcane is patchy throughout a region and is associated with landscape attributes:

In Hawaii, gullies provided a stable habitat for Polynesian rats (*R. exulans*) and supported permanent populations. Damage was greater in areas highly dissected by gullies (Fellows and Sugihara 1977).

Redhead (1973, 1980) and Redhead and Saunders (1980) showed that Queensland sugarcane crops can only be considered as a temporary habitat due to the disturbances associated with cultivation. Under these circumstances, non-crop habitats were important refuges for *R. sordidus* during the harvest period. Higher population densities and higher levels of crop damage were recorded in crops in close proximity to non-crop refuges.

McDougall (1946b, 1947) did not consider that the availability of non-crop habitats limited the success of *R. sordidus* populations in Queensland sugarcane growing areas. It was suggested that the staggered nature of harvesting within a district allowed *R. sordidus* to utilise mature cane awaiting harvest as a refuge. It was further suggested that unharvested crops were important refuges for dispersing individuals. These findings are difficult to interpret as dispersal periods were not substantiated with data and general movement data were not presented.

A patchy landscape results in a non-uniform distribution of damage throughout a region (Redhead 1980). Despite this, thallium sulphate baits have been used extensively for the control of *R. sordidus* in Queensland sugarcane growing areas since the 1940's (Hitchcock 1975; Hitchcock and

Kerkwyk 1975, 1987; Redhead and Saunders 1980). Annual widespread aerial application of baits has been the norm since 1967. Control procedures that rely on widespread aerial baiting are non-selective and costly, with many baits being applied to areas where control is not necessary (Ralph 1982; Redhead and Saunders 1980). The ability to direct control effort to locations where it is most needed is essential if the control process is to be cost-effective.

This aim of this study is to determine the influence of local site attributes on the spatial distribution of crop damage throughout a sugarcane growing region and to determine the damage potential associated with each combination of attributes.

6.2 METHODS

The Herbert River District is an agricultural mosaic of sugarcane crops, native forests and grasslands, swamps, drainage channels and improved pastures.

The canegrowing area of the Herbert River District was divided into 1 km² cells. Three hundred and sixty one cells were chosen at random and a crop (field of sugarcane) was randomly selected within each cell. Within each crop, a site of approximately 150m x 50m was selected such that it was more than 20m from the perimeter of the crop.

The following data were collected at each site:

Crop damage: Five randomly located transects, each consisting of 200 consecutive stalks, were inspected for rodent damage. Crop damage was expressed as the number of bitten stalks per 1000 stalks.

Weed cover: In-crop weed cover was assessed visually within each field. Weed cover was expressed as 0%-5%, 6%-25%, 26%-50%, 51%-75% or 76%-100%. The dominant weed species were also recorded.

Soil type: The soil type at each site was determined from detailed soil maps of the district (Wilson and Baker 1990). *R. sordidus* is a colonial animal that constructs elaborate networks of burrows and runways. It was considered that soil attributes such as drainage, binding and the ease of burrowing through the surface and the soil profile may influence the establishment of populations within a crop. A score for each of these four attributes was generated for each soil type from information obtained from the Queensland Department of Primary Industries. The four individual scores for each soil type were summed to give a total soil score. The range of total soil scores was partitioned into three equal classes representing poor, fair and good soil types with respect to those attributes that may influence burrow establishment and maintenance (Table 6.1).

Refuge availability: Non-crop habitats (refuges) are not utilised equally by *R. sordidus*, the order of utilisation being grassland and swamp > open forest > closed forest and grazed areas (Chapter 3). The type of the major refuge associated with (less than 1 km) each site was recorded.

The effect of individual site attributes on the pattern of damage within the district was determined by χ^2 tests of independence.

Log-linear models were used as a preliminary analysis to investigate the significant associations within the data set. Logit models were then used to determine the relationships between the three explanatory variables (weed

Table 6.1

Classification of soil types with respect to those attributes that may influence burrow establishment and maintenance.

Soil type ¹	Drainage score ²	Binding score ³	Ease of digging score		Total soil score	Soil class
			Surface ⁴	Profile ⁵		
Th, Cn, Hb	4	3	3	3	13	Good
Bw,Ag	4	3	2	3	12	
Hv	4	2	3	3	12	
Tr	3	3	3	3	12	
Lc,Pa,Pl, Lu	4	2	2	3	11	Fair
Mk	4	1	3	3	11	
Mw	3	3	3	2	11	
An,At,As	3	2	3	3	11	
Rg	2	3	3	2	10	
Pt,Mn,Ln Rp,Br,Yr Sn,Tb	2	3	1	1	7	Poor
Md	1	3	2	1	7	
Lh	1	3	1	1	6	

1 Soil type reference code (Wilson and Baker 1990).

2 Soil drainage: 4 good; 3 fair; 2 poor (fluctuating water table); 1 poor.

3 Soil binding: 3 good; 2 fair (possible collapse); 1 poor.

4 Soil surface: 3 easy (friable); 2 moderate (hard set); 1 hard (very hard set).

5 Soil profile: 3 easy; 2 moderate; 1 hard.

cover, refuge type and soil type) and their effect on crop damage, the response (or dependent) variable. In this case the hypothesis to be tested was: *If crop damage is uniformly or randomly distributed throughout the*

district, all defined site types should be equally represented across levels of the response variable.

Logit models were used in preference to general log-linear models as the former incorporate the multiway comparisons between the explanatory variables (as well as all lower order implied marginal associations) regardless of their statistical significance to the fit of the model. This removes the deviance from the data which is not related to the response variable (Knoke and Burke 1980).

A series of models was fitted to the data in order to assess whether the distribution of observations across levels of the response variable was influenced by either main or interaction effects amongst the explanatory variables. Individual effects were added to the model using a stepwise procedure, with the order of inclusion dictated by the magnitude of the reduction in deviance attributed to the effect (Fienburg 1980). Only those effects that contributed a significant ($p < 0.05$) reduction in the residual deviance were included in the model, except where the inclusion of an effect was necessary to satisfy the requirement that the model be hierarchal.

The goodness of fit of a particular model was determined using the Likelihood Ratio statistic (χ^2_{LR}) rather than the Pearson Chi-Square statistic (χ^2) as the former can be easily partitioned into additive parts representing the contribution of individual components of the model. Final model selection was based on the criterion that all significant associations evident within the data be included and that the model provide an adequate representation of the observed data.

The logit values and odds ratios describe the effect of the explanatory variables (weed cover, refuge type and soil type) on crop damage. Within a model, the magnitude of the logit values represent the relative strength of the effects being compared. The additive nature of logit effects allows logit

values to be calculated for each combination of site attributes. The odds of a particular combination of site attributes resulting in either low or high damage can be calculated as the exponential transformation of the corresponding logit value. Odds ratios are multiplicative with departure from unity being a measure of strength (Everitt 1980).

The logit values and odds ratios derived from the selected model were also used to generate an index of damage potential for sites defined by specific combinations of site attributes.

6.3 RESULTS

Damage within the 361 sites ranged from 0% to 21% damaged stalks with the majority of estimates clustered at the lower end of the range (Figure 6.1). The frequency distribution was divided into three equal areas and crop damage at each site classified as low, moderate or high (Table 6.2).

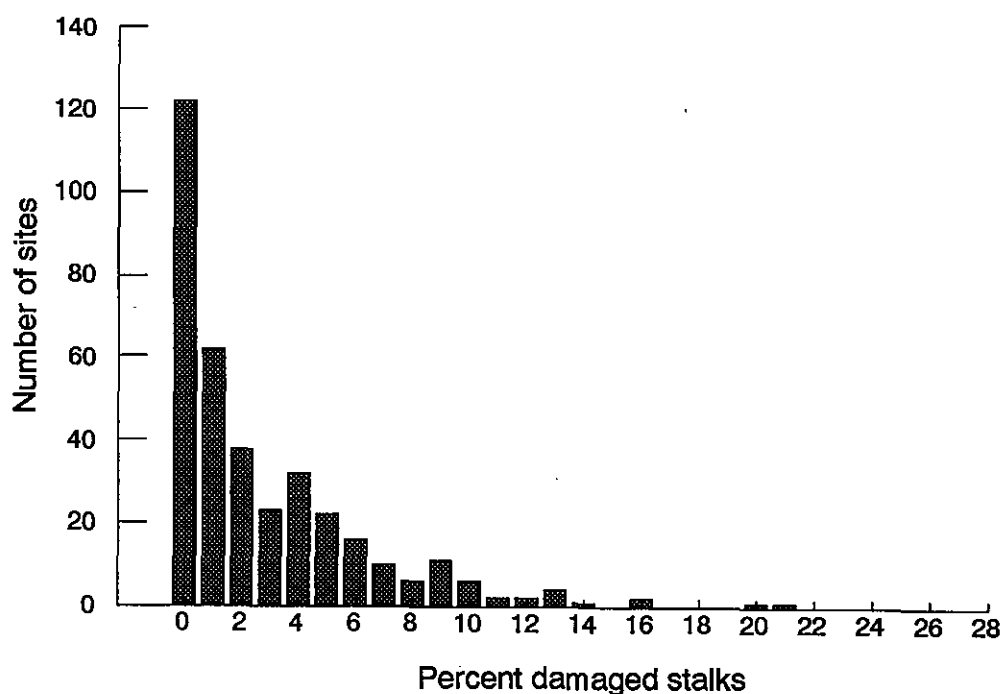


Figure 6.1 The frequency distribution of crop damage

Table 6.2

Classification of sites into damage classes

Crop damage (% damaged stalks)	Damage class	Number of sites	% of Total sites
< 1.0	LOW	123	34.1
≥ 1.0 - 3.75	MODERATE	117	32.4
≥ 3.75	HIGH	121	33.5

Crop damage was not uniform throughout the District (Table 6.3) with more low damage sites than expected occurring in the Ingham Line and Estate areas. Conversely, more high damage sites than expected occurred in the Abergowrie and Stone River areas ($\chi^2_{10}=132.0$, $p<0.001$).

Table 6.3

The distribution* of crop damage throughout the Herbert River District.

District	Number of sites	Crop damage (% of sites)		
		Low	Moderate	High
Abergowrie	142	18.3	38.0	43.7
Stone River	63	9.5	25.4	65.1
Fairford	27	22.2	48.1	29.7
Macknade	38	42.1	36.8	21.1
Ingham Line	53	67.9	28.3	3.8
Estate	38	86.8	13.2	0.0
No. of sites (Expected%)**	361	123 (34.1)	117 (32.4)	121 (33.5)

* For each area - percentage of sites in each crop damage category.

** From Table 6.2.

Crop damage was positively associated with weed cover (Table 6.4). More sites with a high weed cover experienced higher damage than expected whilst more sites with low weed cover experienced lower damage than expected ($\chi^2_6=46.58$, $p<0.001$).

Table 6.4

Distribution* of damage based on weed cover

% Weed cover	Number of sites	Crop damage (% of sites)		
		Low	Moderate	High
0 - 5	82	44	34	22
6 - 25	167	43	31	26
26 - 50	61	11	43	46
> 50	51	15	22	63
No. of sites (Expected%)**	361	123 (34.1)	117 (32.4)	121 (33.5)

* For each weed cover class - percentage of sites in each damage class.

** From Table 6.2.

Weeds were not distributed uniformly throughout the District with the Macknade, Ingham Line and Estate areas containing more sites with low weed cover than expected (Table 6.5).

A higher than expected number of sites associated with grasslands and open forest exhibited high crop damage (Table 6.6). At sites where the adjacent refuge was heavily grazed, the number of sites exhibiting low crop damage was greater than expected. This was also the case where refuges were absent ($\chi^2_{10}=23.59$, $p<0.01$).

Table 6.5

Distribution* of weed cover throughout the Herbert River District.

Area	Number of sites	Weed cover (% of sites)		
		Low (0% - 25%)	Moderate (26% - 50%)	High (> 50%)
Abergowrie	142	70.4	20.4	9.2
Stone River	63	38.0	22.2	39.7
Fairford	27	59.2	22.2	18.5
Macknade	38	86.8	5.3	7.9
Ingham Line	53	94.3	18.9	0.0
Estate	38	86.9	13.2	0.0
No. of sites (Expected%)**	361	249 (69.0)	61 (16.9)	51 (14.1)

* For each area - percentage of sites in each weed cover class.

** From Table 6.4.

Table 6.6

The distribution* of crop damage based on adjacent refuge type.

Refuge type	Number of sites	Crop damage (% of sites)		
		Low	Moderate	High
Grassland	21	10	42	48
Swamp/drainage	67	42	27	31
Open forest	115	23	34	43
Closed forest	55	36	31	33
Grazing	40	45	30	25
None	63	44	35	21
No. of sites (Expected%)**	361	123 (34.1)	117 (32.4)	121 (33.5)

* For each refuge type - percentage of sites in each damage class.

** From Table 6.2.

Table 6.7

The Distribution* of refuges within the Herbert River District

Area	Number of sites	Adjacent refuge type (% of sites)					
		Grassland	Swamp/ drainage	Open forest	Closed forest	Grazing	None
Abergowrie	142	4.9	21.8	38.0	16.9	11.0	6.3
Stone River	63	7.9	6.3	60.3	9.5	4.8	11.1
Fairford	27	14.8	7.4	22.2	7.4	3.7	44.4
Macknade	38	0.0	34.2	10.5	23.7	5.3	26.3
Ingham Line	53	9.4	13.2	20.8	15.1	22.6	18.9
Estate	38	0.0	26.3	5.3	15.8	13.2	39.5
No. of sites (Expected%)**	361	21 (5.8)	67 (18.6)	115 (31.9)	55 (15.2)	40 (11.1)	63 (17.5)

* For each area - percentage of sites associated with each refuge type.

** From Table 6.6.

Sites associated with specific refuge types were not distributed uniformly throughout the district. As sites were chosen at random, these data are indicative of the distribution and extent of refuges in each area (Tables 6.7 and 6.8).

A higher than expected number of sites associated with good soil types exhibited high crop damage (Table 6.9). Conversely, more sites on poor soil types exhibited low crop damage ($\chi^2=34.78$, $p<0.001$).

The Abergowrie and Stone River areas contained the highest percentage of sites on good soil types whilst the Fairford, Ingham Line and Estate areas contained the highest percentage of sites on poor soil types (Table 6.10).

Independently, weed cover, refuge type and soil type have been shown to influence the distribution of crop damage throughout the Herbert River District. *Interactions* between site attributes may also influence the pattern of crop damage throughout a district.

Log-linear and logit models were used to determine the relationships between the three explanatory variables (weed cover, refuge type and soil type) and their effect on crop damage, the response (or dependent) variable. The GLIM (release 3) statistical package was used for all analyses (Baker and Nelder 1978).

All 361 sites were incorporated into the models after being allocated to classes on the following basis:

- Damage at each site was classed as either LOW or HIGH depending on whether the estimate was below or above the median damage estimate for all sites (n=361).
- Weed cover at each site was classified as LOW (<25%) or HIGH (>25%)

Table 6.8

The density (number km⁻²) of refuges associated with sites within the Herbert River District.

Area	Number of sites	Refuge density* (% of sites)			
		Zero	One	Two	Three
Abergowrie	142	6.3	30.9	38.0	24.6
Stone River	63	11.1	57.1	25.4	6.3
Fairford	27	44.4	40.7	14.8	0.0
Macknade	38	26.3	71.1	2.6	0.0
Ingham Line	53	18.9	62.3	18.9	0.0
Estate	38	39.5	47.4	13.2	0.0
No. of sites (Expected%)	361	63 (17.5)	169 (46.8)	90 (24.9)	39 (10.8)

* For each area - percentage of sites in each refuge density class. Refuge density is the number of refuges within 1 km of the site.

Table 6.9

Distribution* of damage based on soil classification.

Soil classification	Number of sites	Crop damage (% of sites)		
		Low	Moderate	High
Good	113	15	36	49
Fair	85	40	39	21
Poor	163	45	26	29
No. of sites (Expected%)**	361	123 (34.1)	117 (32.4)	121 (33.5)

* For each soil classification - percentage of sites in each damage class.

** From Table 6.2.

Table 6.10

The distribution* of soil classes within the Herbert River District.

Area	Number of sites	Soil class (% of sites)		
		Good	Fair	Poor
Abergowrie	142	58.5	14.8	26.8
Stone River	63	30.2	30.2	39.6
Fairford	27	14.8	14.8	70.4
Macknade	38	10.5	71.1	18.4
Ingham Line	53	3.8	9.4	86.8
Estate	38	2.6	23.7	73.7
No. of sites (Expected%)**	361	113 (31.3)	85 (23.5)	163 (45.2)

* For each area - percentage of sites in each soil class.

** From Table 6.9.

Refuges were partitioned into four classes based on their relative utilisation by *R. sordidus* (Chapter 3):

- (1) Grassland/swamp
- (2) Open Forest
- (3) Closed forest/grazing
- (4) No adjacent refuge.

Soil type at each site was classified as GOOD, FAIR or POOR based on the accumulated score of four attributes - drainage, binding, ease of digging through the soil surface and profile (Table 6.1).

The distribution of the response variable (crop damage) and the three explanatory variables (weed cover, refuge type and soil type) across the 361 sites is given in Table 6.11.

Table 6.11

The distribution of sites cross-classified by damage, weed cover, refuge type and soil type.

SOIL TYPE	DAMAGE WEED COVER REFUGE TYPE	LOW		HIGH	
		LOW	HIGH	LOW	HIGH
GOOD	Grassland/swamp	5	1	17	10
	Open forest	8	2	12	12
	Closed forest/grazing	5	3	9	9
	None	10	2	4	4
FAIR	Grassland/swamp	14	3	2	2
	Open forest	10	3	13	6
	Closed forest/grazing	10	1	5	5
	None	9	0	2	0
POOR	Grassland/swamp	17	1	6	10
	Open forest	15	6	15	13
	Closed forest/grazing	29	7	7	5
	None	20	3	5	4

A series of log-linear models was fitted to the data of Table 6.11 (Table 6.12). The model that includes all of the significant associations within the data set is Model 8: [RWS][DW][DSR] indicating that weed cover has an effect on damage [DW] as do the individual and combined effects of refuge type and soil type [DSR].

Although Model 7 adequately describes the data, the [Soil.Refuge] interaction of Model 8 provides the opportunity to investigate the role of soil type and refuge type interactions in the damage process.

Table 6.12

Assessment of the fit of various models to the site data. Numbers within parentheses identify the previous model against which the reduction in deviance associated with the inclusion of the component is assessed.

Model	Deviance	d.f.	-Deviance	d.f.
1. [RWS][D]	94.09	23		
2. [RWS][DW]	60.72	22	33.37 (1)	1 *
3. [RWS][DS]	69.61	21	24.48 (1)	2 *
4. [RWS][DR]	74.84	20	19.25 (1)	3 *
5. [RWS][DW][DS]	39.47	20	21.25 (2)	2 *
6. [RWS][DW][DR]	44.85	19	15.87 (2)	3 *
7. [RWS][DW][DS][DR]	23.05	17 +	16.42 (5)	3 *
8. [RWS][DW][DSR]	8.20	11 +	14.85 (7)	6 *
9. [RWS][DS][DWR]	22.60	15	0.45 (7)	2
10. [RWS][DR][DWS]	20.31	14	2.74 (7)	3

D=damage, W=weeds, R=refuge, S=soil type

* The inclusion of the component makes a significant contribution to the model ($p < 0.05$).

+ The model provides an adequate fit to the observed data ($p < 0.05$).

Table 6.12 shows that weed cover has the strongest effect on crop damage (deviance reduction of 33.37). The lack of a strong association between weed cover and refuge type and/or soil type (models 9 and 10 respectively) indicates that the influence of weed cover is independent of these other site attributes.

Information relating to the derivation of the estimated logits and the odds of sustaining either low or high damage for the twenty four combinations of site attributes is given in Appendices 6 to 9.

Figure 6.2 shows that the odds of sustaining high crop damage are always higher for sites with a high weed cover regardless of soil type or refuge type.

The odds of sustaining low crop damage are greater at sites characterised by low weed cover except when they occur on good soil types and are adjacent to a refuge. Sites with high weed cover are generally associated with high damage provided that an adjacent refuge is present (Figure 6.2).

Figure 6.2 also shows that the odds of high crop damage at sites characterised by good soil types are high if an adjacent refuge is present. The strength of this association follows the same trend as the relative utilisation of the adjacent refuge type (grasslands > open forest > closed forest/grazing). For sites on other soil types, the magnitude of the odds of sustaining high damage are not correlated with the relative utilisation of adjacent refuge types.

The logit values associated with high damage range from 2.38 to -1.99 (Appendix 9). This range was partitioned into three equal classes representing low, moderate and high crop damage **potential**. Each of the twenty four combinations of site attributes was assigned to a damage potential class based on the logit value for that combination (Table 6.13).

As verification of the logit analysis, each of the 361 sites was assigned to a damage potential class based on the combination of attributes at each site. The actual damage estimates of sites within each damage potential class were then compared. The mean damage estimates of each class (Low: $1.48 \pm 0.20\%$, $n=145$; Moderate: $3.71 \pm 0.31\%$, $n=129$; High: $5.06 \pm 0.42\%$,

n=87) differed significantly, providing independent evidence that the logit model adequately predicts damage (one-way ANOVA: arcsine[\sqrt{p}] transform $F_{2,358}=36.61$, $p<0.001$; multiple comparison: $t_{214(\text{mod-high})}=2.65$, $p<0.05$; $t_{272(\text{low-mod})}=6.23$, $p<0.001$; $t_{230(\text{low-high})}=8.66$, $p<0.01$).

Table 6.13

Damage potential classes for each combination of site attributes based on the estimated logits of sustaining high damage.

Soil type	Refuge type	Weed cover	
		Low	High
Good	Grassland/swamp	HIGH	HIGH
	Open forest	MODERATE	HIGH
	Closed forest/grazing	MODERATE	HIGH
	None	LOW	MODERATE
Fair	Grassland/swamp	LOW	LOW
	Open forest	MODERATE	HIGH
	Closed forest/grazing	LOW	MODERATE
	None	LOW	LOW
Poor	Grassland/swamp	LOW	MODERATE
	Open forest	MODERATE	HIGH
	Closed forest/grazing	LOW	MODERATE
	None	LOW	MODERATE

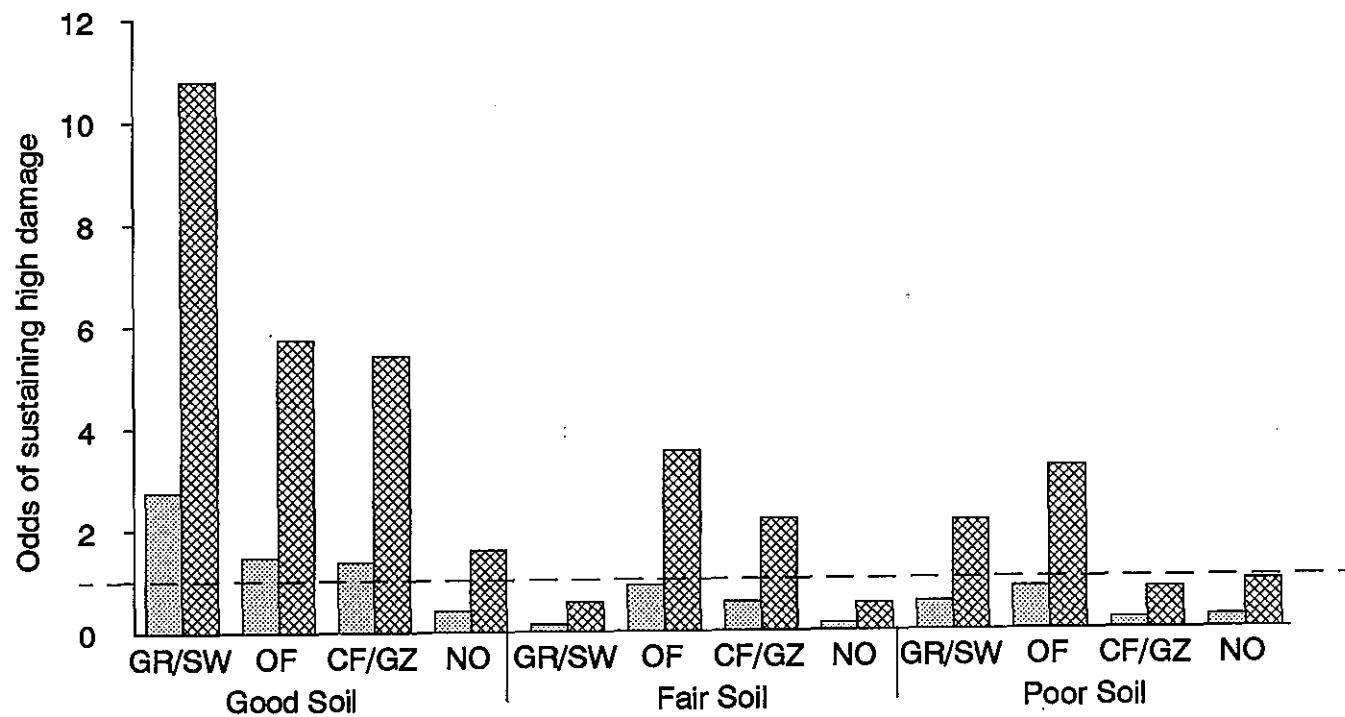


Figure 6.2 The relationship between the odds of sustaining high crop damage and site characteristics

Weed Cover: Low (dotted pattern), High (cross-hatched pattern)
 Adjacent refuge: GR/SW Grassland/swamp, OF Open forest, CF/GZ Closed forest/grazing, NO None

-- : point at which the odds of sustaining HIGH or LOW damage are equal.

6.4 DISCUSSION

Crop damage is not uniform throughout the Herbert River District as not all locations have an equal potential for damage. Damage at a particular location is influenced by weed cover, the type of refuge associated with the site and soil type. It is important to realise that the level of crop damage is determined not only by the individual contributions of these attributes, but also by interactions between attributes.

Weed cover has the strongest influence on crop damage and its effect is independent of the other attributes. Sites with high levels of weed cover were consistently associated with higher crop damage than comparable sites with low weed cover, regardless of soil type and refuge type.

The effect of refuge availability on crop damage is closely linked to weed cover. Sites with high weed cover are generally associated with high damage provided that a refuge is present. From a rodent perspective, crops with low weed cover ($\leq 25\%$) may be considered as low quality crops compared to those with high weed cover ($>25\%$) whilst refuge quality can be ranked as grasslands and swamps > open forests > closed forests and grazing areas on the basis of their relative utilisation (trap success) by *R. sordidus* (Chapter 3).

The influence of soil type on crop damage is also linked to refuge availability. Sites characterised by good soil types can expect high crop damage if a refuge is present. The effect of soil type is to modify the normal influences due to weed cover and refuge availability. The damage at a given location that is normally dictated by the status of weed cover and refuge type is amplified by the presence of good soil types, whereas fair or poor soil types have little effect on the expected level of damage.

In general, damage to crops on soil types that do not restrict burrow construction or maintenance throughout the wet season is closely linked to the relative importance of the associated refuge. If all other site characteristics are equal, crop damage will be higher at sites on these soil types.

The significance of these site attributes to the damage process can be explained in terms of the population processes that must take place before significant damage can occur, viz:

- . Invasion;
- . Establishment;
- . Breeding.

Ploughed fields, harvested areas and crops less than two months old do not support significant populations of *R. sordidus* and so invasion must occur on an annual basis. Invasion occurs from non-crop refuges that are not subject to the disturbances associated with cultivation (Chapter 3). These non-crop habitats are the most temporally stable component of the system and the quality of the refuge determines the potential for crop invasion.

The availability of high quality refuges alone may not be sufficient to explain the extent of crop invasion and the ease of movement between refuge and crop should also be considered (Lenore and Merriam 1985, Merriam *et al* 1991). Factors such as the distance to the nearest significant refuge and the type and extent of corridors (for example, drainage channels and watercourses) connecting the refuge to the crop may also contribute to the potential for colonisation. The significance of this site attribute has yet to be determined.

R. sordidus is a colonial animal that constructs elaborate networks of burrows and runways. The potential for establishment within a crop

depends, in part, on the ability to construct burrow networks and in certain situations soil characteristics may be a limiting factor in this process. Breeding occurs over the wet season and soils that waterlog readily or cannot support burrows over this period because of poor structural characteristics affect the potential for establishment and hence breeding.

In-crop weeds have been shown to influence both the onset of reproduction (Chapter 3) and, on a local scale, the level of damage at harvest (Chapter 4). This study provides independent evidence of the importance of weeds in the damage process and also shows that this influence is significant at a regional level of scale. Agricultural practices are changing rapidly in the Herbert River District due to the introduction of minimum tillage techniques, green cane harvesting and trashblanketing. In 1982, green cane accounted for 1.2% and 3.6% of the sugarcane processed by the Victoria and Macknade mills respectively. By 1987, the input of green harvested cane into these mills had risen to 72% and 64% respectively (Churchward and Poulsen 1988). Green cane harvesting and trashblanketing were introduced to overcome problems associated with harvesting in wet weather, however the trashblanket that results from green cane harvesting is extremely effective in suppressing weed growth during the early growth stages of the crop. A direct comparison of trashblanket and conventional crops was not undertaken in this study but it can be inferred that the smothering of weeds during the breeding season should result in a general reduction of damage in trashblanket crops.

The attributes and interactions responsible for damage at a particular location are shown in Figure 6.3. In summary, highest damage can be expected at locations that possess the following characteristics:

- . High in-crop weed cover;
- . Well drained, friable soil;
- . Close to grassland, swamp or open forest refuges;

and by inference,

- . Conventional tillage techniques;
- . Areas highly dissected with creeks or drainage channels.

Conversely, lowest damage is associated with:

- . Low in-crop weed cover;
- . Isolation from refuges;

and by inference,

- . Heavy trashblanket techniques;
- . A site surrounded by crops with similar low damage characteristics.

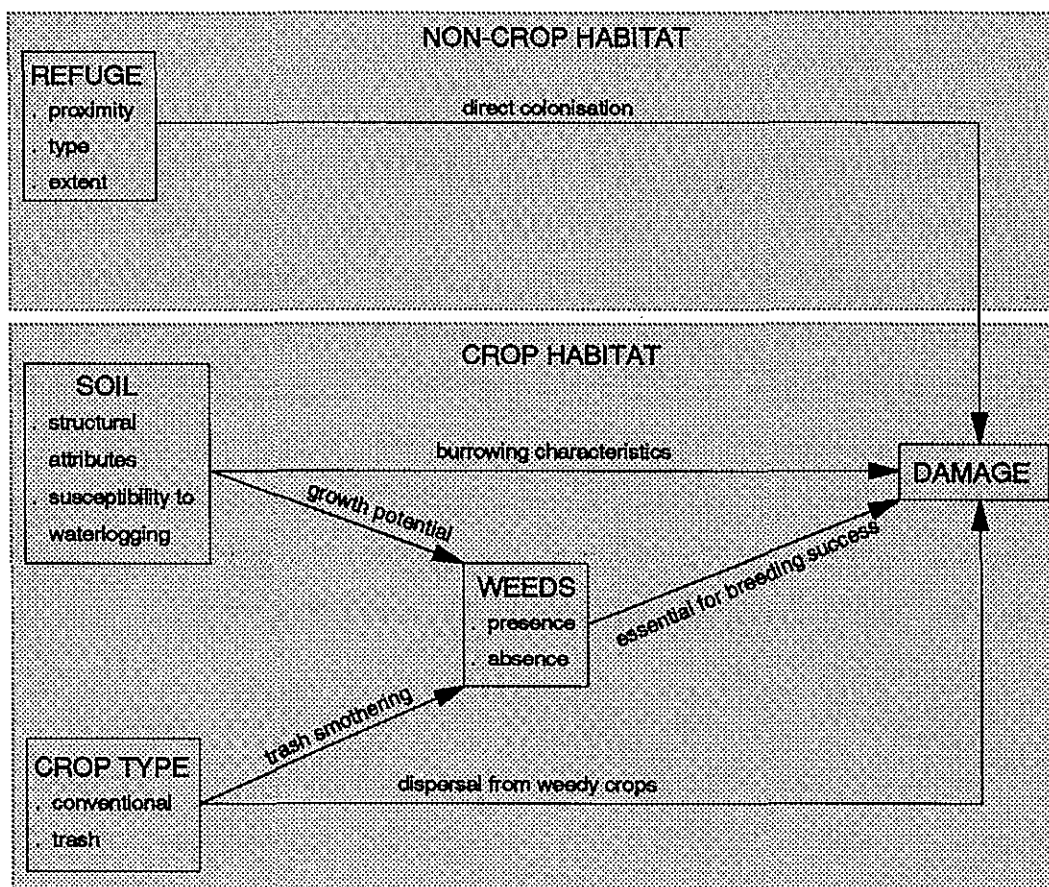


Figure 6.3 The influence of site attributes on rodent damage

At the individual site level it has been shown that the likelihood of sustaining damage is strongly influenced by site attributes. A damage potential index (high, moderate, low) has been assigned to each combination of these attributes based on the logit estimates of sustaining high damage.

It has also been shown that the damage potential categories are consistent with the observed crop damage estimates and efficiently partition the observed crop damage estimates into three distinct categories. The one anomaly of low damage associated with grassland refuges and less than optimal soil types remains unexplained.

The use of site attributes rather than rodent population indices to determine crop damage potential will greatly reduce the time and effort required to allocate control priorities. It will also overcome the problem in heterogeneous environments of the questionable accuracy of crop damage prediction models which rely on solely on population indices (Hannson 1977; Hastings 1982).

To be an effective management tool, a crop damage model must explain crop damage at both the individual site level and the regional level. The observed distribution of damage within the six major areas of the Herbert River District is: Abergowrie & Stone River > Fairford & Macknade > Ingham Line & Estate (Table 6.3). All sites were chosen at random and so the combinations of site attributes associated with each area are indicative of the prevalence of these combinations within each area and reflect the geography of the area.

The dominant geographic attributes of each area are given in Table 6.14. The observed distribution of damage within the six areas parallels the prevalence of those combinations of site attributes in each area that give rise to high damage potential.

Table 6.14

Dominant geographic attributes of each area and their association with damage.

Area	Damage*	Dominant area attributes		
		Weeds**	Refuges***	Soils****
Abergowrie	High number of sites with high damage.	Low number of sites with high weed cover.	High number of sites adjacent to open forest refuges. Very few sites not associated with refuges. Many sites associated with multiple refuges.	High number of sites on good soils.
Stone River	High number of sites with high damage.	Variable.	High number of sites adjacent to open forest and grassland refuges. Many sites associated with multiple refuges.	Variable.
Fairford	High number of sites with moderate damage.	Relatively uniform distribution of sites within weed classes.	High number of sites adjacent to grassland refuges. Many sites not associates with any refuge.	High number of sites on poor soils.
Macknade	High number of sites with low to moderate damage.	High number of sites with low weed cover.	High number of sites adjacent to swamp/drainage refuges. No grassland refuges. High number of sites not associated with any refuge.	High number of sites on fair soils.
Ingham Line	High number of sites with low damage.	High number of sites with low weed cover.	High number of sited associated with grazing areas.	High number of sites on poor soils.
Estate	High number of sites with low damage.	High number of sites with low weed cover.	Very low number of sites adjacent to grassland or open forest refuges. High number of sites not associated with any refuge.	High number of sites on poor soils.

* From Table 6.3, ** From Table 6.5, *** From Table 6.7 and 6.8, **** From Table 6.10

The Abergowrie area is a narrow valley, highly dissected by watercourses and bordered by open forest, hence the preponderance of sites associated with open forest and swamp refuges. Most sites are associated with refuges and many are associated with multiple refuges.

The Stone River area is similar to Abergowrie but it is not as highly dissected by watercourses hence the low percentage of sites associated with swamp/drainage refuges.

The Estate area consists of a low-lying open plain and extensive swamplands. Open forest and grassland refuges are scarce and many sites are not associated with refuges of any kind.

Fairford is also an intensively cultivated plain bordered by grassland and open forest. It is well drained and most sites are surrounded by sugarcane and are not associated with refuges.

The Macknade area is a large coastal area dissected by wet gullies hence the higher percentage of swamp/drainage and closed forest refuges. The central plain is intensively cultivated and many sites are not associated with refuges.

Ingham Line supports both agriculture and grazing and most sites are associated with a single refuge area.

To assess the sensitivity of the crop damage potential model at a regional scale, aerial photographs and soil maps were used to categorise the damage potential of each 1 km² cell of the Herbert River District (Table 6.15). The damage potential for each cell was categorised as high, moderate or low depending on the most prevalent combination of refuge and soil attributes in each cell (from Table 6.13). In-crop weed cover is a

temporal factor and low weed cover was assumed when allocating a damage potential to each cell. The use of damage potential categories based on low weed cover provides a more realistic estimate of regional damage potential given the high preponderance of low weed cover sites throughout the district during this study (Table 6.5). In addition, the increasing use of pre-emergent herbicides and trashblanketing techniques should result in an increase in the proportion of low weed areas in the near future.

At a regional level of scale, the crop damage potential model based on site attributes partitions the six areas into two distinct damage potential groups that are consistent with the observed damage estimates from each area. The Abergowrie and Stone River areas contain a high percentage of high damage potential cells and a low percentage of low damage potential cells. Conversely, the Estate and Ingham Line areas contain a low percentage of high damage potential cells and a high percentage of low damage potential cells. The Fairford and Macknade areas both contain an average percentage of low damage potential cells but also contain varying percentages of high damage potential cells and cannot be considered as a distinct group (Table 6.15).

The lack of sensitivity of the model in partitioning the areas into three levels of damage potential is most probably due to the high variability of cell types in the Fairford and Macknade areas. Fairford has a high number of cells associated with open forest and grassland refuges but this is offset by many cells that are not associated with any refuge. The Macknade area has a large number of cells associated with swamp/drainage refuges and many cells not associated with any refuge.

Table 6.15

The distribution of damage potential within the Herbert River District based on the predominant attributes of 1 km² cells.

Area	Observed damage*	Percentage of cells in each damage potential category ⁺		
		Low	Moderate	High
Abergowrie	high	13 (22)	52 (86)	35 (59)
Stone River	high	29 (34)	37 (43)	34 (40)
Fairford	moderate	35 (45)	31 (40)	34 (43)
Macknade	moderate	35 (27)	45 (35)	20 (15)
Estate	low	52 (69)	36 (47)	12 (16)
Ingham Line	low	57 (61)	28 (30)	15 (16)

* from Table 6.3.

+ number of sites in parentheses.

An understanding of the combinations of attributes that confer a specific damage potential on a site allows the district to be divided into general areas of low, moderate and high damage potential. In turn, this allows control to be directed to areas where it is most needed.

As the damage potential at a given location is largely determined by local site attributes such as soil type and refuge availability, a Geographic Information System (GIS) was developed to map areas of low, moderate and high damage potential within the Herbert River and Mackay districts.

All data were stored and manipulated in dBase IV. Maps were produced using Mapinfo software. Each district was divided into 1 km² cells and the soils and habitats within each cell classified as follows:

Soils The percentage cover of each soil type was estimated to the nearest 10% from 1:100 000 soil maps (DPI, land use series). The suitability of each soil type was classified as optimal or sub-optimal on the basis of drainage, permeability and physical attributes (Table 6.1). The sub-optimal class consisted of all soil types classified as fair or poor in Table 6.1.

Habitats The percentage cover of each habitat type was estimated to the nearest 10% from 1:25 000 aerial photographs (Sunmap series). Sugarcane, open forest, mangrove and closed forest habitats were classified individually. Grasslands, swamp and grazing habitats were classified collectively as grasslands.

Crop damage potential for each cell was classified as low, moderate or high based on the combination of the predominant non-crop habitat type, soil type and level of in-crop weed cover (Table 6.13)

The distribution of soils and predominant non-crop habitats within the Herbert River district are shown in Figures 6.4 and 6.5). The distribution of areas of low, moderate and high damage potential for the Herbert River District is shown in Figures 6.6 (assuming low in-crop weed cover) and 6.7 (assuming high in-crop weed cover).

The distribution of soils and predominant non-crop habitats within the Mackay district are shown in Figures 6.8 and 6.9). The distribution of areas of low, moderate and high damage potential for the Mackay District is shown in Figures 6.10 (assuming low in-crop weed cover) and 6.11 (assuming high in-crop weed cover).

The ability to direct control to areas where it is most needed is essential if the cost-effectiveness of the control process is to be maximised. The crop damage potential model based on site attributes adequately explains observed damage at the individual site level and (with lower sensitivity) the regional level. It can therefore be used as a management tool to increase the efficiency of the control process.

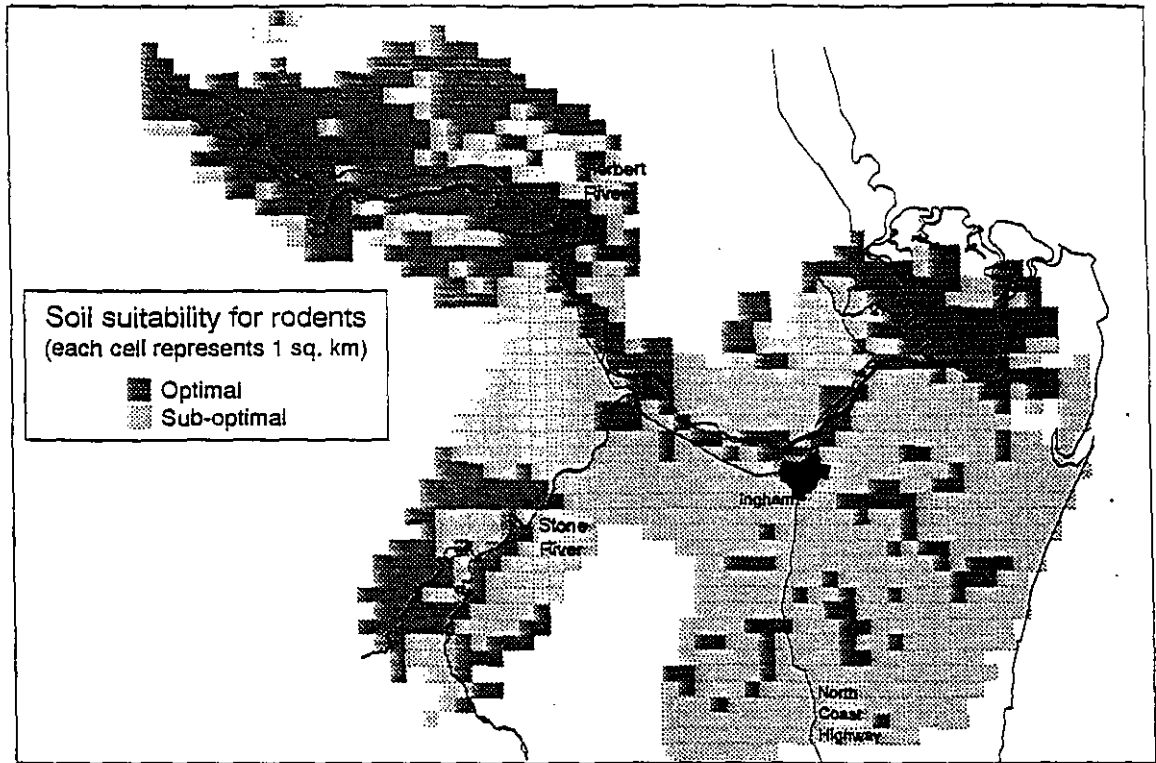


Figure 6.4 The distribution of soils suitable for rodents within the Herbert River District

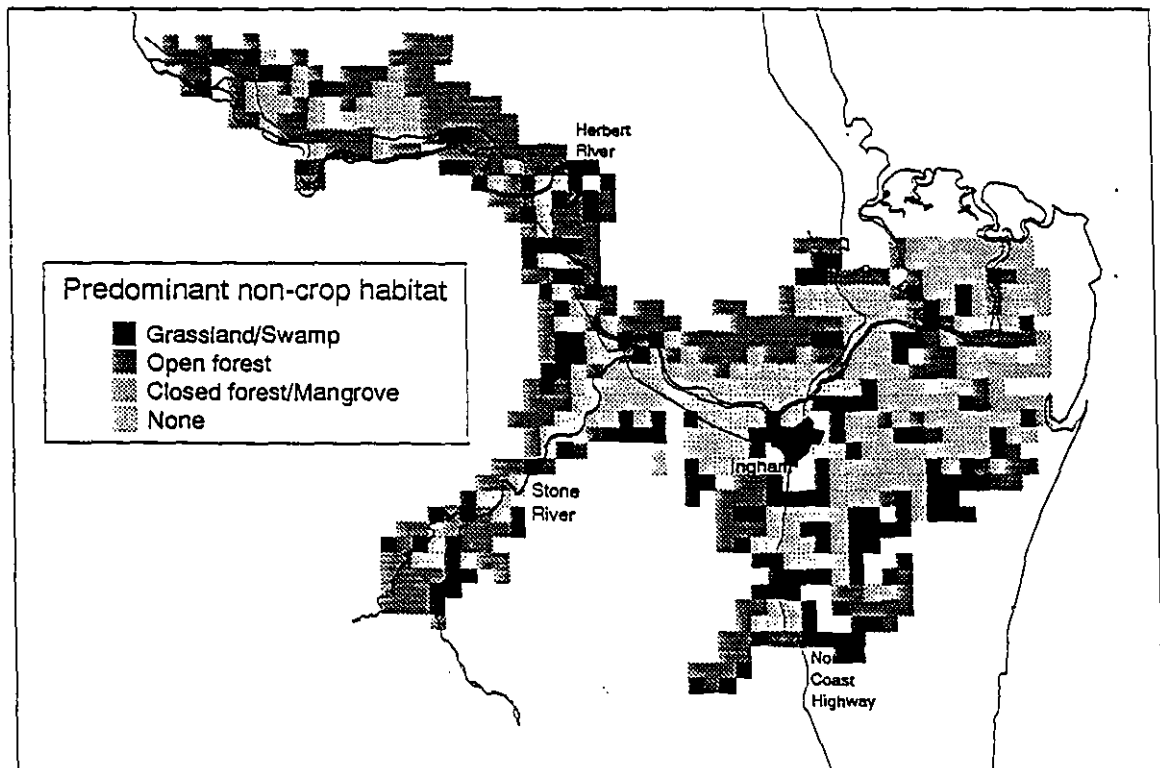


Figure 6.5 The distribution of non-crop habitats within the Herbert River District

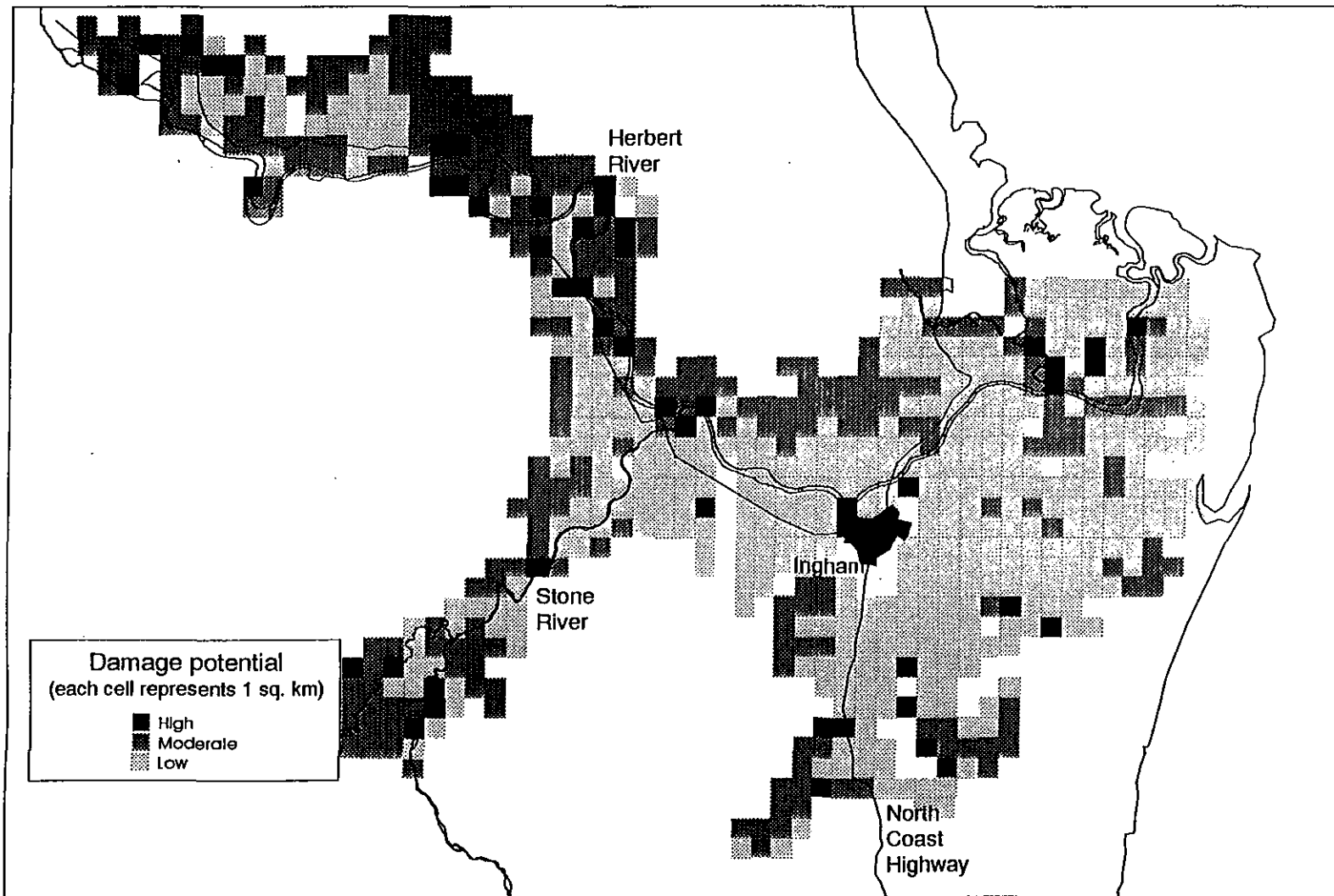


Figure 6.6 Crop damage potential within the Herbert River District (assuming low in-crop weed cover)

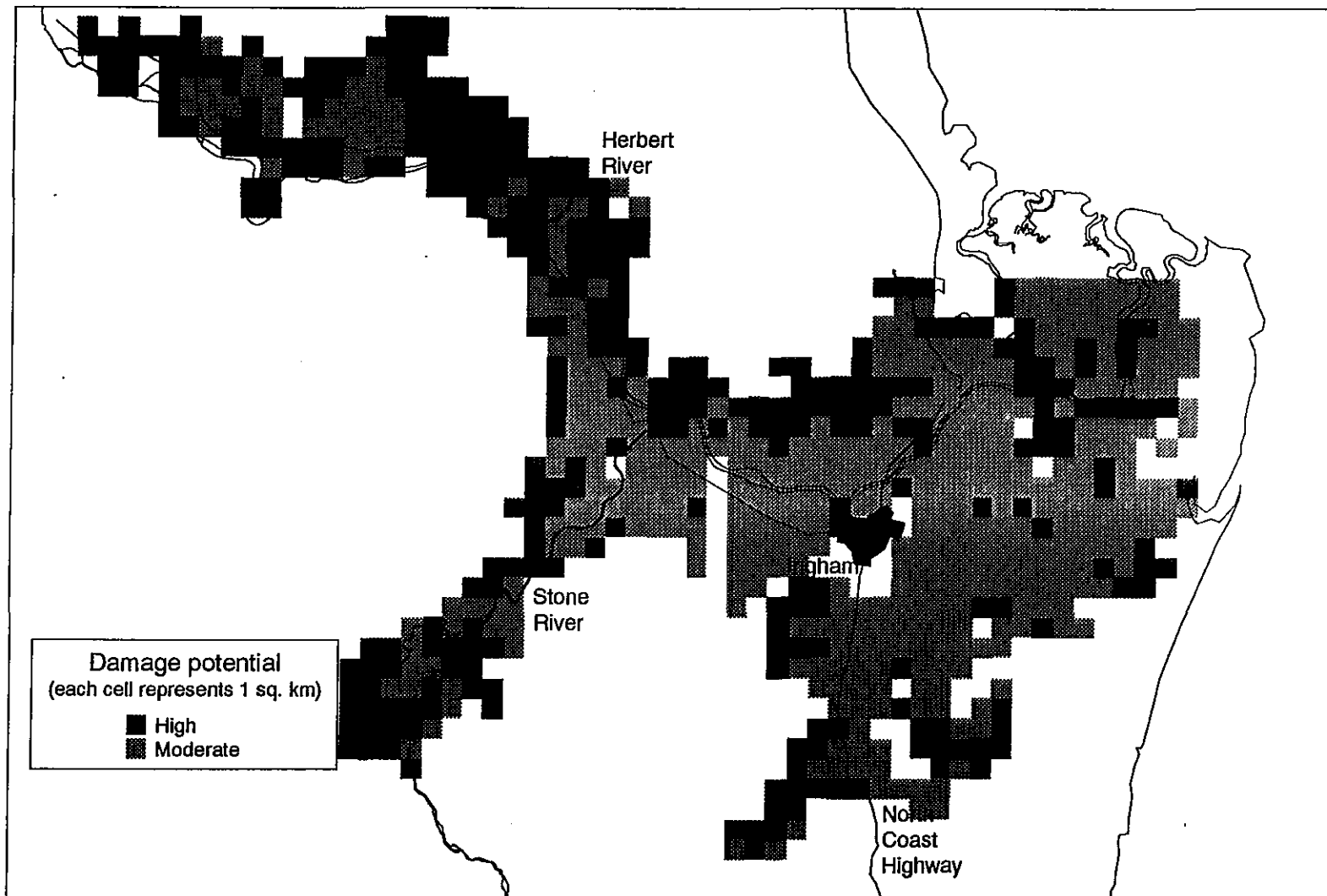


Figure 6.7 Crop damage potential within the Herbert River District (assuming high in-crop weed cover)

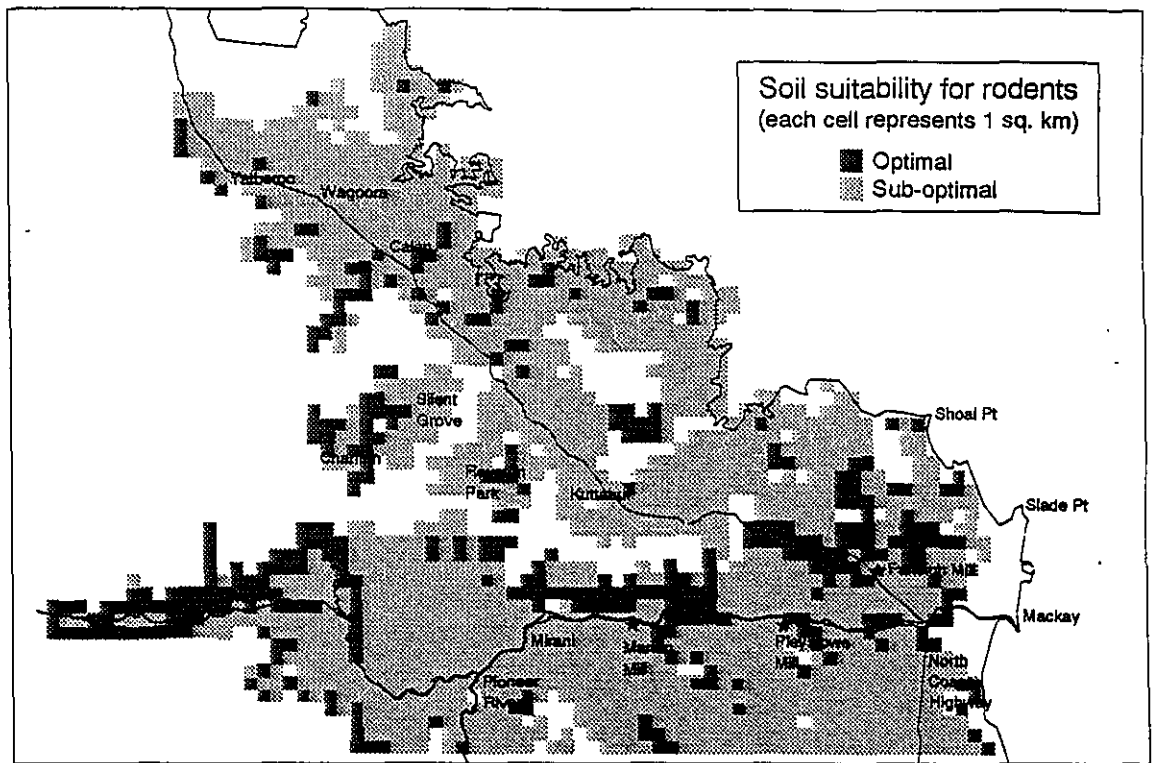


Figure 6.8 The distribution of soils suitable for rodents within the Mackay District

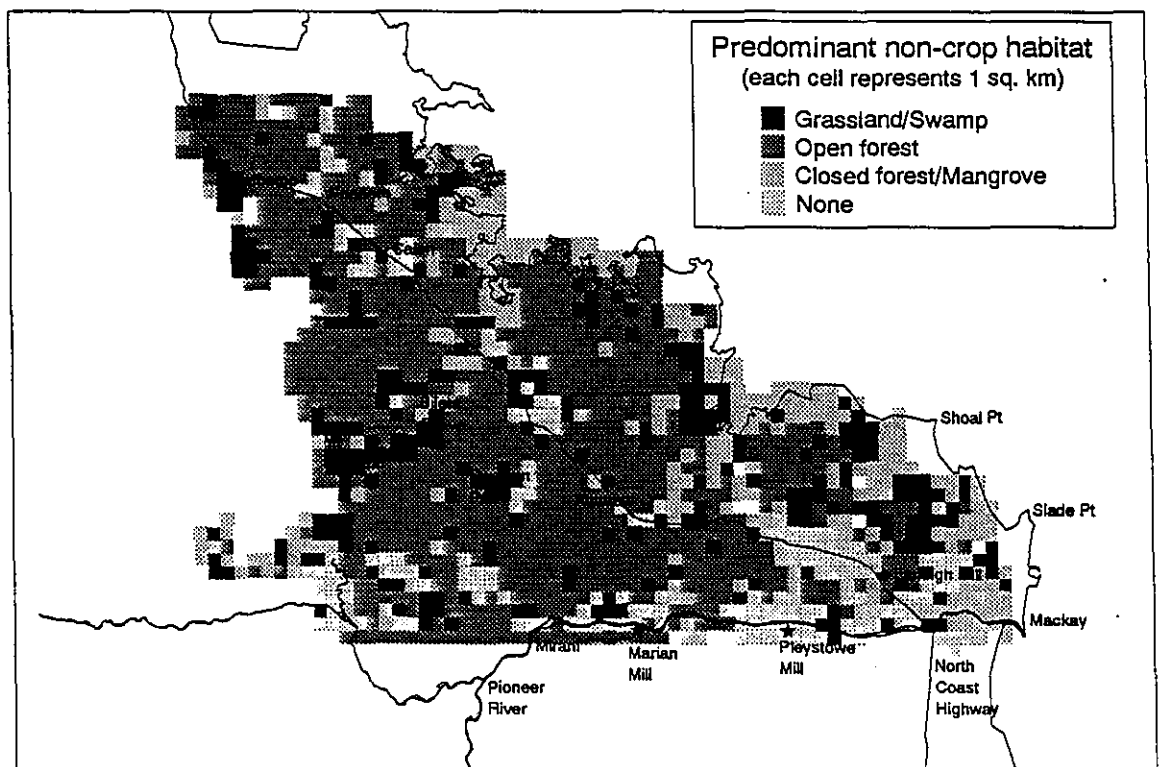


Figure 6.9 The distribution of non-crop habitats within the Mackay District

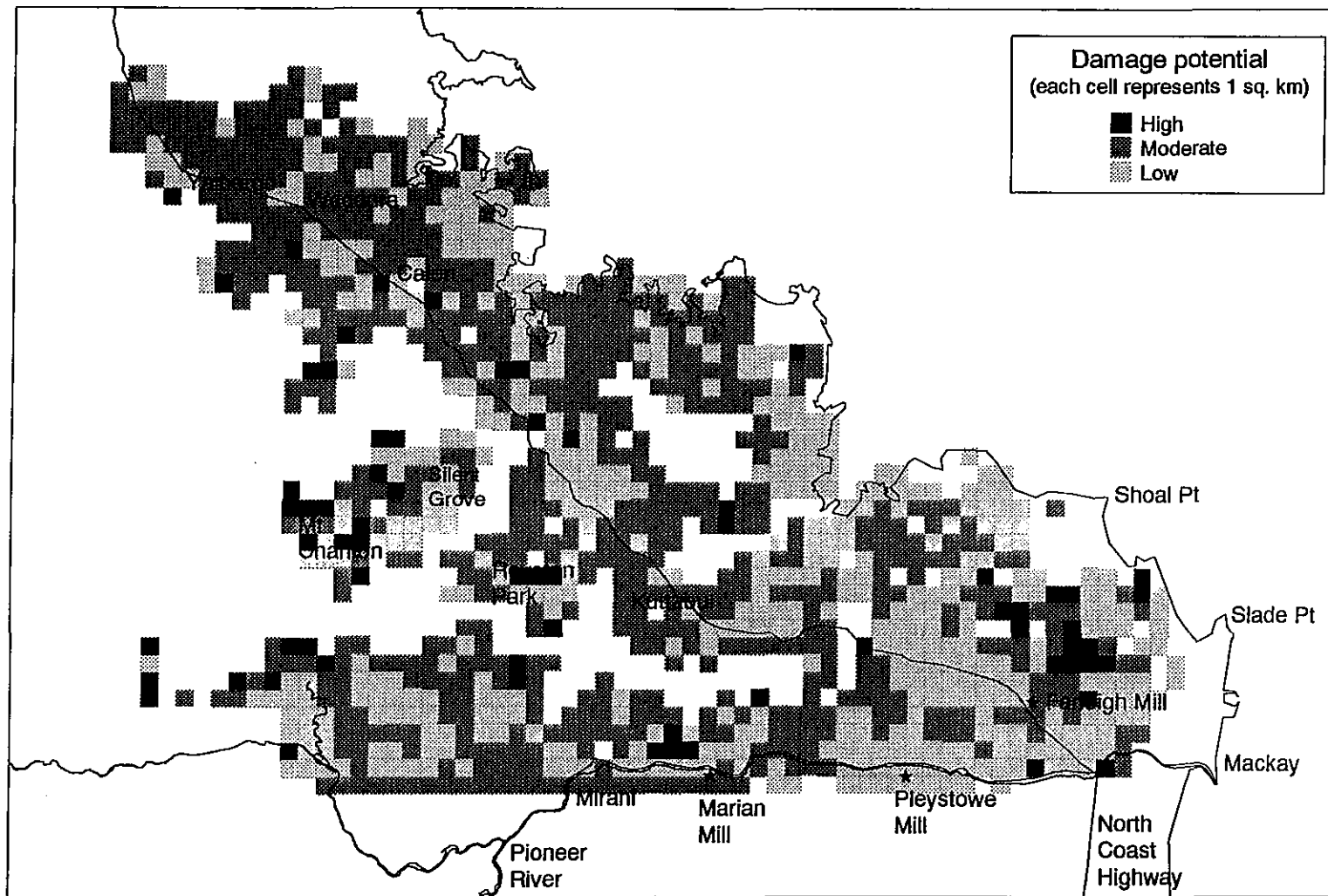


Figure 6.10 Crop damage potential within the Mackay District (assuming low in-crop weed cover)

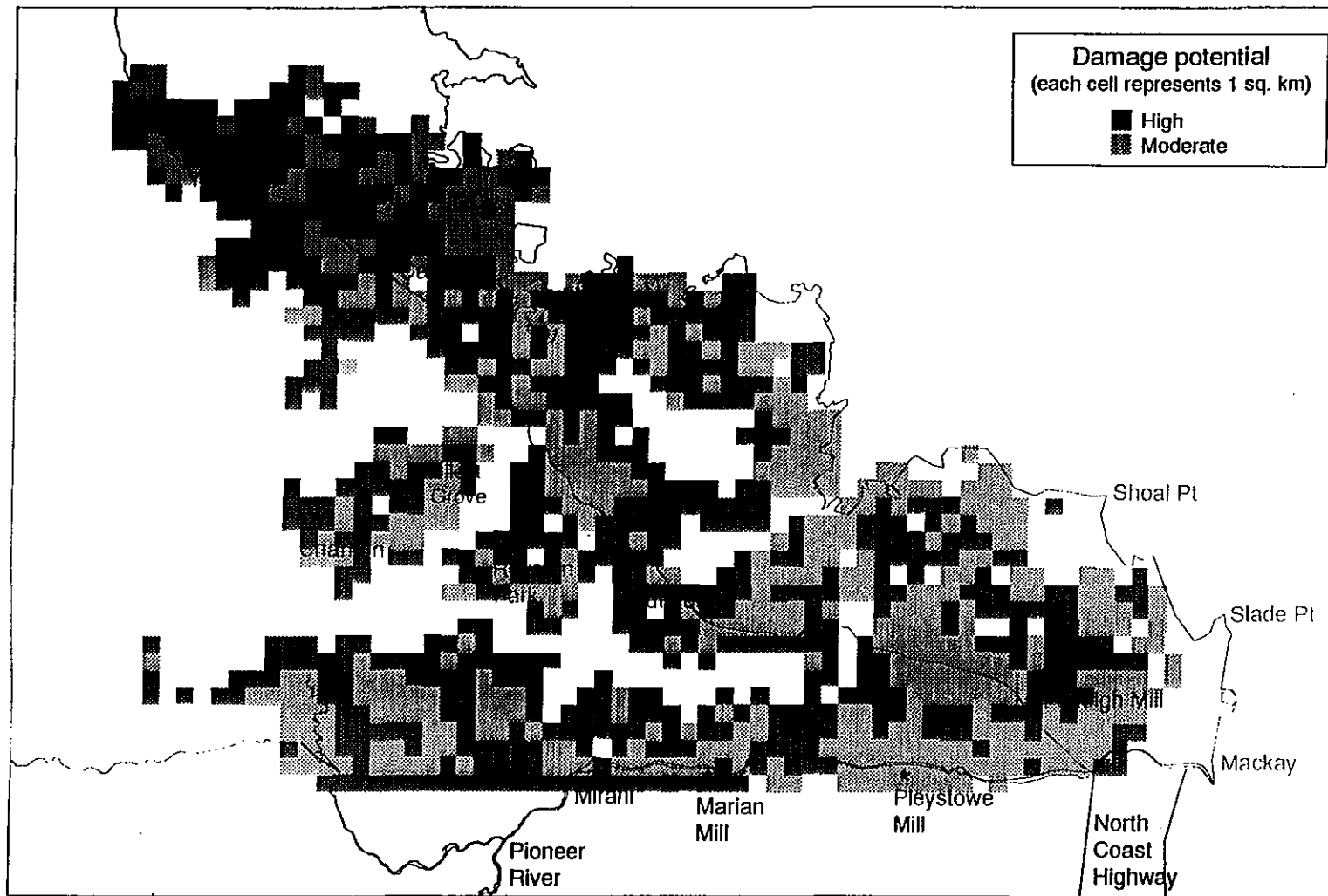


Figure 6.11 Crop damage potential within the Mackay District (assuming high in-crop weed cover)

SUMMARY AND MANAGEMENT IMPLICATIONS

7.1 THE POPULATION CYCLE

The population density of *R. sordidus* in the Mackay and Herbert River District cycles annually with the amplitude of the cycles being dependent on environmental conditions that dictate breeding success and mortality.

Despite the effects of environmental factors on population density, population processes in each year follow a predictable annual cycle (Figure 7.1).

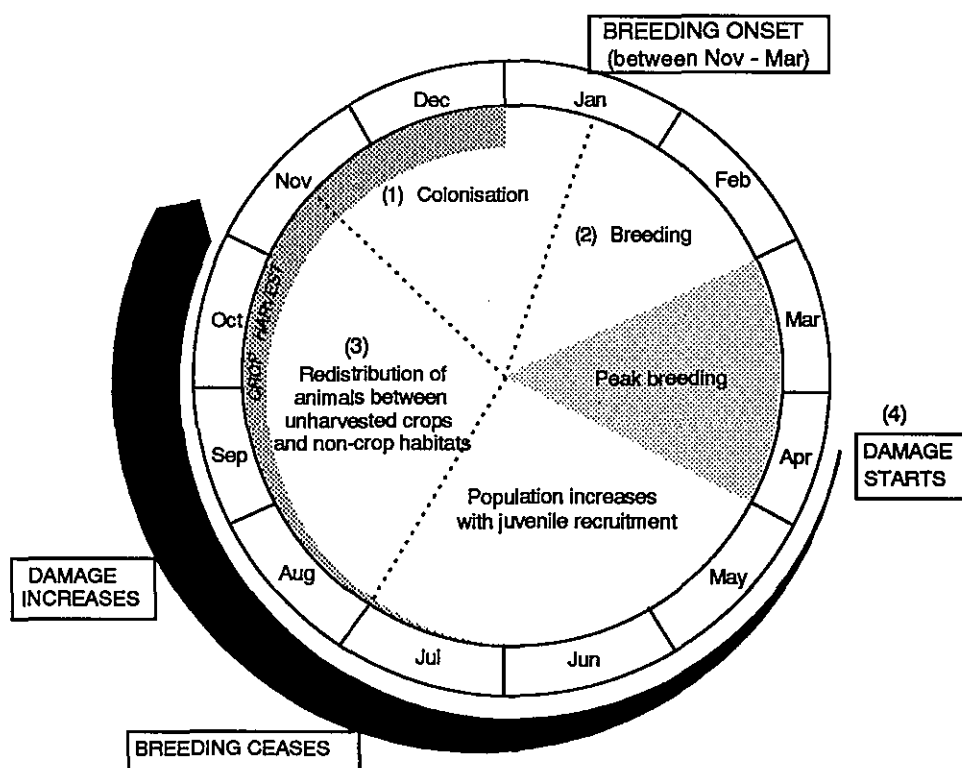


Figure 7.1 Annual population cycle of *R. sordidus* in sugarcane crops of the Herbert River district (Wilson and Whisson 1989)

The population cycle is closely related to the crop cycle. Conventional crops are not invaded until they are two months old. At this stage of crop development, the disturbances due to cultivation have ceased and the crop

provides cover for the colonising individuals. Crops are colonised by mature, non-breeding individuals from surrounding non-crop habitats, colonies are established and the mature population remains stable until breeding commences.

A well defined breeding season occurs each year and commences between November and March. The onset of breeding is associated with the first appearance of summergrasses in and around crops. Breeding intensity peaks one to three months after the first pregnancies occur and declines rapidly thereafter. Breeding ceases in July/August regardless of climatic conditions.

Juveniles enter the population at the peak of the breeding season and peak population size occurs one to two months later. In general, the population size decreases over the June/July period due to a decrease in breeding intensity and the breakdown of breeding colonies.

The beginning of the harvest season coincides with a large redistribution of animals between crops and refuge areas. Animals which survive this redistribution over the July - December period provide the nucleus of populations that will invade crops the following season.

Significant crop damage does not occur until after the peak of the breeding season. The pattern of damage to sugarcane correlates with stomach contents. The diet of *R. sordidus* changes dramatically between the breeding and non-breeding seasons. Over the breeding season, diet consists almost entirely of non-cane vegetation and seeds. Once the breeding season has finished, there is a dramatic switch to cane. Previous studies have shown that *R. sordidus* cannot survive and breed when fed solely on sugarcane. As seed and vegetation form the major part of the diet over the breeding period it is likely that weeds provide the level of nutrition

required to sustain breeding.

The overall success of the population in any given year is dependent on the time of onset of reproduction. If conditions favourable for reproduction occur early (November, December), then populations have the potential to increase rapidly and attain high densities before breeding ceases.

Continued monitoring over a number of years is necessary to verify the processes governing the performance of *R. sordidus* populations but it is obvious that a one to two month extension of the breeding season can greatly affect the potential for crop damage.

7.2 THE ROLE OF WEEDS

The relationship between the onset of breeding and the first appearance of summer grasses, coupled with the dietary switch between the breeding and non-breeding season indicates that breeding is dependent on the availability of a non-cane food source. Studies involving weeded and unweeded sections of fields have shown that in-crop weeds play an important role in determining the potential for crop damage.

Weed control can be achieved in two ways:

- . Herbicide treatment;
- . Trash-blanketing.

The elimination of weeds from a crop through the use of herbicides resulted in a significantly lower population throughout the entire cycle compared with the population in non-weeded areas. At the end of the breeding season, population density in the unweeded areas increased rapidly as juveniles

entered the population. A similar increase did not occur in the weeded areas where juvenile recruitment was less than 50% of that in the unweeded areas.

The suppression of the population due to the removal of weeds resulted in a 60% reduction in damage to the harvested crop. Stomach content analyses of rodents trapped in weeded areas showed that seed and non-cane vegetation still predominated in breeding females, indicating that they were forced to forage over a much larger area than their counterparts in unweeded crops.

The practice of green cane harvesting and trash-blanketing should result in a general reduction of damage throughout the district as the trash-blanket effectively smothers weeds. The amount of damage to these crops will most probably depend on the proximity to weedy, conventional crops and favourable non-crop refuges. In extensive trash-blanketed areas, damage reduction should be similar to that obtained with herbicide treatment. In areas where there is a mosaic of both crop types, damage to trash-blanketed crops could be as high as in neighbouring weedy, conventional crops due to dispersal.

7.3 THE DAMAGE PROCESS

For a particular location to sustain significant damage, several processes must occur:

- . Invasion;
- . Establishment;
- . Breeding.

Conventional crops less than two months old are free of rodents and so invasion must occur on an annual basis. Invasion occurs from stable refuges (non-crop areas) that are not subject to the major disturbances of cultivation and harvest. The quality and size of the refuge determines the size of the refuge rodent population and hence the potential for crop invasion. Refuge quality can be ranked on the basis of rodent utilisation as grasslands and swamps > open forests > closed forests and grazed areas.

As *R. sordidus* is a grassland animal it is not surprising that grasslands are utilised more than any other non-crop area. Woodlands and the grassy fringes of drainage channels also support substantial populations whereas the low light penetration and sparse ground cover associated with closed forests result in a low level of utilisation. Grazing paddocks are also poorly utilised as low grass height, regular disturbance by cattle and soil compaction make colonisation and establishment difficult.

The proximity of high quality refuges alone, may not be sufficient to explain the extent of crop invasion. The ease of rodent movement between refuges and crops may need to be considered. Factors such as the distance to the nearest significant refuge and the type and extent of corridors (for example, drainage channels) connecting the refuge to the crop may also influence the potential for invasion.

The potential for establishment depends, in part, on available shelter, food and the ability to construct burrow networks. In-crop weeds and soil characteristics are important in this process. *R. sordidus* is a colonial animal that constructs elaborate networks of burrows and runways. Breeding occurs over the wet season and soils that waterlog readily or cannot support burrows over this period because of poor structural characteristics can limit the potential for establishment.

7.4 THE SPATIAL DISTRIBUTION OF DAMAGE

Rodent damage is not uniform throughout a district. The severity of damage at a particular location is dependent on specific site characteristics that influence invasion, colonisation, breeding and survival.

The strongest association is between weed cover and damage. Sites with high weed cover are consistently associated with more damage than comparable sites with low weed cover, regardless of soil and refuge type.

The effect of refuge availability on crop damage is linked to weed cover. Generally, sites with high weed cover are associated with high crop damage provided that a refuge is present.

The influence of soil type on crop damage is linked to refuge availability. Sites characterised by good soil types can expect high damage if an adjacent refuge is present. If all other site characteristics are equal, damage will be higher in crops on good soil types. In general, damage to crops on soil types that do not restrict burrow construction or maintenance during the wet season is determined by the relative importance of the adjacent refuge.

It is important to realise that these characteristics do not operate independently. Damage potential is determined not only by the contribution of individual characteristics but also by the interactions between characteristics.

Highest damage can be expected at a site that possesses the following characteristics:

- High in-crop weed cover;

- . Well drained, friable soil;
- . Close to substantial grassland or open forest refuges;

It can also be assumed that high damage sites will have the following characteristics:

- . Conventional tillage techniques;
- . Area highly dissected with creeks or drainage channels.

Conversely, lowest damage is associated with:

- . Low weed cover (herbicide treatment);
- . Isolation from refuges;
- . A site surrounded by crops with similar characteristics.

It can be assumed that trash-blanketed crops will also experience low damage if they are isolated from refuges and are surrounded by weed free crops.

7.5 DAMAGE POTENTIAL

Rodent damage within a region is patchy as not all locations have a similar potential for damage. The ability to direct control effort to locations where it is most needed is essential if the cost-effectiveness of the control process is to be maximised.

The site characteristics and interactions that explain the observed pattern of

crop damage together with supporting information from aerial photography and soil maps allow the district to be divided into general areas of low, moderate and high damage potential.

At present, the damage potential of each 1km² cell can only be based on the predominant combination of refuge type and soil type that have been shown to confer a specific damage potential on a location. As the model is refined, it should be possible to re-draw the boundaries with greater precision and provide a damage potential index for smaller areas.

7.6 MANAGEMENT IMPLICATIONS

It is clear that the long-term, cost-effective control of rodents in sugarcane should rely on an integrated management program which combines both chemical and biological control methods applied in an orderly sequence. The objective of such a control program should be to prevent the problem from occurring rather than to apply treatments in a reactive manner in an attempt to control large populations.

A three phase management program is necessary:

- . Population monitoring to provide estimates of the overall level of potential damage within a region;
- . Management of cropped areas to reduce the extent of colonisation and establishment;
- . Strategic baiting of high-risk areas at the correct phase of the population cycle in years when damage is expected to be high.

Implementation of such a program is a decision for representatives of the sugar industry since the program relies on procedures at three levels. There are separate and distinct roles for growers, Pest Boards and the Bureau of Sugar Experiment Stations.

In deciding on the method of implementation, the following should be given consideration:

- . Coordination of the activities at the three levels is essential since the program must be implemented on a regional scale. Rodents invade crops from refuges and populations are re-distributed between crops at harvest. Regional programs will prevent individual growers from inheriting a problem from neighbouring properties;

- . The management program must be implemented every year. The potential long-term benefit will be lost if it is implemented for a few years and then neglected for a year or two because there does not appear to be any significant rodent problems. It must be realised that populations of *R. sordidus* have the potential to increase rapidly given favourable environmental conditions;

- . The objective of this program is to reduce both the extent of invasion and the level of establishment within crops by reducing both the quality of refuge habitats and the use of weeds as an in-crop food source. The full benefits of the program can be realised only when control extends throughout a region;

- . Rodent control must be regarded as an integral part of farm management and, as for other farm practices, its priority for implementation should be judged on the expected benefit to production.

Responsibilities for the successful implementation of the program are:

Canegrower responsibilities

- . Eliminate in-crop weeds over the breeding season (December - April) through the use of herbicides and/or trash-blanketing.
- . Keep crop margins weed-free since breeding animals from the crop will forage widely to obtain this preferred food source.
- . Where possible, manage grasslands by mowing or heavy grazing to render them unsuitable for use as "between crop" refuges.
- . Where possible, convert grasslands into closed forests (for example, along creek banks and the slopes of steep, wet gullies).
- . Encourage canopy closure in open forests. Do not burn open forests in an attempt to rid the area of rodents. Regular firing opens the canopy, encourages grass growth and provides rodents with a favourable habitat.
- . Ensure that headlands and grass verges are closely mown over the June - January period to frustrate movements between crops.
- . If individual canefields are to be baited, baits should be applied during the early stages of the breeding season, that is, around December. A delay of one month can lead to significant damage later in the season.
- . Clean up any undisturbed grassy areas around the farm over the December - July period. Small areas can support large colonies of rodents.

Regional responsibilities

- . Implement monthly monitoring of rodent populations and weed cover between October and May.

- . Assess damage prior to harvest to develop correlations between population size, environmental conditions and subsequent damage. These data can then be interpreted at the industry level and used to refine the prediction of the expected overall level of damage.

- . Bait areas of specific damage potential based on the expected level of overall damage. For example, in a year where monitoring suggests that a high overall level of damage is expected, bait areas of high and moderate damage potential. In year where monitoring suggests that only moderate damage will occur throughout the region, bait only areas of high damage potential. In years where low overall damage is expected, do not bait any areas.

- . If the full suite of management recommendations are implemented on a regional scale, in most years baiting should not be necessary. Only in rare circumstances would the baiting of low damage potential areas be necessary.

Industry responsibilities

- . Provide the expertise to establish early warning systems of potential crop damage (monitoring systems) for all major sugar producing districts that are affected by rodents.

- . Provide the necessary expertise to interpret data arising from monitoring programs and provide an annual assessment of overall

damage potential for each region.

- . Recommend which areas of each district require additional control in the form of baiting.
- . Coordinate studies to refine the location of low, moderate and high damage potential areas in each region.
- . Implement studies to refine the control process in anticipation of changes in agricultural practice and bait registration requirements.

7.7 CONCLUSION

These studies have provided an understanding of the processes responsible for rodent damage together with specific management recommendations designed to reduce crop damage. Changes in agricultural practice, more attention to crop cleanliness and the modification of non-crop areas to make them less suitable as refuges for *R. sordidus* will have a beneficial effect on crop damage.

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APPENDIX 1

Habitat and soil characteristics of areas defined in October 1990

Mill area	Site code	Soil description	Non-crop habitats
Cattle Creek	2	Brown loam; variable sand and loam content	low to moderate fragmentation; area bordered and fragmented by closed and open forest; most grasslands grazed
	4	Brown loam variable sand and loam content	very highly fragmented by drainage channels; steep terrain
Marian	2	Reddish brown loam; high sand and gravel content; loose surface	moderate to high fragmentation; patchy grassland/ open forest; bordered by extensive open forest and closed forest on hills
	4	light gray/brown sandy loam	low to moderate fragmentation; area bordered by extensive open forest and grassland; high percentage of crops bordering non-crop habitat
	6	dark brown clay loam	moderate to high fragmentation; patchy open forest/ grassland/ grazing; fairly intensive grazing in area
Pleistowe	1	heavy dark brown loam	low fragmentation; bordered by open forest/ grazing/ grassland;
	5	heavy dark brown loam	low fragmentation; bordered by grazed open forest; non-crop habitats managed eg. grasses on river bank slashed
Racecourse	1	light coloured; high clay content	moderate fragmentation; patchy open forest and grazing areas
	3	heavy dark brown loam	low fragmentation; habitats strictly managed eg. banks of creeks grazed; area bordered by extensive grassland/ open forest/ grazing; high percentage of crops border non-crop habitats
Farleigh	1	reddish brown sandy loam	fairly low fragmentation except near perimeter; extensive open forest (mostly grazed) through middle of area
	2	brown gravelly loam	highly fragmented area; crops <u>always</u> close to non-crop habitats; mostly grazed open forest and grassland

Mill area	Site code	Soil description	Non-crop habitats
Marian north	1	gray/brown clay loam; variable gravel content	highly fragmented; mostly grazed open forest
	2	black loam; variable colour and surface characteristics	moderate to high fragmentation; bordered by grazed grassland or open forest
	3	gray loam fairly hard-setting	moderate to high fragmentation; bordered by grazed open forest and grassland
Farleigh north	8/1	gray-brown soil; fairly hard-setting	very high fragmentation
	8/2	brown clay loam	moderate fragmentation
	9/1		extensive open forest; high fragmentation
	9/2		<500m to patchy grassland bordering creek; low fragmentation
	9/3	Brown loam to hard-setting gray loam	<500m to extensive open forest; fairly low fragmentation; road verges not maintained
	9/4		>500m to extensive open forest; low fragmentation
	9/5	brown loam	<500m to isolated swamp and extensive open forest
	9/6		0m to moderate open forest; low dissection <u>but</u> patches of open forest
	9/7	gray clay loam	high fragmentation
	9/8	gray clay loam	all crops <200m to extensive open forest; low fragmentation
	9/9	gray clay loam	all crops <500m to extensive open forest low fragmentation
	9/10	very hardsetting gray clay loam	all crops <200m to extensive open forest; low fragmentation
	9/11	gray loam	bordered by open forest and grazing; isolated grassland/ open forest; low dissection by creeks and drainage
	9/12	gray loam	all crops close to extensive open forest/ grazing/ grassland; moderate fragmentation
	9/13	gray loam	very small area of cane; all crops close to drainage or extensive open forest
9/14		All crops bordered by open forest or extensive drainage channel; high fragmentation	
9/15	gray clay loam	patchy open forest; cane area bordered by creek;	

Mill area	Site code	Soil description	Non-crop habitats
Farleigh north	9/16	gray loam; fairly hard set	fairly large cane area; high percentage of crops close to remnant open forest or creeks
	9/17	gray loam	all crops <200m to moderate grassland and open forest; fairly low fragmentation;
	9/18	gray loam	all crops close to open forest; low fragmentation
	9/19	fine, gray/brown loam	creek runs through middle of area; all crops close to open forest

APPENDIX 2

The number of 'new' *R. sordidus* recorded on Day 5 of each trapping session compared to the total number of individuals recorded for the trapping session

Month	Treatment area	Site 1		Site 2		Site 3		Site 4	
		Total	Day 5	Total	Day 5	Total	Day 5	Total	Day 5
Dec	Conventional	(12)	(2)	7	0	3	0	1	0
	Trash-blanket	(9)	(2)	13	0	22	0	17	1
Jan	Conventional	30	3	11	1	8	0	3	0
	Trash-blanket	14	1	14	1	18	0	22	0
Feb	Conventional	27	0	34	2	21	2	24	2
	Trash-blanket	11	0	11	0	18	1	11	0
Mar	Conventional	16	1	32	0	20	2	15	1
	Trash-blanket	(7)	(1)	20	2	16	1	7	0
Apr	Conventional	8	0	(23)	(4)	18	1	8	0
	Trash-blanket	4	0	17	1	21	2	(17)	(2)
May	Conventional	16	1	43	2	34	2	16	3
	Trash-blanket	16	1	(26)	(3)	(30)	8	17	2
Jun	Conventional	18	1	29	0	-	-	13	0
	Trash-blanket	18	1	25	1	-	-	21	0
Jul	Conventional	-	-	26	2	25	2	(8)	(1)
	Trash-blanket	-	-	26	2	-	-	13	1
Aug	Conventional	8	0	20	2	(18)	(2)	4	0
	Trash-blanket	(6)	(1)	13	1	-	-	14	1
Sep	Conventional	21	2	43	3	-	-	20	2
	Trash-blanket	-	-	22	0	-	-	29	2

() Occasions when the proportion of the total number of individuals captured on the last night was greater than 0.1.

APPENDIX 3

**Adult sex ratio and age structure of the marked population from
Day 1 to Day 5 of trapping sessions**

Month	Site	Day	Adult sex ratio			Age structure ¹			
			Male	Female	χ^2_1	Juvenile	'Adult'	'Old adult'	χ^2_1
Jan	1 Conventional	1	3	3		1	3	3	
		2	9	6	0.01	1	8	7	0.11
		3	13	10	0.13	1	10	13	0.10
		4	13	10	0.13	1	10	13	0.10
		5	16	10		1	12	13	
Feb	1 Conventional	1	3	6		0	3	6	
		2	10	11	0.30	0	4	17	0.15
		3	13	12	0.07	0	4	21	0.01
		4	15	12	0	0	4	23	0
		5	15	12		0	4	23	
	2 Conventional	1	6	3		2	3	6	
		2	16	6	0.10	3	4	15	0.00
		3	19	9	0.01	3	6	19	1
		4	21	9	0.01	3	6	21	0.05
		5	22	10		3	6	22	0.01
Mar	2 Conventional	1	4	14	0.01	1	1	17	
		2	5	17	0.003	1	3	19	
		3	5	18	0.02	1	3	20	
		4	7	23	0	1	3	22	
		5	7	23		1	3	22	
	2 Trash-blanket	1	3	4		1	6	1	
		2	6	4	0.11	3	9	1	
		3	8	5	0.19	4	12	1	0.08
		4	8	5	0.19	5	12	1	0
		5	8	7		5	12	1	
May	2 Conventional	1	3	7		6	4	6	
		2	7	14	0.39	7	6	14	0.21
		3	10	16	0.07	11	8	17	0.01
		4	12	17	0.002	13	9	19	0.01
		5	13	18		13	9	20	
Sep	2 Conventional	1	6	12	0.39	0	4	14	0.11
		2	9	16	0.23	0	5	20	0.33
		3	12	19	0.08	1	7	24	0.13
		4	15	20	0.004	2	9	26	0.00
		5	16	22		2	10	28	3

¹ Due to a low number of juveniles, this class was only included in analysis in May

$\chi^2 H_0$: Sex ratio (or age structure) on Day x does not vary significantly from that on Day 5

APPENDIX 4

Major characteristics of the populations in each treatment area of each site

Population attribute	Occurrence at each site	
	Conventional	Trash-blanketed (unweeded)
Colonisation (>1 individual per 100 trap nights)	December/January	November/December
Breeding season		
Duration	Variable (February - May)	Incidence of breeding low throughout study
Peak	March (Sites 1,2,3) No breeding at Site 4	
Entry of juveniles into the population (i.e. juveniles representing $\geq 10\%$ of the total trappable population)	April/May	February/March
Sex ratio	Similar between sites each month. Site 4 not considered due to low sample size.	Similar between sites each month.
Population levels (December to June)	Variable between sites	Variable between sites

APPENDIX 5

**Number of individuals marked and trap effort each month in
a) conventional and b) trash-blanketed areas**

a) Conventional areas

Month	Sex					Total	Number of traps set
	Juvenile male	Mature male	Juvenile female	Mature female	Number of pregnancies		
Dec	2	12	5	3	0	23	200
Jan	0	35	1	23	1	59	200
Feb	2	71	12	47	1	132	200
Mar	2	36	2	66	41	107	200
Apr	8	11	13	40	14	72	200
May	25	29	26	53	2	133	200
Jun ¹	10	13	11	29	0	63	120
Jul ²	20	23	3	43	0	89	160
Aug	4	21	2	37	0	65	200
Sep ³	4	36	3	40	0	84	120

¹ Harvest of Site 3 trash-blanketed area - trapping not possible

² Site 1 not trapped due to cane lodging

³ Harvest of Site 3 conventional area

b) Trash-blanketed areas

Month	Sex					Total	Number of traps set
	Juvenile male	Mature male	Juvenile female	Mature female	Number of pregnancies		
Dec	3	25	7	26	0	61	160
Jan	1	30	0	29	0	60	160
Feb	3	31	7	11	1	52	160
Mar	3	27	4	15	2	50	160
Apr	5	21	18	15	2	59	160
May	9	28	24	28	2	89	160
Jun ¹	7	25	5	29	0	66	120
Jul ²	6	17	0	16	0	39	120
Aug	3	17	0	13	0	33	120
Sep ³	7	18	5	21	0	51	120

¹ Harvest of Site 3 - trash-blanketed area only

² Site 1 not trapped due to cane lodging

³ Harvest of Site 1 - trash-blanketed area only

APPENDIX 6

The observed and expected cell frequencies of site types classified by weed cover, soil type, refuge type and crop damage. Expected cell frequencies (Exp) and [Exp] were derived from Models 7 and 8 respectively.

Weed cover	Soil type	Refuge type*	Crop damage					
			Low			High		
			Obs	(Exp)	[Exp]	Obs	(Exp)	[Exp]
Low	Good	GR/SW	5	8.23	5.17	17	13.78	16.83
		OF	8	5.26	7.92	12	14.34	12.08
		CF/GZ	5	6.63	5.99	9	7.37	8.01
		NONE	10	8.39	9.73	4	5.61	4.27
	Fair	GR/SW	14	10.44	13.84	2	5.56	2.16
		OF	10	12.75	11.19	13	10.25	11.81
		CF/GZ	10	11.09	9.21	5	3.91	5.79
		NONE	9	9.07	9.00	2	1.93	2.00
	Poor	GR/SW	17	15.21	14.54	6	7.79	8.46
		OF	15	16.91	16.38	15	13.09	13.62
		CF/GZ	29	26.87	29.45	7	9.13	6.55
		NONE	20	20.76	19.57	5	4.23	5.43
High	Good	GR/SW	1	1.56	0.83	10	9.44	10.17
		OF	2	1.38	2.08	12	12.62	11.92
		CF/GZ	3	2.39	2.01	9	9.61	9.99
		NONE	2	1.76	2.27	4	4.24	3.73
	Fair	GR/SW	3	1.71	3.16	2	3.29	1.84
		OF	3	2.30	1.82	6	6.70	7.18
		CF/GZ	1	2.64	1.79	5	3.36	4.21
		NONE	0	0.00	0.00	0	0.00	0.00
	Poor	GR/SW	1	3.86	3.46	10	7.14	7.54
		OF	6	5.00	4.62	13	14.00	14.38
		CF/GZ	7	5.38	6.55	5	6.62	5.45
		NONE	3	4.02	3.43	4	2.98	3.57

* GRassland/SWamp, Open Forest, Closed Forest/GraZing

APPENDIX 7

Logit effects corresponding to the odds of sustaining either low or high damage (derived from Model 7)*.

Site attribute		Logit estimates of sustaining high damage ($\text{Log}_e [m_{2jk}/m_{1jk}]^m$).
Weed cover $U_{dw(i)}$	Low	-0.449 (0.449) ⁺
	High	0.916 (-0.916)
Refuge type $U_{dr(ik)}$	Grasslands/swamp	0.137 (-0.137)
	Open forest	0.478 (-0.478)
	Closed forest/grazing	-0.318 (0.318)
Soil type $U_{ds(i)}$	None	-0.839 (0.839)
	Good	0.760 (-0.760)
	Fair	-0.357 (0.357)
	Poor	-0.411 (0.411)
Constant (U)		-0.039

* There are three sets of estimated parameter effects contained within this model: $U_{dw(i)}$, $U_{dr(ik)}$ and $U_{ds(i)}$. The logit estimates corresponding to these U-terms were generated using the expected values given in Table A1.

** m_{1jk} Observed number of sites with high damage and characterised by weed cover "j", refuge type "k" and soil type "l".
 m_{2jk} Observed number of sites with low damage and characterised by weed cover "j", refuge type "k" and soil type "l".

+ The odds of sustaining low damage ($\text{Log}_e [m_{1jk}/m_{2jk}]$) are in parentheses.

APPENDIX 8

Logit estimates corresponding to the effect of the soil type/refuge type interaction ($U_{dsr(ijk)}$) on the odds of sustaining high damage (derived from Model 8⁺).

Site attributes		Logit estimates of sustaining high damage ($\text{Log}_e[m_{2jk}/m_{1jk}]^{**}$).
Soil type	Refuge type	
Good	Grassland/swamp	1.504 (-1.504) ⁺
	Open forest	0.875 (-0.875)
	Closed forest/grazing	0.811 (-0.811)
	None	-0.405 (0.405)
Fair	Grassland/swamp	-1.447 (1.447)
	Open forest	0.379 (-0.379)
	Closed forest/grazing	-0.095 (0.095)
	None	-1.504 (1.504)
Poor	Grassland/swamp	-0.118 (0.118)
	Open forest	0.287 (-0.287)
	Closed forest/grazing	-1.099 (1.099)
	None	-0.938 (0.938)

* There are four sets of parameter effects contained within this model: $U_{dw(i)}$, $U_{dr(ijk)}$, $U_{dsr(i)}$ and $U_{dsr(ijk)}$. The logit effects for the three main effect parameters are the same for both Model 7 and Model 8 as the marginal totals from which they are generated are equivalent.

** m_{1jk} Observed number of sites with high damage and characterised by weed cover "j", refuge type "k" and soil type "l".
 m_{2jk} Observed number of sites with low damage and characterised by weed cover "j", refuge type "k" and soil type "l".

+ Logit effects on the odds of sustaining low damage ($\text{Log}_e[m_{1jk}/m_{2jk}]$) are in parentheses.

APPENDIX 9

Logit estimates* and odds ratios of sustaining either low or high damage for each combination of site attributes.

Site attributes			Low vs high damage		High vs low damage	
Weed cover	Soil type	Refuge type	Logits	Odds	Logits	Odds
Low	Good	GR/SW	-1.02	0.36	1.02	2.76
		OF	-0.39	0.68	0.39	1.48
		CF/GZ	-0.32	0.73	0.32	1.38
		NONE	0.89	2.44	-0.89	0.41
	Fair	GR/SW	1.94	6.96	-1.94	0.14
		OF	0.11	1.12	-0.11	0.90
		CF/GZ	0.58	1.79	-0.58	0.56
		NONE	1.99	7.32	-1.99	0.14
	Poor	GR/SW	0.61	1.84	-0.61	0.55
		OF	0.20	1.22	-0.20	0.82
		CF/GZ	1.59	4.90	-1.59	0.20
		NONE	1.43	4.18	-1.43	0.24
High	Good	GR/SW	-2.38	0.09	2.38	10.80
		OF	-1.75	0.17	1.75	5.75
		CF/GZ	-1.69	0.18	1.69	5.42
		NONE	-0.47	0.63	0.47	1.60
	Fair	GR/SW	0.57	1.77	-0.57	0.57
		OF	-1.26	0.28	1.26	3.53
		CF/GZ	-0.78	0.46	0.78	2.19
		NONE	0.63	1.87	-0.63	0.53
	Poor	GR/SW	-0.76	0.47	0.76	2.14
		OF	-1.16	0.31	1.16	3.19
		CF/GZ	0.22	1.25	-0.22	0.80
		NONE	0.06	1.06	-0.06	0.94

+ From Model 8, logit estimates are:
 For high damage: $\log_e(m_{2jk}/m_{1jk}) = U + U_{dw(i)} + U_{dsr(jk)}$
 For low damage: $\log_e(m_{1jk}/m_{2jk}) = U + U_{dw(i)} + U_{dsr(jk)}$
 where U and $U_{dw(i)}$ are obtained from Table A2 and $U_{dsr(jk)}$ is obtained from Table A3.

* GRassland/SWamp, Open Forest, Closed Forest/GraZing