Theoretical and practical aspects of feral pig control

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Declaration

Except where otherwise indicated
this thesis is my own work.

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October 1987

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Abstract

This thesis is about the evaluation of feral pig control. The evaluation is divided into three parts; firstly surveying of populations of feral pigs or their sign, secondly modelling the processes occurring during control, and thirdly field evaluation of the effects of control on populations of feral pigs or their sign. The control methods evaluated were shooting from a helicopter, and poisoning with warfarin.

The evaluation of shooting from a helicopter occurred on the floodplains and surrounding woodlands of the Mary and Adelaide Rivers in the Northern Territory. A method of helicopter aerial survey using randomly selected transects was developed and evaluated prior to its use in the evaluation. The accuracy and precision of one strip transect and eight line transect estimators were tested by surveying a known population of carcasses of feral pigs. Most of the estimators were accurate and of high precision. In an area of combined floodplain and woodland, the most accurate was the Fourier series estimator. The survey method was used to estimate an 80% kill of feral pigs by shooting. A functional response model was fitted to the kill data. The model estimated a 95% kill after 0.24h/km^2 of shooting compared to the actual duration of shooting of 0.13h/km^2.

The evaluation of the effects of poisoning with warfarin initially involved developing and testing survey methods. The evaluation occurred in Namadgi National Park in the Australian Capital Territory in mixed forest, woodland and grassland. Methods for measuring the spatial extent and frequency of pig rooting and pig dung were developed and evaluated. Randomly selected, unmarked and marked plots were investigated, but the marked plots were measured most intensively. The methods for estimating the extent of pig rooting and counts of pig dung were repeatable, with no significant difference between replicate measurements. Poisoning with warfarin resulted in a 2% drop in the frequency of plots with rooting but an 87% drop in the number of dung pellets counted on plots after one month. An independent estimate of the kill was 94% after 14 days, calculated from deaths of feral pigs marked previously with radio-transmitters. The effect on pig abundance was also estimated (97% kill after one month) by a mathematical model of the poisoning. The model was derived from similar models used to study the epidemiology of infectious diseases.

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Chapter 1

Introduction

This thesis is about the evaluation of control of feral pigs (Sus scrofa) and their impact; how control can be evaluated and what control achieves. The thesis concentrates on developing and evaluating methods of surveying feral pigs and feral pig sign. The methods are then used to evaluate field control. The field evaluations are compared to, or supplemented by, development and application of theoretical models of feral pig control. The central hypothesis to be tested is that control of feral pigs does not affect population density of pigs or the extent of their sign.

The thesis is structured as follows. The development and evaluation of survey methods are described in Chapters 2 and 3. The most accurate, precise or repeatable survey methods are then applied to the field evaluations of shooting from helicopters in Chapter 4 and poisoning in Chapter 5. The two methods are however not directly compared in the field as shooting from a helicopter was evaluated in mostly open floodplain habitat and poisoning in mixed forest, woodland and grassland. Included in each of Chapters 4 and 5 are mathematical models of each method of control. The models are derived from first principles then applied to the field evaluation. An overall discussion of the results is given in Chapter 6, which also discusses the broader implications of the activities and draws parallels with results in other areas of wildlife management.

1.1. Why feral pigs are controlled

Pigs are not native to Australia. They were introduced with white settlement (Tisdell 1982). The ancestors of feral pigs are domestic pigs whose ancestors are wild boar which are native to Europe and Asia (Bratton 1977).

Feral pigs in Australia are of interest to science because of their adaptability and survival strategies and of interest to the wider community because of their economic and environmental impacts and their value as an economic resource.

1.1.1. Economic impact

The annual economic cost of feral pig damage to agriculture in Australia has been estimated at $70 million (Tisdell 1982). The accuracy of this estimate is unknown.

Damage has been reported to pastures (Pullar 1950, Hone 1980), crops (Pullar 1950, Giles 1976, Pavlov 1980, Tisdell 1982), forests and fences (Pullar 1950, Tisdell 1982), and predation of lambs (Rowley 1970, Giles 1976, Plant et al. 1978, Pavlov et al. 1981, Pavlov and Hone 1982). In an early review Fennessy (1966) considered that the impact of feral pigs on lamb production was unknown. Feral pigs can be infected with pathogens that cause endemic diseases such as tuberculosis (Corner et al. 1981), leptospirosis (Keast et al. 1963), swine brucellosis (Norton and Thomas 1976), Murray Valley encephalitis and Ross River virus (Gard et al. 1976) and sparganosis (Giles 1980). Corner et al. (1981) considered that feral pigs were probably a dead-end host for tuberculosis.

In a potentially useful model for describing what influences the extent of damage by a pest, Cherret et al. (1971) suggested that the extent of damage was a function of five variables; the destructive potential per pest, the duration of exposure, the resistance of the host or object being attacked, the number of pests and the value of each item damaged. Norton (1976) suggested a simpler classification which combined the destructive potential and the resistance into one term, the actual damage per pest. No attempt has yet been made to apply that classification to the economic impact of feral pigs.

Feral pigs may have a role as a reservoir of infection of exotic livestock diseases such as foot and mouth disease, rabies, swine fever and African swine fever (Gee and Whittem 1973, Geering 1981, Hone and Bryant 1981, Meischke and Geering 1983).

Overseas there has been more research published on the economic effects of wild boar and feral pigs. Pasture damage has been reported in the USA (Barrett 1971). Crop damage has been reported in Poland (Mackin 1970, Andrzejewski and Jezierski 1978, Gorynska 1981), Malaya (Diong 1973) and the USA (Wood and Barrett 1979). Gorynska (1981) reported significant correlations between the area of crop damage and numbers of wild boar ($r=0.55$, $df=21$, $P<0.01$) and the value of compensation for damage and the square of wild boar numbers ($r=0.61$, $df=21$, $P<0.01$). In contrast, Mackin (1970) and Andrzejewski and Jezierski (1978) reported no significant correlation between the extent of crop damage and abundance of wild boar. In a discussion of pests generally, Woods (1974) considered there was rarely a linear relationship between the number of pests and the extent of damage.

1.1.2. Environmental impact

Feral pigs commonly root up the ground to feed on plant roots and soil invertebrates. Rooting is the disturbance of the soil by use of the snout. Studies on rooting in forests and other habitats have concentrated on where rooting occurs (Bratton 1974, 1975, Jezierski and Myrcha 1975, Bratton et al. 1982), when it occurs (Jezierski and Myrcha 1975, Howe and Bratton 1976, Barrett 1978, Wood and Roark 1980, Genov 1981, Bratton et al. 1982, Alexiou 1983), its spatial extent (Jezierski and Myrcha 1975, Singer 1981, Cooray and Mueller-Dombois 1981, Bratton et al. 1982, Ralph and Maxwell 1984) and its influence on plants (Barrett 1971, Bratton 1974, 1975, Spatz and Mueller-Dombois 1975, Wood and Brenneman 1977, Hone 1980, Howe et al. 1981, Alexiou 1983, Stone 1985) and animals (Singer et al. 1984).

Environmental effects of feral pigs in Australia have not been studied intensively. Alexiou (1983) reported changes in plant species composition in sub-alpine woodland. Frith (1973) broadly discussed possible impacts. Tisdell (1982) noted that there had been little research on the environmental effects of feral pigs in Australia, including the effects on native forests and woodlands, though many foresters considered feral pigs were pests.

The effect of feral pigs/wild boar on mountain forests and other vegetation types has been studied most intensively in Great Smoky Mountains National Park (GSMNP), Tennessee. The pigs reduced the cover of herbs and the number of plant species in gray beech forest (Bratton 1975). Exclosure studies showed that the effect on ground flora was related to the time since colonisation by pigs, and exclusion of pigs resulted in significant increases in plant biomass (Bratton et al. 1982, Singer et al. 1984). Lacki and Lancia (1983) reported increased soil organic matter, cation exchange capacity and acidity in areas of wild pig rooting. Lacki and Lancia (1986) reported increases in shoot elongation in areas of heavy pig rooting. The effect was considered to be associated with enhanced nutrient mobilisation in soil rooted by pigs. Reductions in leaf litter and in the abundance of red- backed voles (Clethrionomys gapperi) and the northern short-tailed shrew (Blarina brevicauda), along with accelerated leaching of phosphorus, calcium and magnesium from leaf litter were reported by Singer et al. (1984). However they reported no significant effect of feral pig rooting on sediment yield.

Lucas (1977) reported that feral pigs in forests in the USA had many detrimental effects, and Wood and Barrett (1979) recorded adverse effects of feral pigs in longleaf pine (Pinus palustris) forests in the USA.

The effects of feral pigs on native vegetation in Hawaii have been described by Spatz and Mueller-Dombois (1975), Stone (1985) and reviewed by Loope and Scowcroft (1985). Foraging on tree ferns (Cibotium glaucum) depressed the fern density and a native grass (Deschampsia australis) was replaced by an exotic grass (Holcus lanatus) in areas of rooting. Spatz and Mueller-Dombois (1975) partly investigated the effect of pig rooting by simulating the process through artificial digging of the soil. Challies (1975) reported the deleterious effects of feral pigs on the vegetation of Auckland Island, New Zealand, and how impacts appear to be related to the time since introduction of pigs.

Damage to forest seedlings and young trees were reported in New Zealand forests (Bathgate 1973). Harrington (1976) reported that studies in Iran had indicated the importance of rooting by wild boar in enhancing regeneration of forage plants of benefit to other wildlife and in suppressing forest insects. However Bobek and Perzanowski (1984) considered that no unequivocal evaluation of the impact of wild boar on Polish forests could be made due to lack of data.

Clearly feral pigs can have impacts on agriculture, forestry and the environment. Whether the impacts are regarded as deleterious or beneficial depends on the management aims of the area concerned.

Tisdell (1982) and Auld and Tisdell (1986) argued that the economic assessment of the effects of feral pigs in Australia needed to recognise the effects of damage and the game value of the animals. Auld and Tisdell (1986) estimated the annual game value of feral pigs at $30-35 million in Australia. The effect in Australia of game hunting and harvesting on populations of feral pigs or the impacts of feral pigs are not known. Barrett (1971, 1978) formulated a management plan for feral pigs on a private cattle ranch in California based on game hunting to regulate pig density and control damage to pastures.

1.2. Control of feral pigs

Many methods of control of feral pigs and their damage have been, and are being used in Australia and overseas (Giles 1976, 1977, Hone et al. 1980, Appleton 1982, Tisdell 1982, Breckwoldt 1983), especially poisoning, trapping, hunting, shooting from the ground and from helicopters, fencing and habitat alteration. Biological control has been attempted in Pakistan (Tisdell 1982) using swine fever, but this did not reduce damage or pig populations (Anon 1970). Holloway (1973) considered that current control technologies were adequate and had effectively controlled feral pigs in New Zealand. Habitat alteration was described as an elegant method of pest control (Caughley 1980). The method has had little application for feral pigs as the species is a habitat generalist (Bratton 1977). Feral pigs can colonise most ecosystems some of which may not be able to be easily manipulated such as some relatively intact forests.

Several poisons have been or are being used legally or illegally for control of feral pigs in Australia; sodium monofluoroacetate (1080), phosphorus (SAP, CSSP) and fenthion ethyl (Lucijet) (Bryant et al. 1984, McIlroy 1985). Evaluation of poisoning with sodium monofluoroacetate (1080) has shown that a 73% reduction in abundance of feral pigs can be achieved in the short-term (one to two months) (Hone 1983). However several problems with the use of 1080 for control of feral pigs have been identified. Vomiting of 1080 bait can occur (Hone and Kleba 1984, Rathore 1985, O'Brien et al. 1986) thus providing poisoned food for non-target species. Rathore (1985) reported that the high incidence of vomiting was prevented by dosing feral pigs with metoclopramide, but Hone and Kleba (1984) and O'Brien et al. (1986) reported the opposite effects - no effect on the incidence of vomiting after ingestion of metoclopramide. Despite this Coblentz and Baber (1987) recommended the use of 1080 poison and metoclopramide for the control of feral pigs on Isla Santiago in the Galapagos.

Mortality of feral pigs can be very low after ingestion of 1080-poisoned bait (Hone and Kleba 1984) and there is no antidote to treat victims of accidental poisoning. O'Brien (1985) reported that the LD_{50} to pigs of 1080 was 4.4 mg/kg which was higher than the 1.0 mg/kg reported by McIlroy (1983). The high body weight of pigs means that many non-target species may be at risk in Australia because of the high concentration of 1080 in poisoned bait (McIlroy 1983). The above problems have led to evaluation of an alternative poison, warfarin, which in pen experiments caused mortality of up to 92% (Hone and Kleba 1984).

There has been limited evaluation of the efficiency and costs of other control methods. Some fences are pig-proof and many are not (Plant 1980, Hone and Atkinson 1983). Netting fences can limit movements of feral pigs but are more costly than plain wire or electric fences (Hone and Atkinson 1983).

Trapping had little impact on feral pig populations in GSMNP (Fox 1972, Fox and Pelton 1977). Fox and Pelton (1977) evaluated the effects of trapping and shooting and found that the cost per pig of shooting at night on foot, was less than that for shooting by day which in turn cost less than trapping. Shooting by night from vehicles cost the most. Trapping success was significantly and negatively related to the age of adjacent pig rooting. Diong (1973) reported that trapping, with snares, could reduce local populations of pigs in Malaya.

A limitation of trapping is that some pigs are not captured. Piglets less than six to eight weeks old were never trapped in an intensive study in Poland (Jezierski 1977). Barrett (1978) considered that in California old boars often attempted to tip over traps to obtain bait rather than enter the trap. Andrzejewski and Jezierski (1978) reported that some wild boars in Poland were never caught in traps. All such individuals were older than one year and were believed to be immigrants to the study area. Giles (1980) noted that in western New South Wales (NSW) the sex ratio of trapped pigs was biased in favour of females.

Turvey (1978) described the use of trapping and other control methods and reported that trapping was widely used in north-west NSW. If low numbers of feral pigs were killed per year, then trapping was more cost effective than poisoning, and when high numbers of pigs were killed then poisoning was more cost effective. However Turvey relied on questionnaire data from farmers so the results are of unknown accuracy. Boreham (1981) used trapping in what is now Namadgi National Park in the Australian Capital Territory (ACT), and concluded that trapping was the most effective control method then available. Baber and Coblentz (1986) after extensive trapping in two sites in California, caught 66.7% and 77.7% of pigs at least once. Coblentz and Baber (1987) reported a trapping success rate of 14 pigs captured in 91 trap nights.

A limitation of both trapping and poisoning is the need for feral pigs to eat the bait. In one study Hone (1983) estimated that 23% of feral pigs at a site did not eat the pellet bait used for poisoning. Hone et al. (1985) reported that the daily ingestion of bait by free-ranging feral pigs varied significantly between seasons, from one to three kg/pig. Coblentz and Baber (1987) measured bait removal to estimate the efficiency of poisoning. This estimation assumed bait removal at adjacent sites to be independent. As some of the bait sites were only 10-30m apart the assumption is suspect. Transects were only 135-275m long so a pig could easily remove all baits along a transect. If that occurred then the efficiency of poisoning was grossly overestimated. The analysis also assumed that all pigs would eat the bait, goat meat, yet the meat was not recorded in the natural diet of the feral pigs studied.

Shooting from a helicopter has been used to control feral pigs in swamps in NSW

(Hone 1983, Bryant et al. 1984, O'Brien 1985). O'Brien (1985) reported a decline in the kill rate (pigs shot/h) over several years of shooting from helicopters in the Macquarie Marshes in NSW. It was noted in that study that the optimal frequency of shooting was not known, nor was the cost relative to other control methods. Saunders and Bryant (in press) estimated that 80% of feral pigs in an area were shot from a helicopter. Feral pigs that survived may have changed their behaviour in response to the shooting, as evidenced by two of six pigs that were radio-collared and known to be in the area but which were not seen from the helicopter during shooting. Hence some pigs survived by not being seen, rather than pigs escaping from shooters.

In none of the previous studies has there been close integration of the ecological basis of any control method. The ecological basis of control has been explored by several authors. Tipton (1977), Giles (1980) and Hone and Robards (1980) discussed the effects of control on population dynamics but did not experimentally examine the effect of the control methods themselves. Tipton (1977) reported that the optimal control strategy, within cost constraints, was to remove 60% of the 0.5 to 1.0 year old age class and 40% of the over 2.5 year old class each fall (autumn) and spring. The resultant finite rate of increase of the population was 0.85/yr. When food supply varied between years then the control could be reduced to obtain the same result. Giles (1980) calculated that instantaneous reduction of population size by at least 70% was necessary to keep abundance of feral pigs below that of pre-control levels for at least one year. Hone and Robards (1980) reported the expected effect of control on a closed feral pig population which grew exponentially with an instantaneous rate of increase of 0.6/yr. Annual control which killed 70% of pigs then alive, achieved eradication in 9.5 years, compared to biannual control of 70% which produced eradication in 3.5 years. Food supply was assumed to be high in each year. When food supply was variable between years then the populations were generally lower but eradication still took as long. However Caughley (1980) showed that a hypothetical population increasing by logistic growth with an instantaneous rate of increase of 0.6/yr and subjected to continual control throughout the year at a level of 70% control, survived for 42 years before eradication.

Calculations by Giles (1980) indicated that a major source of variation in the rate of increase of pig populations was variation in juvenile mortality. No control method currently used specifically aims to increase juvenile mortality to get maximum depression of the rate of increase of a population.

In the present study, the aim was to increase our understanding of the effect of two control methods; shooting from a helicopter and poisoning with warfarin.

1.3. Surveying

The evaluation of the effects of control on pig populations or their impacts requires a survey method or methods which estimate the abundance of feral pigs or their sign prior to and after control. Such methods are now reviewed.

Survey data are of three types; presence/absence, density index (relative density) or true density. Presence/absence data are used for mapping the distribution of animals. Recent attempts to map the distribution of feral pigs in Australia have demonstrated broad agreement but also some notable differences. Maps by Frith (1973), Tisdell (1982) and Strahan (1983) differ in the presence or absence of several colonies of feral pigs in Western Australia and the extent of isolation of colonies in eastern NSW. The differences appear to be associated with the authors rather than some extraordinary capacity of feral pigs to appear and disappear or be eradicated locally.

Most surveys of feral pigs have aimed to obtain density indices or estimates of true density. Many methods are available for counting wildlife populations. Norton-Griffiths (1975), Eberhardt (1978b), Eberhardt et al. (1979), Caughley (1980), and Seber (1982, 1986) described in detail most of the survey methods. A variety of survey methods has been used for feral pigs or wild boar, but no universally accurate or precise method has been developed. Similarly there is no standardisation of survey variables. Barrett (1982) outlined briefly some of the methods, but I will discuss them in more detail.

Track counts and drive counts (by beating) were used by Pucek et al. (1975), Dzieciolowski (1976) and Bobek and Perzanowski (1984) in Polish forests in winter snow. Dzieciolowski (1976) reported a significant ($P<0.05$) but weak correlation ($r=0.389$, $df=24$) between the results of drive counts and the number of tracks of wild boar. The track counts were indices of population density but the accuracy of the drive counts was not known.

Diong (1973) used the number of pigs killed in small known areas in Malaya to obtain a "rough estimate" of pig abundance over a wide area. Line transects were used by Singer and Ackerman (1981) in forests in GSMNP, USA. The transects were used to obtain estimates of true density by walking along existing trails and converting observed density to true density by Eberhardt's (1968) power function. However Burnham et al. (1980) concluded that the power function was not generally useful as an estimator of true density and hence the density estimate by Singer and Ackerman (1981) was probably inaccurate. Saunders and Bryant (in press) used an index, manipulation. index method (Eberhardt 1982) to estimate true population size of feral pigs. The indices were obtained by aerial survey. Coblentz and Baber (1987) used an area count on Isla Santiago and assumed it was an accurate count.

Capture-recapture was used by Henry and Conley (1978) to estimate true density by the Petersen estimate. Jezierski and Myrcha (1975), Jezierski (1977) and Andrzejewski and Jezierski (1978) used a calendar of captures method to estimate true density. Barrett (1971, 1978) used the ratio of tagged and recognised pigs to untagged pigs, to estimate population density, supplemented by aerial reconnaissance of pig sign. How the latter aerial observations were used was not specified. Giles (1980) used Schnabel and Jolly-Seber estimates, a cumulative catch equation and frequency of capture models (Poisson, negative binomial and geometric) to estimate true density of a pig population. Only the Jolly-Seber estimate and the negative binomial and geometric models allow for unequal catchability of feral pigs which has been reported in several studies (Barrett 1971, Jezierski 1977, Giles 1980).

Baber and Coblentz (1986) showed that capture probabilities can vary between individuals and times. They used two capture-recapture models (M_b and M_h) in program CAPTURE (Otis et al. 1978) to estimate true density of populations, but reported that at each of two sites the appropriate model was different because of varying pig behaviour. At one site the accuracy of the estimate of pig numbers was compared to a Petersen estimate and a removal estimate, and all were in close agreement (63, 71 and 63 pigs respectively). The Petersen estimate assumed equal probability of capture and recapture (Caughley 1980) and the appropriate model from program CAPTURE (M_h) assumed a constant probability of capture that varied between individuals (Baber and Coblentz 1986). The accuracy of the estimate from model M_b was not tested. Coblentz and Baber (1987) also used mark-recapture models, namely the generalized removal model (M_{bh}) in program CAPTURE (Otis et al. 1978). The latter study estimated the size of the pig population on Isla Santiago, in the Galapagos. The authors cautioned that the estimates may not be accurate. That is not surprising as in two habitats on the island, the number of pigs was estimated by "comparing the number of pigs and pig sign" with those in other habitats. No details of how the comparisons were made were given. The number of pigs in those two habitats accounted for 64% of the estimated total number of pigs on the island.

Indices of population density of feral pigs have been obtained by area counts (Hone and Pedersen 1980, Hone 1983), spotlight strip transects (Hone 1983), aerial survey strip transects (Pavlov et al. 1981, Hone 1983, Saunders and Bryant in press, Wilson et al. in press), bounty payments on pig snouts (Giles 1980, Woodall 1983) and dung counts on plots (Ralph and Maxwell 1984). The precision of the spotlight transect counts and the data from aerial survey (Hone 1983) was very low. The ratio of the standard error to the estimate was 31%-54% for the aerial survey and 30%-33% for the spotlight counts (Hone 1983) but was lower (25%) in surveys by Wilson et al. (in press). Barrett (1982) noted that many indices of pig abundance have been used but they have been rarely compared to known populations of feral pigs. He did not give an example and I do not know of any.

In the studies of Mackin (1970) and Gorynska (1981) the methods used to obtain estimates of wild boar were only vaguely described and so the accuracy of the estimates can not be assessed. Despite the plethora of survey methods, accurate estimates of the abundance of feral pigs over extensive areas have not been obtained. There have been sets of guesses of the number of feral pigs in Australia; 0.5-1.5 million (McKnight 1976), 8.7-10.1 million (Flynn 1980) and 3-6 million (Tisdell 1982). The usual caveat on the accuracy of guesses (Caughley 1980) should be applied to each of the above.

In the present study methods were needed to survey feral pigs or their sign in open floodplain, forest, woodland and grassland. For the thesis, aerial survey was chosen for open floodplain and open woodland habitats while ground transect surveys were used in forest, woodland and grassland.

The methods of control of populations of feral pigs have evolved from a combination of field experience and experiments. Not all the practices have been tested exhaustively because it is virtually impossible to do so. Experiments to evaluate three poisons in each of three bait types with four delivery systems, in each of four seasons become too costly to apply in the field. An alternative approach is to develop mathematical models of the control methods, based on relevant field and laboratory data. A review of modelling follows.

1.4. Modelling

The principal use of mathematical models in pest control is to provide guidelines for evaluating various control strategies (Conway 1977, Conway and Comins 1979). If the values of parameters used in a model can be estimated then the models may also be of predictive value.

There have been surprisingly few attempts to integrate the many patterns and processes which are involved when controlling vertebrate pests such as feral pigs and to express the results in a mathematical form or model. Gentry (1971) developed a mathematical model of programs for eradication of rats. The model was based on a series of simultaneous integral equations which described changes in the number of rats of different ages. Natural changes in abundance were described and the effects of sterilisation and poisoning examined. Batcheler (1982) developed a simple probability model to estimate the number of random encounters with poisoned bait that were required to kill a pest. This was based on the poison content and piece-weight distribution of poisoned baits. Grant et al. (1984) described a Leslie matrix model to evaluate the effect of pesticides on non-target populations. The effects of four hypothetical coyote (Canis latrans) control programs using sodium monofluoroacetate were simulated. Modelling has been used more extensively for evaluating chemical and other control of invertebrate pests such as cattle ticks (Sutherst et al. 1979).

Hone (1986a) developed probabilistic models which estimated the probability of an animal dying in a poisoning program. The probabilistic approach reflected underlying uncertainty in describing the effects of all factors and interactions that may determine how many or what percentage of animals die. The models estimated the probability of an animal dying as the product of the probability of an animal eating the poisoned bait and the probability of dying given that the animal has eaten the poisoned bait.

Models of poisoning were developed for four ecological situations; each combination of random and non-random search, and random and non-random bait dispersion. The models for random and non-random bait dispersion were based on type II and type III functional response relationships for mice (Peromyscus maniculatus) feeding on wheat (Real 1979). However Taylor (1977) reported different results for mice (Onychomys torridus) feeding on mealworms, namely a type II functional response for both dispersion patterns. Similarly, Short (1985) reported type II functional responses for kangaroos (Macropus rufus), sheep (Ovis aries) and rabbits (Oryctolagus cuniculus) feeding on plants. The data of Taylor and Short indicate type II functional responses though it should be noted that neither tested the fit of a type III response to their data. On the basis of the above, the distinction between bait dispersion patterns by Hone (1986a) was probably not necessary. Similarly the labelling (May 1981) of a type II functional response as the "invertebrate" response and the type III as the "vertebrate" response is not appropriate.

The disc equation (Holling 1959, 1965, 1966) and later elaborations of the functional response (Pulliam 1974, Charnov 1976, Belovsky 1984, Fujii et al. 1986) assume that prey density is constant during predation. The random predator equation (Rogers 1972, Lawton et al. 1974) allows for prey removal and is hence more analagous to feral pigs feeding on bait. Hone (1986a) suggested Pulliam's (1974) equation may be useful for modelling poisoning situations where bait is randomly distributed and the pest's search pattern is non-random. The model is appropriate when the pest does not remove a substantial proportion of the bait. Hone (1986a) also suggested that when both bait dispersion and the pest's search pattern are non-random, then the model of Caraco and Pulliam (1984) could be used to describe bait removal. Their model, which is the same as that suggested by Cowie (1977), assumes a linear relationship between prey (bait) removal and prey (bait) abundance, and that the handling time per unit of prey (bait) is negligible compared to the time spent by a pest at a bait station. From the above, and as alternate food is nearly always available, the two-prey (bait and non-bait) equivalent of the random predator equation (Lawton et al. 1974) is a more appropriate model for the functional response relationship than those used by Hone (1986a). Hence the four categories of models described in that study can be reduced to one general category and model.

The models of Hone (1986a) assume that the probability of an animal dying from poisoning is similar between individuals in the population. The probability of dying may not be constant however because of behavioural differences between animals. An analagous situation has been described for capture probabilities in trapping animals for estimating abundance (Otis et al. 1978). Incorporation of variable probabilities in the models of Hone (1986a) is an area for future research and is not attempted here.

This Chapter has reviewed why and how feral pigs are controlled and how such control can be evaluated by surveying and modelling. The next two Chapters describe the development and evaluation of survey methods. The evaluation builds on existing knowledge described in this Chapter.

Chapter 2
Aerial surveying

Aerial surveys are often used to estimate abundance of large mammals. Surveys usually aim to obtain indices, or estimates of true population density with acceptable levels of precision. Many survey and environmental factors can influence counts in aerial survey (Graham and Bell 1969, Caughley 1974, Caughley et al. 1976) usually resulting in negative bias (underestimating density). Many methods have been used to correct for this bias such as multiple regression (Caughley et al. 1976), paired observers (Magnusson et al. 1978) and photography (Norton-Griffiths 1975). These and other methods were reviewed by Pollock and Kendall (1987). They concluded that total ground counts were the best method for correcting for visibility bias in aerial survey. Seber (1982) noted the need for evaluation of the various estimators on known populations.

Parallel development of on-ground line transects have concentrated on better models for defining the detection function (Eberhardt 1968, 1978a, Burnham et al. 1980, Seber 1982, Burnham and Anderson 1984, Buckland 1985). The detection function describes the decreasing probability of seeing an animal at increasing distance from the observer. Burnham and Anderson (1984) and Hone (1986b) have emphasised the need for distance data in transect counts and the use of established criteria for evaluation of methods. Ground and aerial survey techniques appear to be converging analytically but no study has reported an evaluation of line transect methods relative to an aerial survey of a known population. Alldredge and Gates (1985) evaluated line transect estimators for aerial survey of dolphins but did not independently estimate true density. Pollock and Kendall (1987) argued against widespread use of line transect estimators in aerial survey, as the critical assumption that all animals were seen on the transect line may not be correct in areas of thick vegetation or if animals are underwater.

Aerial survey has been used in Australia to monitor the abundance of feral pigs (Pavlov et al. 1981, Hone 1983, Saunders and Bryant in press, Wilson et al. in press). These studies used observed counts to obtain indices of abundance of feral pigs. Aerial survey of feral pigs can be used to estimate population density before, during and after control. A potential use is in the event of an outbreak of an exotic livestock disease such as foot and mouth disease. Aerial survey could be used rather than ground survey techniques because of concern about accidental dissemination of disease pathogens by ground staff or equipment. Such aerial survey would require a precise index of population density or a precise and accurate estimate of density. The former is more easily obtained by the use of well-established sample survey methods (Cochran 1977). The latter option would be useful but would require development and evaluation of new methods of aerial survey. This Chapter reports the first stage of such development and evaluation. Past developments of both aerial and ground transects are utilised particularly in the application of distance data.

Of the many factors known to influence counts of animals by aerial survey, the effects of weather, time of survey and observers have been studied in some detail. Short and Bayliss (1985) reported an effect of cloud cover on counts of kangaroos (Macropus rufus and M. giganteus) and Hill et al. (1985) reported an effect of time of day on counts of kangaroos (M. giganteus). Effects of observers on counts of large mammals have also been reported (moose Alces alces, LeResche and Rausch 1974; kangaroos M. rufus, Caughley et al. 1976; dolphins Tursiops truncatus, Leatherwood et al. 1978; feral horses Equus caballus, Frei et al. 1979; kangaroos M. rufus, M. giganteus, Short and Bayliss 1985). The effects of each of these treatments except time of day, have not been studied previously for aerial survey of feral pigs. Wilson et al. (in press) reported no significant effect of time of day on counts of feral pigs by fixed-wing aerial survey.

To develop and evaluate an aerial survey method for feral pigs in open floodplain and open woodland habitats, the effects of days, time of day, weather and observers on observed population density were investigated by applying a new survey method. This was complemented by a test of the method's accuracy and precision from counts of objects at a known density. For this latter experiment a known population of feral pigs was not available but a known population of carcasses of feral pigs were located in an area available for survey.

2.1. Methods

Site

The area studied was on the floodplain and surrounding area of the Mary and Adelaide Rivers (12° 30'S, 130° 30'E) in the Northern Territory (Figure 2.1). The area of about 400 km^2, is flat with broad floodplains of each river spreading in an east-west direction as the rivers flow north. The surveys were conducted in October 1985 (dry season) and March 1986 (wet season).

Prior to the study, the site was divided into three habitats on the basis of plant species composition. The first habitat was wet, open floodplain with abundant surface water. This habitat is virtually treeless with large areas of green grasses and herbs to a height of 1-2m. The second habitat was Eucalyptus woodland which occurs on the slightly higher land adjacent to the open floodplain. The common tree species in the woodland are E. tetradonta and E. miniata which reached heights of 10-15m. There is very little understorey in the woodland except for grasses. The third habitat was wet swamp of paperbarks, characterised by large areas of paperbark Melaleuca spp. trees. Abundant surface water occurs under the trees, with green grasses and herbs.

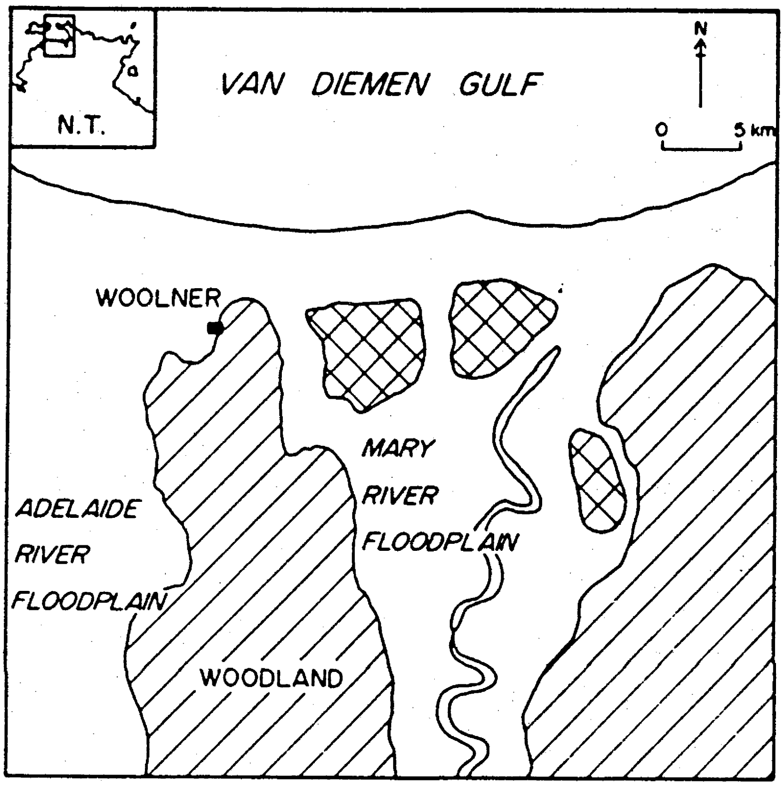
Design

A preliminary survey in October 1985 tested the effects on observed population density of four treatments; days (two), time of day (early morning and late afternoon), observers (two) and habitats (wet open floodplain and wet paperbark swamp). A split-plot randomised block design was used, with time of day as the sub-plot factor and other treatments as main-plot factors. Two blocks were used, with all treatments assumed to be fixed. In the preliminary survey, transects were initially selected at random without replacement for the first flight, then the same transects were reflown on each subsequent flight.

For the test of accuracy a known population of carcasses of feral pigs was surveyed in March 1986. Many studies of the accuracy of aerial and ground survey methods have used known populations of inanimate objects (pins, Watson et al. 1969; blocks, sacks and deer carcasses, Robinette et al. 1974; dots, Caughley et al. 1976; stakes, Burnham et al. 1980; beans, Hone 1986b). Surveys of inanimate objects are not replacements for surveys of wild animals but can be useful areas for research in the development of survey methods. That is the context of the experiment reported here. Feral pigs had been shot as part of a control program and the number of pig carcasses was known from detailed records. A total of 618 carcasses were surveyed in an area of 223 km^2 of which 472 carcasses were in 96 km^2 of open floodplain habitat and 146 carcasses in 127 km^2 of adjacent open woodland. They were surveyed during the day immediately after the shooting which had taken two days.

Survey Methods

Figure 2-1: Map of study area in the Northern Territory. Hatched areas are woodland and cross-hatched areas are paperbark swamps.



Transects were flown in each habitat and, other than in the preliminary survey, were selected at random with replacement. The transects were flown east-west to minimise effects of sunshine glare, and were of variable length as the habitats were of variable width. Counts were made by observers in the back seat of a Jet Ranger helicopter with the side doors removed for counting. Each observer counted on only one side of the flight path. A navigator was seated with the pilot in the front of the helicopter and used 1:100,000 topographic maps for navigation. Survey altitude was 46m (150ft) and speed 90km/h (50 knots). When a group of pigs was sighted the helicopter hovered so an accurate count of the group could be obtained. This was done to prevent undercounting of large groups, a problem reported by Sinclair (1973) in surveys of large mammals and in counts of inanimate objects (Hone 1986b). Also the technique was designed to prevent an association between group size and distance such that at greater distances large groups were more likely to be seen than small groups. Eberhardt et al. (1979) reported that in aerial surveys of otters (Enhydra lutris), sightability of groups was dependent on group size. Burnham et al. (1980) emphasised the need to avoid such a relationship.

Pigs that were sighted were recorded in one of four strip-width classes (0-25,26-50,51-75,76-100m). The strip-widths were delimited by tape on a pole that projected perpendicular to the flight path from under the helicopter body and just in front of each observer. The accuracy of the strip-width markers was checked by flying over objects on the ground that were at known distances apart. Surveys were flown during the two hours after sunrise (about 0610h) and two hours before sunset (about 1840h).

The cloud cover (on a scale of 0 to 8), time (mins) of finishing or starting a survey relative to sunrise or sunset, duration (mins) of each flight and distance (km) of surveying over each habitat were recorded for each survey flight.

Analysis

The preliminary survey was analysed by fixed-factor, split-plot analysis of variance (Snedecor and Cochran 1967), after transformation of observed densities to common logarithms after adding one. The transformation was necessary to achieve homogeneity of variances. The residual variances were estimated from the sum of the block effects with other treatments. Observed density was estimated by the ratio method (Jolly 1969, Cochran 1977, Caughley and Grigg 1981), using data pooled from all four strip-width classes (0-100m).

For the full surveys in both seasons the effects of cloud cover, time of survey, duration and distance of survey were examined by correlation analysis, for each observer, season and habitat. The effects of observers on observed density were examined by Newman-Keuls test for each habitat. Chi-square analysis was used to test the numbers of individuals and numbers of groups of feral pigs in each strip-width class and the frequency distributions of group sizes seen by each observer.

The densities of carcasses and associated standard errors were calculated using one strip transect estimator, the ratio method, and eight line transect estimators; Cox's method (Eberhardt 1978a, Seber 1982), the Fourier series, negative exponential, half-normal, exponential power series, exponential polynomial (using program TRANSECT) (Burnham et al. 1980), hermite polynomial and hazard rate estimators (Buckland 1985). The ratio method is simply the total count of carcasses divided by the total area sampled and does not correct for visibility bias. All other estimators correct for, or attempt to correct for, visibility bias. For each of the last seven estimators (Fourier series, negative exponential, and so on) an estimate of population density (D) was obtained from the following equation;

$$D = np \times f(0) / L$$

where np was the number of animals sighted, L was the total length of transect and f(0) was the probability density function of observed perpendicular distances for each of the seven estimators, in this case when distance equals 0 (Burnham et al. 1980). Only one observer counted carcasses for the accuracy experiment and as the observer counted on only one side (not 2) of the helicopter then the equation for estimating density for all estimators except the ratio, was modified from its usual form (Burnham et al. 1980) to that above, by halving the denominator.

For each line transect estimator calculated by program TRANSECT, the variance of the density estimate was calculated by assuming that the variance of the number of carcasses counted was twice the number of carcasses counted (var(n) = 2n) following Eberhardt (1978b) and Burnham et al. (1985). Program TRANSECT (Burnham et al. 1980) underestimated the variance by assuming the number of animals counted equalled the variance of the number (var(n) = n).

During aerial surveys the bottom of the observer's field of view was nearly straight down, so the frequency distribution of the number of pigs or carcasses counted in each strip-width class was not "left-truncated" (Alldredge and Gates 1985).

The effects of strip width on the accuracy of Cox's method were also examined.

The effects of increasing strip width and of increasing distance to the strip width were tested for the ratio method. In the first analysis the strip width increased from 0-25m to 0-50m to 0-75m and to 0-100m. Secondly the strip width of 25m started directly under the helicopter then was from 26-50m, then 51-75m and finally 76-100m from the helicopter flight path. Sampling intensity was 4.2% for the 25m strip width, 8.3% for the 50m strip, 12.5% for the 75m strip and 16.7% for the 100m strip width.

Estimates of true density of carcasses were obtained for the floodplain habitat and for the combined floodplain and woodland habitats. There were insufficient data for separate estimates in the woodland as time for surveying that habitat was too short to get sufficient data for the line transect estimators. Surveying had to be suspended when dingoes, feral pigs and birds of prey started feeding on and hence removing carcasses, thereby preventing us from knowing true density.

2.2. Results

The analysis of variance of the preliminary survey results showed no significant (P>0.05) effect of days (F=0.319, df=1,7), times of day (F=1.140, df=1,8), observers (F=0.158, df=1,7) and habitats (F=0.015, df=1,7) or any of their interactions on the observed density of feral pigs.

Correlation analysis showed no significant relationships between cloud cover, time of day or duration of flights and observed population density (Table 2.1). There was one significant negative correlation of survey day and observed population density (Table 2.1) and two positive and one negative correlation of distance of survey and observed population density (Table 2.1).

Further testing of the effect of observers showed there were no significant differences between observers in observed population density within habitats within seasons (Table 2.2). In contrast there were highly significant differences between observers in the number of pigs counted in each strip-width class within habitats and seasons (Table 2.3). In the dry season surveys, the left observer counted most pigs in the outer strip class (75-100m) in contrast to the right observer who counted more pigs in the inner strip in the paperbark habitat and in the second strip in the floodplain habitat. In the wet season data there were no clear trends. Counts of pig groups showed broadly similar results (Table 2.4) but showed less variation across strip-width classes than counts of individual pigs. There were no significant differences in the frequency distributions of group sizes recorded by the two observers (Table 2.5), although the right-side observer usually counted more smaller groups.

Most of the estimators gave estimates of the density of carcasses not significantly different from the true density (Table 2.6). The exponential polynomial estimator significantly overestimated true density for the floodplain habitat and the ratio method underestimated when strip width was wide (Table 2.6).

The most accurate estimator in the floodplain habitat was the ratio method when the strip width was 0-25m (Table 2.6). The second most accurate estimator was the hazard rate, the third was the exponential power series and the fourth was the Fourier series estimator (Table 2.6). In the combined floodplain and woodland habitats the Fourier series estimator was the most accurate (Table 2.6). The second most accurate estimator was Cox's method (W=25m), the third was the half-normal and the fourth was Cox's method (W=50m). In both situations there was a slight tendency to overestimate true density. The estimator with the lowest standard error in the floodplain habitat was the Fourier series and in the combined floodplain and woodland habitat was the hazard rate estimator (Table 2.6).

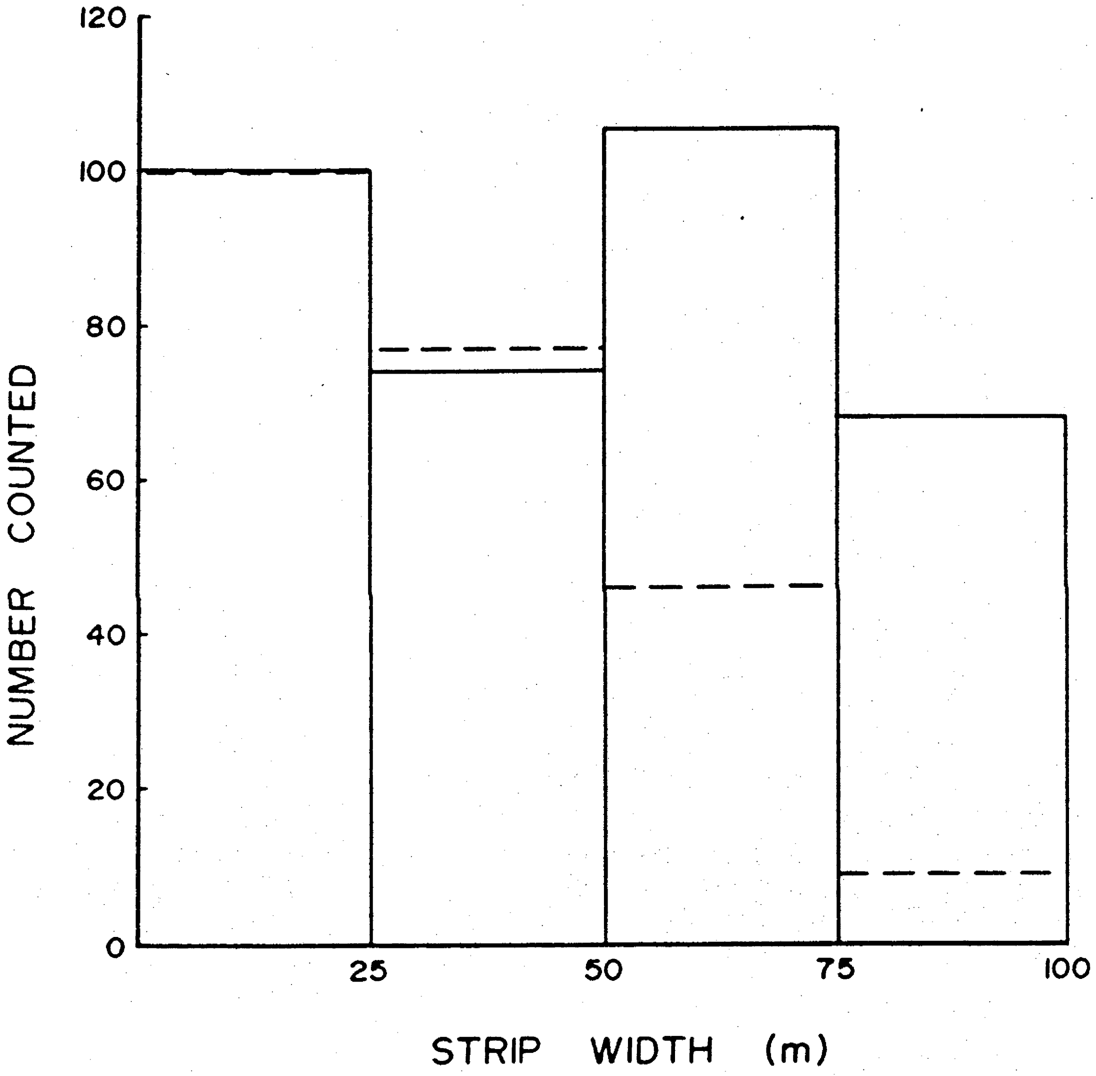
On the open floodplain the ratio method gave significantly biased estimates of density as strip width increased (Table 2.6). The narrow inner strip width of 25m gave accurate estimates though the precision of the estimate was low (coefficient of variation 48%). When analysed for each 25m strip width the estimated density and accuracy quickly declined; 5.03 carcasses/km^2 (0-25m), 3.89 (26-50m), 1.60 (51-75m) to 0.46 (76-100m). The density estimates for the floodplain and woodland combined were accurate when strip width was narrow but significantly negatively biased when strip width was wide (Table 2.6). Again the precision was low (coefficient of variation 48%). As the strip width was displaced out from the flight path the density estimates and their accuracy for the combined floodplain and woodland declined (2.14 carcasses/km^2, 0-25m; 1.95, 26-50m; 1.15, 51-75m; 0.23, 76-100m).

The decline in the number of carcasses counted in successive strip widths was more rapid than the decline in the number of live feral pigs counted while surveying the same area at the same time of year (Figure 2.2). The data shown are for the combined floodplain and woodland habitats.

2.3. Discussion

The results in this study indicate that the method of aerial survey from a helicopter developed in this project has application to feral pigs. The absence of effects on observed density attributable to cloud cover, days or time of day indicates that survey data can be pooled over those factors. The occasional effects of survey day or distance of survey suggest that those factors have minor overall

Figure 2-2: The number of carcasses of feral pigs (dashed lines), and number of live feral pigs (solid lines) counted in each strip-width class during aerial survey. The numbers of each have been adjusted to a similar value of 100 in the inner strip.



effects on observed density within the range of levels examined in this work. With the large number of correlation tests conducted, a few significant results would be expected even if there were no real effects.

The results show that observers can return similar observed densities but have very different sightability curves (the number of animals counted in each strip-width class). The wide strip width (100m) blurred over all such differences between observers. The shape of some of the sightability curves such as those of the left observer in the dry season, prevents their use in line transect estimation. Such differences in sightability curves suggest the observers had different search patterns. Differences in fatigue or boredom would have resulted in different observed densities. The differences could also be related to experience as only the right-side observer had previously done aerial survey. The results show a need to check observers' sightability curves before they are used in extensive surveys. Such checking should complement other training such as that outlined by Dirschl et al. (1981).

The accuracy of many line transect estimators for counting carcasses shows that models that satisfy the criteria outlined by Burnham et al. (1980) and Burnham and Anderson (1984) have application to aerial survey, especially from a helicopter where, as done here, the helicopter can hover to get accurate counts of group size. The decreasing accuracy with increasing strip width in the present study agrees with results of earlier studies for many species and objects (Caughley 1974, Caughley et al. 1976, Beasom et al. 1981, Hone 1986b).

The precision of some estimators was high, especially the one-term Fourier series. However Buckland (1985) reported that the one-term Fourier series estimator may underestimate the standard error of the density estimate. The precision of the line transect estimators was higher than that of the strip transect estimator (ratio method) as reported by Burnham et al. (1985).

Cox's method gave accurate estimates of density on the open floodplain and in the combined data for both habitats when strip width was 25m and accurate but slightly higher estimates when strip width was 50m. The precision of both estimates was higher (coefficient of variation 32% and 28% respectively) than that of the ratio method. Eberhardt (1978a) noted that if the underlying sightability curve was half-normal then Cox's method could slightly overestimate. The sightability curve was similar to a half-normal distribution in the present study. The narrower strip width produced the more accurate estimates but the estimate was sensitive to small changes in the data. If one pig carcasse in the inner strip

(0-25m) had been incorrectly tallied into the outer strip (26-50m) the density estimate would have fallen from 5.60 to 5.14 carcasses/km^2. Conversely if the reverse had happened the estimate increased from 5.60 to 6.06. The effect of such recording errors will be more critical when low numbers of animals are counted.

Cox's method satisfies two (model robustness and pooling robustness) of the four criteria (model and pooling robustness, shape criterion and efficiency) that Burnham et al. (1980) suggested any estimator should meet. The method does not satisfy the shape criterion (p169 but compare with p162) and was not considered an efficient estimator. Burnham et al. (1980) suggested the method could be subjective in the selection of strip widths for ungrouped data but that was not a problem here. They also noted the method had the advantage over many others in that the density estimate is easy to calculate.

The results in the present study suggest that Cox's method could be applied cautiously to data in other aerial surveys. Beasom et al. (1981) reported an effect of strip width on counts of white-tailed deer (Odocoileus virginianus). Observed density was 6.65 deer/km^2 when strip width was 100m and 9.06 deer/km^2 when strip width was 50m. Using that data, Cox's method estimated the population density of white-tailed deer as 11.48 deer/km^2 which was substantially higher than the reported densities. More testing is needed to determine if Cox's method overestimated population density or Beasom's data underestimated population density.

Buckland (1985) argued that a shoulder in the detection function was necessary for reliable density estimation. Each of the estimators, other than Cox's method that gave accurate estimates of population density satisfied the shape criterion. The negative exponential and exponential polynomial series estimators, that usually overestimated density, did not have a shoulder in the calculated sightability curves and hence did not satisfy the shape criterion.

The slower decline in the sightability of live feral pigs compared to carcasses suggests that the sightability of live pigs was higher than that of carcasses. That was probably because of live pigs flushing from cover as the helicopter approached. The accuracy of the line transect estimators and the higher sightability of live pigs, suggests that the survey method could be used to estimate the population density of feral pigs. The results indicate that the Fourier series estimator would be the best analysis. The results support the conclusions of Burnham et al. (1980), Alldredge and Gates (1985) and Seber (1986) that the Fourier series estimator is the best line transect estimator currently available.

The experimental analysis of survey methods described in this Chapter has shown that some analyses have potential for use in evaluation of control of feral pigs in open habitats. In forest habitats aerial survey has less application, so alternative methods of survey need to be evaluated. In the next Chapter, a description is given of the development and evaluation of methods for measuring the extent and frequency of rooting and the abundance of feral pigs in forest habitats.

Table 2-1: Correlation coefficients between survey variables and observed density of feral pigs in each season and habitat for each observer (L, left and R, right). *P<0.05, **P<0.01

SEASON, HABITAT & OBSERVER		SURVEY DAY	CLOUD COVER	TIME OF DAY	DURATION	DISTANCE	DF
Dry Season							
Paperbark	L	0.408	−0.385	0.353	−0.447	0.103	10
	R	0.084	0.289	0.153	0.308	0.196	10
Floodplain	L	−0.437	0.610	−0.265	0.359	0.648*	8
	R	−0.688*	0.290	−0.301	0.483	0.610	8
Pooled	L	0.350	−0.024	0.259	−0.298	−0.436	10
	R	0.112	0.261	−0.035	0.251	−0.371	10
Wet Season							
Paperbark	L	−0.775	0.133	0.732	−0.492	0.964*	2
	R	0.764	0.669	−0.604	−0.257	−0.322	2
Floodplain	L	−0.737	0.345	0.202	−0.290	−0.291	5
	R	−0.590	0.739	0.392	−0.125	−0.349	5
Woodland	L	−0.523	−0.325	0.190	0.127	0.389	7
	R	−0.064	0.020	0.193	−0.241	−0.801**	7
Pooled	L	−0.499	0.096	−0.065	0.216	0.045	13
	R	−0.369	0.344	−0.052	0.257	−0.224	13

Table 2-2: Indices of pig density (pigs/km^2) (SE) for each observer in each season and habitat. The right-side observer was the same in each season, but the left-side observer was different.

SEASON & HABITAT	OBSERVER LEFT	 RIGHT	NEWMAN–KEULS TEST
Dry Season			
Paperbark	12.26 (2.22)	9.62 (1.59)	0.97 NS
Floodplain	2.62 (1.00)	1.68 (0.77)	0.75 NS
Wet Season			
Paperbark	3.33 (3.16)	1.94 (0.32)	0.44 NS
Floodplain	7.81 (2.24)	12.61 (2.70)	1.37 NS
Woodland	0.62 (0.30)	1.70 (0.59)	1.63 NS

Table 2-3: The number of feral pigs counted in each strip width by each observer in each season and habitat. There were too few data in the wet season in the paperbark to calculate a Chi-square statistic. **P<0.01.

SEASON & HABITAT	OBSERVER	STRIP WIDTH (m) 0–25	26–50	51–75	76–100
Dry Season					
Paperbark	L	39	150	243	362
	R	250	140	126	104
(X^2=317.8**, df=3)					
Floodplain	L	0	5	53	105
	R	3	48	31	38
(X^2=69.8**, df=3)					
Wet Season					
Paperbark	L	0	0	1	23
	R	0	1	13	0
Floodplain	L	18	115	195	43
	R	169	97	212	122
(X^2=114.3**, df=3)					
Woodland	L	2	31	2	29
	R	28	42	73	37
(X^2=48.2**, df=3)					

Table 2-4: The number of groups of pigs in each strip width counted by each observer in each season and habitat. There were too few data for analysis in the wet season in the paperbark and woodland habitats. Degrees of freedom differ between analyses because of pooling low numbers. $^{**}P<0.01$, NS not significant.

SEASON & HABITAT	OBSERVER	STRIP WIDTH (m)			
		0–25	26–50	51–75	76–100
Dry Season					
Paperbark	L	7	24	25	25
	R	34	21	19	23
($X^2=17.7^{**}$, df=3)					
Floodplain	L	0	4	4	6
	R	3	5	7	2
($X^2=0.5$, df=1, NS)					
Wet Season					
Paperbark	L	0	0	1	2
	R	0	1	1	0
Floodplain	L	6	19	22	10
	R	47	26	29	23
($X^2=15.6^{**}$, df=3)					
Woodland	L	1	5	2	2
	R	5	6	6	4

Table 2-5: The frequency distributions of group sizes observed in aerial survey by observers in wet and dry seasons in each habitat. In the Chi-square analysis the degrees of freedom are different due to pooling of low numbers. All tests were non-significant.

SEASON & HABITAT	OBSERVER	GROUP SIZE 1-10	11-20	21-30	31-50
Dry Season					
Paperbark	L	56	13	12	5
	R	85	25	10	2
(X^2=5.1, df=3)					
Floodplain	L	10	5	2	1
	R	14	4	1	1
(X^2=0.8, df=2)					
Wet Season					
Paperbark	L	2	0	1	0
	R	1	1	0	0
(not tested)					
Floodplain	L	42	10	5	0
	R	108	10	5	2
(X^2=5.0, df=2)					
Woodland	L	8	1	1	0
	R	15	5	0	1
(X^2=0.1, df=1)					

Table 2-6: Estimates of density (D) (carcasses/km^2) and standard errors (SE) of pig carcasses derived from nine transect estimators. True density was 5.02 carcasses/km^2 on the floodplain (F) and 2.79 carcasses/km^2 for the combined floodplain and woodland (FW). The number of parameters (P) in each estimator is shown. The differences between the density estimates and the true density were compared by Student's t tests the values of which are shown. The degrees of freedom for the t tests were 27 for the floodplain and 54 for the combined habitats. *P<0.05, **P<0.01, NS not significant, SW=strip width, W= half of strip width.

ESTIMATOR	P		D	SE	t
Ratio					
SW=0-25m	-	F	5.03	2.42	0.01 NS
		FW	2.14	1.03	0.63 NS
SW=0-50m	-	F	4.46	1.79	0.31 NS
		FW	1.90	0.76	1.17 NS
SW=0-75m	-	F	3.51	1.33	1.14 NS
		FW	1.62	0.57	2.05*
SW=0-100m	-	F	2.74	1.00	2.28*
		FW	1.27	0.43	3.53**
Cox's					
W=25m	-	F	5.60	1.79	0.32 NS
		FW	2.82	0.90	0.03 NS
W=50m	-	F	6.00	1.68	0.58 NS
		FW	3.02	0.85	0.27 NS
Fourier series	1	F	5.31	1.50	0.19 NS
		FW	2.80	0.58	0.02 NS
Exponential power series	2	F	5.29	1.52	0.18 NS
		FW	2.48	0.63	0.49 NS
Half-normal	1	F	5.75	1.33	0.55 NS
		FW	2.93	0.66	0.21 NS
Negative exponential	1	F	8.86	2.27	1.69 NS
		FW	4.46	1.11	1.51 NS
Exponential polynomial	2	F	9.05	1.90	2.12*
		FW	4.60	0.94	1.93 NS
Hermite polynomial	2	F	5.37	1.31	0.27 NS
		FW	2.50	0.73	0.40 NS
Hazard rate	2	F	4.93	1.02	0.09 NS
		FW	2.28	0.50	1.02 NS

Chapter 3

Ground surveying

3.1. Ground surveys - random, unmarked plots

During studies in forests, estimates of population density of feral pigs have been difficult to obtain or verify. Problems of sightability of the pigs appear to limit use of many direct survey methods and hence the extent of rooting has been examined to monitor trends in populations of feral pigs. For example, Belden and Pelton (1975) suggested that a "rooting extent index" had potential for monitoring population trends, but they did not calculate values, maybe because of the subjective nature of the method. Pig rooting was recorded in Tennessee (Conley 1977) with rooting scored qualitatively on line transects. Jezierski and Myrcha (1975), Cooray and Mueller-Dombois (1981) and Ralph and Maxwell (1984) recorded the extent of rooting on plots by estimating the percentage of ground disturbed. Alexiou (1983) plotted the location of rooting on maps.

Belden and Pelton (1975), Conley (1977) and Giles (1980) assumed that a significant positive correlation existed between the abundance of feral pigs and the extent of the rooting. The correlation was not tested by those authors but can be tested from data in the literature. Cooray and Mueller-Dombois (1981) reported data (their Table 6.13) which indicated no significant correlation ($r=-0.208$, $df=2$, $P>0.05$). Conversely data from Ralph and Maxwell (1984) (their Table 6) showed a high positive correlation ($r=0.901$, $df=3$, $P<0.05$). These disparate results suggest that further testing is necessary.

The aims of the study described in this section of Chapter 3 were to (i) develop and use an objective method for determining the distribution and relative abundance of rooting (Monitoring), and (ii) develop and test a method for predicting the level of rooting (Prediction).

3.1.1. Methods

Site

The area studied was around Honeysuckle Creek and Nursery Swamp in Namadgi National Park (NNP) (35°30'S, 149°E) in south-eastern Australia (Figures 3.1, 3.2). The topographic features of NNP are wide deep valleys between a series of mountain ranges. Altitude in the study area varies from 870m to 1380m. Vegetation changes from patches of grassland in valleys and Eucalyptus woodland at low altitude to tall open Eucalyptus forest at higher altitude (Anon 1982). Sub-alpine woodlands occur at the highest altitude and in frost hollows at lower altitude. Natural grasslands have been modified by livestock grazing in many of the open valleys. Annual average rainfall is approximately 650mm at low altitude increasing to 1000mm at higher altitudes. Snowfalls are common in winter especially at high altitude.

Feral pigs were first sighted in the area in the mid 1960's following their introduction at the southern boundary of the park (Figure 3.2). This corresponds to a rate of spread of 3.5km/yr, which is slightly higher than that reported (2.5km/yr) for feral pigs in Great Smoky Mountains National Park, Tennessee (Singer 1981). Some feral pig control had been conducted at Honeysuckle Creek during the previous decade (Boreham 1981), though the subsequent effect on pig populations was apparently slight.

Monitoring

Samples were taken during the period January to December 1984 inclusive. The presence or absence of rooting was measured in 29 grids each 1km^2, randomly selected off 1:25,000 topographic maps. Eight parallel transects were surveyed in each grid in an east-west direction with each transect having a starting point located randomly without replacement. Each transect of one kilometre consisted of 50 plots each 5m long by 1m wide, spaced 15m apart. The first plot on each transect was placed 15m from the start of the transect. The presence or absence of rooting, pig dung and pig tracks was recorded on each plot. As no attempt was made to determine the age of rooting, dung or tracks, the various measures represent cumulative distribution and abundance. Rooting was distinguished from scratchings by wombats (Vombatus ursinus) and lyrebirds (Menura novaehollandiae) by the general bulldozed nature of rooting by feral pigs rather than the scratched disturbance caused by the other species. The number of feral pigs observed within 100m either side of each transect was also recorded. The average (+/- SE) duration of each transect was 1.05h (+/- 0.02).

Figure 3-1: Location of Namadgi National Park in south-eastern Australia.

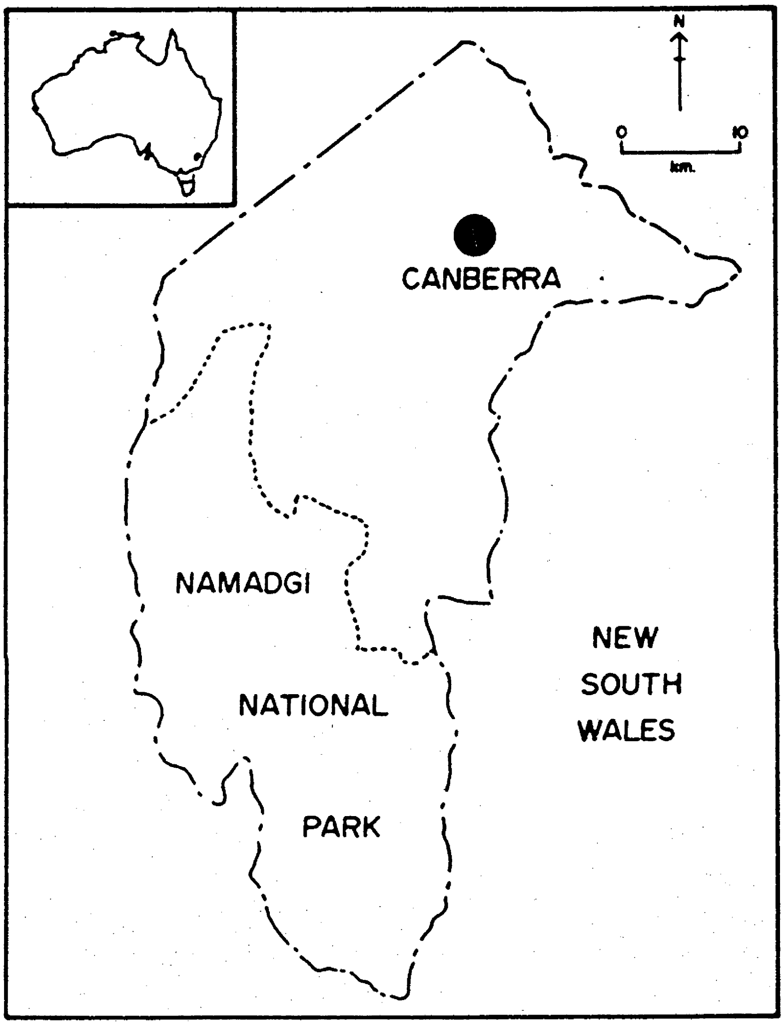
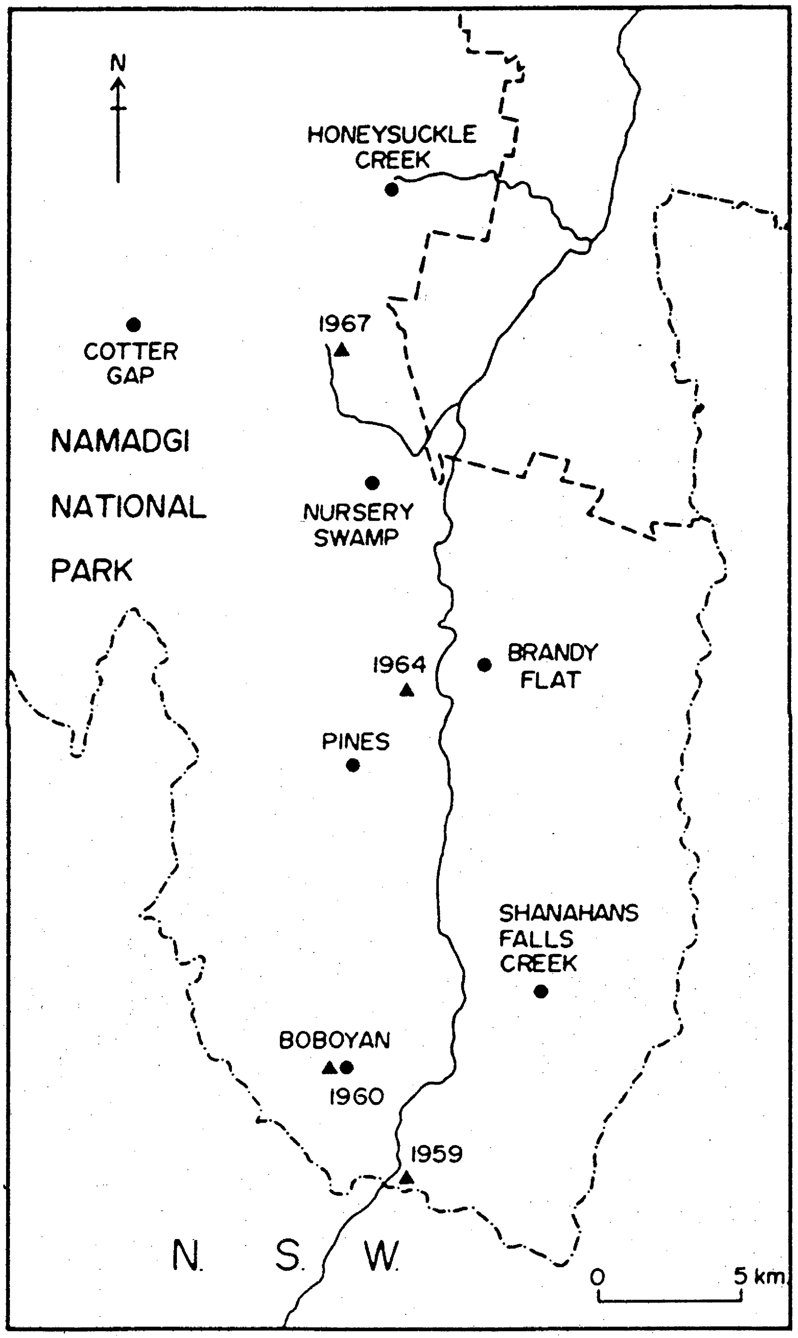


Figure 3-2: Location of study sites and first sightings of feral pigs in Namadgi National Park.



The frequency of occurrence of rooting was assumed to be curvilinearly related to the extent of rooting as occurs in many frequency/density relationships (Caughley 1980). Hence the proportion of plots with pig rooting in each transect (pt) was converted to a linear index of rooting (y) by a Poisson transformation (Caughley 1980 p20).

$$y = - \ln (1 - pt)$$

Estimates of a linear rooting index (LRI) for each $1km^2$ grid were calculated as;

$$LRI = N \bar{y}$$

where N was the total number of possible sampling units (transects) and $\bar{y}$ was the average rooting index per sampled unit (transect). The standard error of LRI was calculated, as outlined by Caughley (1980 p30), as the square root of the summed variances of each grid.

Observed density of feral pigs $(d)/km^2$ was calculated as;

$$d = N \bar{x}$$

where N was the total number of possible transects/km^2 and $\bar{x}$ was the average population density per transect (1km long and 0.2km wide). Observed density was assumed to be an underestimate (index) of true density as some feral pigs do not flush in thick forest, or may move away when an observer approaches.

Prediction

The extent of rooting in $13km^2$ was predicted in a two-stage process. The first stage involved calculating a calibration regression for the extent of rooting in 16 randomly selected $1km^2$ grids and the second stage involved comparing the observed extent of rooting in $13km^2$ with that predicted by the calibration regression. The accuracy of predictions was determined by calculating the 95% confidence interval for the average difference between the observed and expected frequencies of pig rooting.

The regression was derived as follows and is a modification of point-distance methods for estimating animal abundance. The regression requires no a priori assumption of the dispersion pattern of rooting and was calculated between the proportion of plots with pig rooting in a $1km^2$ grid (p) and the observed average number of consecutive plots that had no rooting from the start of a transect (n).

When the average (over the 8 transects per grid) number of consecutive plots with no rooting was zero, then pig rooting was assumed to occur on all plots on all transects. Conversely when the average number of consecutive plots with no rooting was 50 (the length of each transect) then it was assumed no rooting occurred on plots or in the grid. These two assumptions fixed the end points (($n=0$, $p=1.0$) and ($n=50$, $p=0$)) of a regression line without specifying the shape of that line. One equation which satisfies the assumptions is Eberhardt's (1968) power series function;

$$p = 1 - (n/50)^k$$

where p=proportion of plots with rooting per 1km^2 grid, n=average number of consecutive plots with no rooting from the start of transects, and k=regression coefficient. When $k=1$ the regression is a straight line, when $k<1$ the regression is concave and when $k>1$ the regression is convex. The equation can be rearranged to estimate k as the slope of a regression forced through the origin (Snedecor and Cochran 1967, p169) between $-\ln(1-p)$ as the ordinate and $-\ln(n/50)$ as the abscissa for $n>0$.

A second equation satisfying the assumptions of the regression is a modified beta function (Burnham et al. 1980);

$$p = (1 - (n/50))^m$$

where p and n are as above and m is the regression coefficient. This equation can be rearranged to estimate m as the slope of a regression forced through the origin, as above, between $-\ln(p)$ as the ordinate and $-\ln(1-(n/50))$ as the abscissa, for $n<50$. The slope of each regression was estimated as the mean of the ratios of the ordinate over the abscissa (Snedecor and Cochran 1967).

3.1.2. Results

Monitoring

Rooting was present in 27 of 29 grids and in 13.33% of all plots. The frequency of pig rooting varied among grids from 0% to 56.25% of plots. The frequency distribution of the number of plots with rooting per transect was highly skewed, with no rooting on 62 transects, then 29 transects with only one plot with rooting (Table 3.1). The linear rooting index (LRI) was 4903.4 (+/- 323.5 SE) over the 29km^2. The ratio of the SE to the estimate was 6.6%.

The average observed population density of feral pigs was 1.0/km^2 (+/- 0.5 SE). The frequency distribution of the number of feral pigs per transect was highly skewed. On 224 transects no feral pigs were counted. In each of four transects one feral pig was counted, and three, four, five and seven feral pigs were each counted on one transect. Pig dung occurred in 1.09% of plots and pig tracks in 0.14% of plots.

There were significant positive correlations between the percentage of plots in a grid with rooting and pig dung ($r=0.724$, $df=27$, $P<0.01$), feral pig tracks ($r=0.485$, $df=27$, $P<0.01$) and observed pig density ($r=0.443$, $df=27$, $P<0.05$). The regression between the transformed percentage of plots with rooting (PR) and the transformed percentage of plots with dung (PD) was;

$$PR = 2.48PD + 6.47$$

Prediction

The fitted power series function (Figure 3.3) was;

$$p = 1 - (n/50)^{0.14}$$

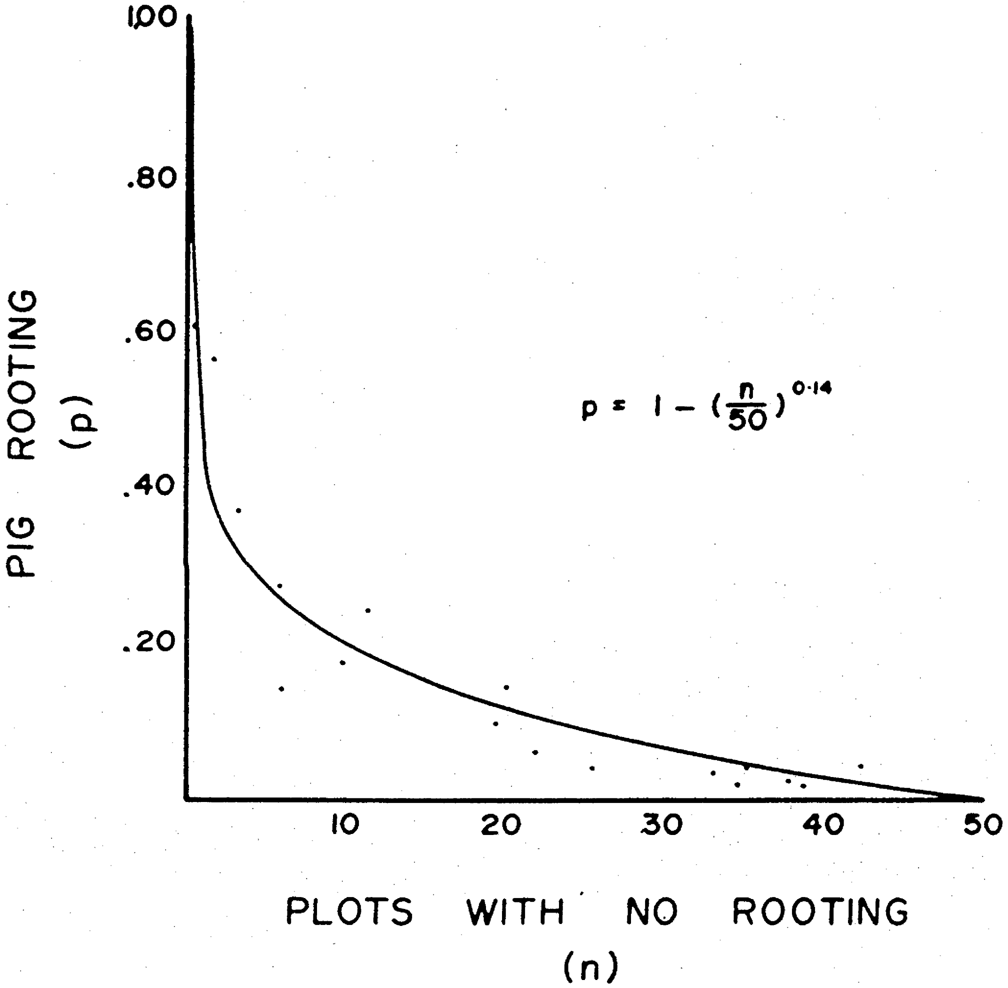
The exponent (0.14 +/- 0.02 SE) was significantly different from zero ($t=7.00$, $df=15$, $P<0.001$). The average observed frequency of rooting in the 13km^2 was 12.77% and the average expected frequency was 14.30%. The average (+/- SE) difference between the observed and expected frequency of rooting was -1.53% (+/- 1.42). The 95% confidence interval of the difference was -4.62% to 1.56%.

The fitted modified beta function was;

$$p = (1 - (n/50))^{3.65}$$

The exponent (3.65) had a standard error of 0.62 and was significantly different from zero ($t=5.89$, $df=15$, $P<0.001$). The observed frequency of rooting in the 13km^2 was 12.77% and the expected frequency was 29.15%. The average (+/- SE) difference between the observed and expected frequency of rooting was -16.38% (+/- 4.98). The 95% confidence interval of the difference was -27.23% to -5.53%, which was wider than the interval for the power series function.

Figure 3-3: The relationship between the proportion of plots with feral pig rooting (p) and the average number of successive plots with no pig rooting from the start of transects (n). Dots correspond to each of 16, $1km^2$ grids and the solid line is the power series function fitted to the data.



3.1.3. Discussion

Monitoring

Rooting by feral pigs was widespread and locally abundant in the forest and woodland. The results indicate that the survey technique has potential for use in mapping and monitoring the distribution and abundance of rooting. Pig rooting can be mapped on a grid basis and the data analysed as the percentage of plots with pig rooting or as the transformed linear rooting index. The regression between the frequencies of rooting and dung indicated that even when no pig dung was present, rooting was. Hence rooting may be a more accurate indicator of past occurrence of feral pigs than dung.

The present technique which used randomly selected transects had advantages over the technique using existing roads and trails outlined by Belden and Pelton (1975) and Howe and Bratton (1976). The edges of roads and trails may be unrepresentative of an area. Conley (1977) reported the use of line transects on which rooting was scored as abundant, common, scarce or none. The present method is more objective. Alexiou (1983) simply mapped the location of pig rooting in selected areas, which would require more field time than the present method.

The percentage of plots with rooting in the present study (13.33%) was lower than that (49.3%-92.0%) reported by Cooray and Mueller-Dombois (1981) in an Hawaiian forest though they used 15m^2 plots compared to 5m^2 plots in this study. Direct comparisons of the spatial extent of rooting in NNP with that reported in other studies is difficult because spatial extent was not directly measured here.

Prediction

The power series function accurately predicted the frequency of rooting in an area of 13km^2. This function should be useful for surveying and mapping the distribution of rooting in forests and woodlands. The modified beta function did not accurately predict the frequency of rooting and was of lower precision than the power series function. The main advantage of the prediction method is the reduction in field-work time which in the present study would have been 60%. The method does not estimate the variance on the frequency of rooting in each 1km^2 grid, but the variance among grids can be estimated by sampling more than one grid.

The results described here indicate that the methods are useful for estimating the frequency of pig rooting in an area. A limitation of the methods is that there is no time limit on the occurrence of rooting or production of dung. For short-term evaluation of pig control a method which measures the occurrence of rooting or accumulation of dung over a defined time period would be more sensitive to control-induced changes in either rooting or dung. Such methods include measurement of rooting or dung on fixed and marked plots, that can be relocated and hence the increment from time 1 to time 2 can be measured. Such an approach was investigated and is described in Section 3.2.

3.2. Ground surveys - random, marked plots

Section 3.1 outlined results of ground survey work using randomly selected and unmarked plots. A complementary study examined survey techniques using randomly selected fixed and marked plots. The results are described here. The study estimated (i) the repeatability and precision of two survey methods for feral pigs - line intercept measurement of rooting and strip counts of dung pellets, (ii) the spatial extent of rooting, (iii) the frequency of occurrence of rooting and dung on plots, (iv) relationships between the extent and frequency of occurrence of rooting and dung, and (v) relationships between the survey results to investigate method accuracy and to assess the usefulness of these methods in control evaluation.

As part of the aims this study tested three alternative hypotheses. The first assumed no relationship between the change in the extent or frequency of rooting from month to month, and the abundance of dung. The second hypothesis assumed the relationship was positive and linear, and the third that the relationship was positive but curvilinear. When pig dung was absent, then rooting decreased at a maximum negative rate but as dung abundance increased then the change in the extent or frequency of rooting became less negative and then more positive. If the relationship was curvilinear then the extent or frequency of rooting did not increase indefinitely with increases in dung abundance, but reached an asymptote. These hypotheses are analogous to numerical response relationships (Krebs 1985).

3.2.1. Methods

Sites

Seven sites were selected with restricted randomisation in the eastern half of Namadgi National Park (NNP); Nursery Swamp (NS), Cotter Gap (CG), Honeysuckle Creek (HC), Brandy Flat (BF), Shanahans Falls Creek (SH), Pine Forest (PI) and Boboyan (BO) (Figure 3.2). Sites selected were at least 5km apart to minimise effects of movement by feral pigs between sites. That distance

Table 3-1: The frequency distribution of the number of plots with rooting per transect in 29km^2 of Namadgi National Park. Each transect contained 50 plots.

NUMBER OF PLOTS WITH ROOTING	NUMBER OF TRANSECTS
0	62
1	29
2	19
3	19
4	6
5	5
6	7
7	4
>7	81
Total	232

was chosen on the basis of limited radio-tracking data (Terrill pers. comm.) for feral pigs in the park that showed feral pigs had home ranges of up to 4-5km^2. Rainfall was recorded monthly at each site and temperatures recorded at Glendale Crossing in the centre of the area.

Design and sampling

At each site data were collected on the spatial extent and frequency of occurrence of rooting, counts of dung pellets and counts of feral pigs. Data were collected monthly from May 1985 to December 1986, with the exception of August 1986, and in July 1986 when spatial extent of rooting was not measured.

Each site consisted of an area of 4km^2 with 25 permanent plots in each of the four, 1km^2 grids for a total of 100 plots per site. Each plot measured 10m x 2m. The number of plots was chosen on the basis of preliminary survey work that showed 48 plots was insufficient to get repeatable dung counts or to get adequate precision on the estimate of the proportion of plots rooted by feral pigs. Each of the plots was selected with restricted randomisation. Plots did not overlap (sampling without replacement) and the distance between plots did not exceed 35m, to facilitate finding plots in the forest.

Plots were not rerandomised between months. The ensuing possible lack of temporal independence was traded off against the practical reality of the time required to relocate 1400 pegs each month. White and Eberhardt (1980) in their study of elk and deer pellets similarly did not rerandomise plots, without apparent significant loss of statistical robustness.

Rooting was recorded using a line intercept method (Lucas and Seber 1977) with the start and end of each area of rooting being measured directly under a tape measure held between two pegs 10m apart at each end of the long main axis of each plot. An area was recorded as rooted if there were obvious signs of ground disturbance by feral pigs and the vegetative ground cover was less than that of surrounding non-disturbed areas.

Dung pellets of feral pigs were counted on a 1m strip either side of the centreline tape measure, so plot size was 20m^2 (10m x 2m). That size and shape was used for comparison with results of Ralph and Maxwell (1984) rather than using a circular plot which has been reported to give more precise results (Neff 1968). However Ralph and Maxwell (1984) used adjacent plots in long transects rather than randomly placed plots. That sampling method may be less precise than the method used in the present study because of serial correlation between adjacent plots.

The number of dung pellets was recorded then the plot was cleared of pig dung. Dung were classed as present if each pellet was still intact and could be picked up without disintegrating. No attempt was made to age dung pellets. Batcheler (1973) reported that assigning ages to dung pellets of possums (Trichosurus vulpecula) was subject to error due to the effect of weather on dung appearance. Dung of feral pigs was differentiated from that of other species on the basis of shape (oval to lobed), composition (fibrous, heterogeneous), colour (black) and odour (putrid). Identification of dung of adult pigs was very easy but that of subadult (6-12mths) pigs required careful examination to avoid confusion with the dung of kangaroos and wallabies. Dung of juvenile (< 6mths) feral pigs was not seen during the study. Fresh dung pellets initially found on plots were placed outside but near plots and checked each month to determine disappearance rates.

Feral pigs seen at each site were recorded and their age (assessed by size into three age classes; juveniles, subadults and adults) and sex recorded whenever possible. Area counts were used to estimate observed density which was assumed to be an index (underestimate) of true population density of feral pigs. Since the plots for dung counts were clustered at each site, the area over which pigs were observed was not the whole site. The proportion of each $4km^2$ site in which pigs were counted was 0.25; that is $1km^2$ at each site. Study in 1984 (Section 3.1) indicated that there were insufficient sightings of feral pigs to use a line or strip transect method (as used by Singer and Ackerman 1981). Burnham et al. (1980) recommended that at least 40 animals had to be recorded to use transect methods, and I did not expect to see that many each month.

Sampling each month revealed changes within seasons and allowed sufficient time for the extent of rooting to change and dung to accumulate but not decay too much that most of it passed beyond the criteria established for counting. Preliminary work in March and April 1985 showed that more than 65% of dung pellets lasted longer than one month in NNP in contrast to Hawaii where most disappeared in two weeks (Ralph and Maxwell 1984).

Analysis

The repeatability of measurements of rooting extent was determined by independently remeasuring each of the 700 plots within a day of each measurement. The difference among sites between the extent of rooting for each site was tested using a paired Student's t test (Snedecor and Cochran 1967). The repeatability between months of counts of dung pellets was examined using Chi-square analysis by comparing the frequency distributions of the number of dung pellets per plot for two successive months. Data from 400 plots were used, from sites where no pig control was occurring.

The standard errors of the percentages of plots with rooting or with dung were estimated from a hypergeometric distribution as sampling was without replacement (Derman et al. 1973).

To examine the application of the data for predicting the extent of rooting or abundance of dung, relationships between the extent of rooting or abundance of dung and the frequency of occurrence of either rooting or dung were determined by least squares regressions forced through the origin. The x variable was either the frequency of occurrence or an index calculated from the first term of a Poisson series (Caughley 1980), where the index (I) was;

$$I = -\ln(1 - f)$$

where f was the proportion of plots with rooting (or dung). For regression it was assumed that the standard deviation of each value of x was proportional to that x (Snedecor and Cochran 1967 p169). The Poisson transformation was investigated as there is commonly a curvilinear relationship between frequency of occurrence data and density indices (Caughley 1980). Batcheler (1973) reported significant correlations between density of possum dung and an index of dung density calculated from the first term of a Poisson series.

The frequency distributions of rooting per plot (length of rooting/10m) and the decay of dung pellets were compared to a negative exponential function fitted by least squares regression after transformation to natural logarithms.

$$y = a\, e^{-bx}$$

For the rooting data, x was the midpoint of each rooting class. For the decay of dung, y was the arcsine of the percentage of dung pellets remaining and included the initial data (0 months, 100% dung present). The coefficient a, is an estimate of the starting point (100% dung pellets) when x=0.

The decay of dung pellets was also compared to a modified exponential function, fitted by least squares regression after rearranging the equation and transformation to common logarithms.

$$y = 100 - a\, x^{b}$$

where y was the percentage of dung pellets remaining, but did not include the initial data and x was the number of months. This equation has the advantage over the simple exponential equation that it solves to the starting point (100% dung pellets) for x=0.

The frequency distributions of numbers of dung pellets per plot for each month and the number of pigs per 0.25km^2 were compared to Poisson distributions by Chi-square goodness-of-fit tests (Snedecor and Cochran 1967).

The corrected number of dung pellets per site (CD) (corrected for decay) was estimated from;

$$CD = (M \ln(f_1/f_2)) \;/\; (1 - (f_2/f_1))$$

where M was the number of dung pellets counted, f_1 the number of reference dung pellets at the start of a month and f_2 the number of reference dung pellets still present at the end of the month (Hill 1981).

The relationship between the mean and variance (Taylor 1961) of the corrected number of dung pellets/site/month was determined by least squares regression. Data were transformed to common logarithms for regression.

Plots were classified as being on or away from trails. Feral pigs move around their home range along such trails. The effects of trails and months on the proportion of plots with dung and on the average number of dung pellets on plots where dung occurred were both tested by two-way fixed factor analysis of variance (Snedecor and Cochran 1967). There was no replication of each trail x month combination so the residual mean square in each analysis was estimated from the interaction mean square.

The difference between successive months in the extent or frequency of rooting was calculated. The relationships between the change in the extent of rooting between months (length of rooting/1000m) and the corrected number of dung pellets (averaged over sites) and average temperature (^{0}C) and rainfall (mm) for the month were determined by regression analysis. Data on temperature and rainfall were combined into a single index of climatic suitability for plant growth. The index was the product of average temperature and rainfall. A high value of the product corresponds to maximum plant growth and a low value to little or no plant growth. The analysis assumed a linear relationship between plant growth and the index. This was assumed to be realistic for the restricted range of temperature and rainfalls that occurred in Namadgi National Park. Initially data were plotted and non-linear relationships transformed. Data on the percentage of plots with pig rooting were similarly analysed.

3.2.2. Results

Rooting

The average difference in rooting at each site between each repeated measurement was 0.00m/1000m (+/- 0.57 SE). This was not significantly different from zero (t=0.00, df=6, P>0.05). The frequency distribution of the extent of rooting per plot (length of rooting/10m) was of negative exponential form (Table 3.2). The most frequent length of rooting was zero. A negative exponential equation fitted to each month's data gave highly significant (P<0.01) correlations (Table 3.3).

The percentage of plots with rooting varied among months from 18.1% to 28.1%. The ratio of the standard error to the mean percentage ranged from 6.0% to 8.2%.

The percentage of the ground rooted by feral pigs differed between sites and months (Table 3.4) and was highest at the Pine Forest (PI), lowest at Brandy Flat (BF) and highest in October and lowest in June 1985 and January 1986. The extent of rooting increased over each winter (June, July, August) and early spring (September, October) and then decreased over late spring (November) and early summer (December). The actual extent of rooting (length of rooting/1000m) of plots was significantly (P<0.05) related in 17/18 months to an index of rooting extent calculated from the percentage of plots with rooting using the first term of a Poisson series (Table 3.5), and was significantly related in each month to the percentage of plots with rooting (Table 3.6).

Dung

In the repeated counts of pig dung there was no significant difference (X^2= 1.744, df=2, P>0.05) in the number of dung pellets per plot from June to July 1985. The frequency distribution of dung per plot was highly skewed with the most common number being 0 then 1, then 2 and so on. The frequency distribution was significantly different from a Poisson distribution in each month (Table 3.7).

The percentage of plots with dung pellets varied among months from 1.0% to 8.3%. The ratio of the standard error to the mean percentage ranged from 12.5% to 38.0%. The average number of dung pellets per plot varied among months from 0.02 to 0.31 and the ratio of the standard error to the mean ranged over the study from 14.3% to 50.0%.

The monthly number of dung pellets per site was significantly related in each month to an index of dung abundance calculated from the first term of a Poisson series (Table 3.8) except in October and December 1986. Similarly the number of dung pellets was significantly related to the percentage of plots with dung (Table 3.9) except for December 1985, October 1986 and December 1986.

The number of dung pellets remaining each month declined (Table 3.10) exponentially in each month (Tables 3.11, 3.12). The estimated intercept of the exponential function (a) varied from 31.38 to 96.88 (Table 3.11) compared to the expected value of 100.0. The modified exponential regression had a higher correlation coefficient than the simple exponential regression in each of 11 months, and the reverse occurred in each of 6 months. The numbers of dung pellets at each site per month corrected for exponential decay are shown in Table 3.13.

The arcsine of the percentage of dung remaining in the first month after establishment was not significantly correlated ($r=-0.311$, $df=14$, $P>0.05$) with rainfall (mm) over the month, average monthly temperature (°C) ($r=-0.468$, $df=15$, $P>0.05$) or average maximum temperature ($r=-0.427$, $df=15$, $P>0.05$) but was significantly correlated with average minimum temperature ($r=-0.550$, $df=15$, $P<0.05$).

The regression between the logarithmically transformed means and variances of the corrected dung counts was significant ($r=0.948$, $df=15$, $P<0.01$). The slope of the regression line was 2.1.

The average proportion of plots with pig dung was significantly higher ($F=17.50$, $df=1,16$, $P<0.01$) on plots with animal trails (0.052) than on plots with no trails (0.033). The proportion was also significantly different among months ($F=6.50$, $df=16,16$, $P<0.01$) being highest (0.191) in June 1985 and lowest (0.022) in December 1986. The average number of dung pellets on plots where dung occurred was significantly higher ($F=6.34$, $df=1,16$, $P<0.05$) on plots with animal trails (0.173) than on plots with no animal trails (0.105). The average number of dung pellets was also significantly different among months ($F=3.50$, $df=16.16$, $P<0.01$) being highest (0.857) in June 1985 and lowest (0.047) in December 1985.

Pigs

The observed population density of feral pigs in the study area was 0.93/km^2 (+/- 0.21 SE). Of pigs observed (122) in the seven sites, 63 (51.6%) were adults, 18 (14.8%) subadults and 41 (33.6%) juveniles. Of pigs that could be sexed, 20 were male and 27 female. These data may have included some recounting of pigs.

The frequency distribution of pigs/0.25km^2 was highly skewed with the most frequent number being 0 (499 subsites). The rest of the distribution was (number of subsites given in parentheses) 1 pig (8), 2 pigs (4), 3 pigs (4), 4 pigs (2), 5 pigs (2), 6 pigs (1), 7 pigs (1), 8 pigs (1), 9 pigs (2), and 19 pigs in 1 subsite. The frequency distribution was significantly different from a Poisson series ($X^2=103.0$, df=1, $P<0.01$).

Relationships between rooting and dung pellets

When calculated between months there was no significant correlation between the percentage area of each site rooted and the average number of dung per site ($r=-0.076$, df=14, $P>0.05$), or the corrected average number of dung pellets ($r=0.015$, df=14, $P>0.05$). When calculated between sites there was no significant correlation between the percentage of a site rooted by pigs and the average number of dung pellets ($r=0.101$, df=5, $P>0.05$) or the corrected average number of dung pellets ($r=0.100$, df=5, $P>0.05$).

The monthly change in the extent of rooting over all sites was calculated between successive months from data in Table 3.4. The regressions were significant between the monthly change in the extent of rooting (length of rooting/1000m) and corrected dung counts, and the product of temperature and rainfall. The linear regression between the change in extent of rooting and corrected dung counts had a correlation of 0.626 (df=13, $P<0.05$). When the corrected dung counts were transformed to their square root, the correlation was 0.649 (df=13, $P<0.01$). The highest correlation (0.653, df=13, $P<0.01$) was with the common logarithms of the corrected dung counts (CD) after adding one.

Change in rooting = $-1.235 + 1.181 \log(CD + 1)$

The linear regression of the change in the extent of rooting and the product of average temperature and rainfall for the month was significant ($r=-0.649$, df=13, $P<0.01$).

The regression between the monthly change in the percentage of plots with rooting and corrected dung counts was highly significant ($r=0.675$, df=14, $P<0.01$). The regression using the square root of the corrected dung counts was significant ($r=0.703$, df=14, $P<0.01$), as was the regression with the corrected dung counts transformed to common logarithms after adding one ($r=0.716$, df=14, $P<0.01$).

Change in plots with rooting = $-6.440 + 6.206 \log(CD + 1)$

The regression of the change in the number of plots with rooting and the product of average temperature and rainfall was significant ($r=-0.643$, $df=14$, $P<0.01$).

Relationships between rooting and number of pigs

Between months the percentage of ground rooted by pigs was not significantly correlated with observed population density ($r=-0.158$, $df=16$, $P>0.05$). Between sites the percentage of each site rooted by pigs was not significantly correlated with observed population density when this was averaged over months ($r=0.131$, $df=5$, $P>0.05$).

Relationships between dung pellets and number of pigs

There were no significant correlations between the number of dung pellets recorded per month and the observed population density of feral pigs at the end of a month ($r=-0.029$, $df=15$), population density at the start of a month ($r=0.390$, $df=15$) or population density averaged over the month ($r=0.247$, $df=15$).

There were no significant correlations between corrected dung counts and observed population density of pigs at the end of a month ($r=-0.041$, $df=15$), at the start of a month ($r=0.373$, $df=15$) or when pig density was averaged over the month ($r=0.151$, $df=15$).

The relationships were examined in more detail with data from Shanahans Falls Creek (SH) where pigs could be seen more easily and were not disturbed except by me. There was no significant correlation ($r=0.099$, $df=15$, $P>0.05$) between the number of dung pellets per month and observed population density of pigs at the end of the month. The correlation was significant with population density at the start of the month ($r=0.516$, $df=15$, $P<0.05$), but not significant with population density averaged over the month ($r=0.392$, $df=15$, $P>0.05$).

When juvenile pigs were excluded from the analysis, as their dung was never seen, and observed population densities at the start and end of each month were averaged, then there was a significant correlation between dung counted and average observed density of adult and subadult pigs ($r=0.512$, $df=15$, $P<0.05$). The regression equation was;

$$\text{Dung}/100 \text{ plots} = 9.6 + 9.4 \text{ (Pigs} > 6 \text{ mths)}$$

There was a significant correlation between corrected dung counts and average observed population density ($r=0.490$, $df=15$, $P<0.05$) of adult and subadult pigs. The regression equation was;

Corrected Dung/100 plots = 13.4 + 9.3 (Pigs >6 mths)

3.2.3. Discussion

The results show that repeatable measures of rooting and counts of dung were obtained by the methods used. Rooting was a more accurate indicator of past feral pig presence than dung counts, as rooting occurred when no dung occurred, and dung counts were more accurate than one or two counts of pigs per month.

For the same number of plots measured, the percentage of plots with rooting was a more precise measure than the percentage of plots with dung as the rooting estimate had a lower coefficient of variation. This was due to the higher average value of the variable measured. Such a result is expected with binomial data (Snedecor and Cochran 1967), where precision is highest when the frequency of occurrence is between 20% and 80% (Batcheler 1973).

The extent of rooting in this study varied between months from 2.2%-4.4%. This extent was similar to that reported for a Polish forest (1%-10%) by Jezierski and Myrcha (1975) and an Hawaiian forest (6%-11%) by Ralph and Maxwell (1984) but lower than that reported for parts of Great Smoky Mountains National Park (0.3%-80%) by Singer (1981) or an Hawaiian forest (14%-38%) reported by Cooray and Mueller-Dombois (1981).

The negative exponential frequency distribution of rooting per plot probably reflects different searching patterns by feral pigs. The large number of short lengths of rooting may have been sites of searching for food, and the longer lengths of rooting were sites where food was found. The negative exponential functions for the frequency distribution of rooting per plot had very high correlations but appear to have poor predictive value. Each equation underestimated the frequency of occurrence of plots with no rooting.

The lack of correlation between the extent of rooting and dung counts or pig counts supports data in Section 3.1. The assumption of Belden and Pelton (1975), Conley (1977) and Giles (1980), that the extent of rooting is positively correlated with population density, is not correct. In the present study the extent of rooting was not correlated with pig counts but in the previous study (Section 3.1) the frequency of rooting on plots was correlated with the frequency of pig dung on plots. Similar comparisons between the abundance of wild boar and the extent of crop damage in Poland have shown statistically non-significant relationships in two studies (Mackin 1970, Andrzejewski and Jezierski 1978), but a significant correlation in another (Gorynska 1981).

The lack of correlation between the extent of rooting and the abundance of pig dung suggests that feral pigs do not, in the process of rooting, cover many dung pellets. If they did then a significant negative correlation would have occurred. The lack of correlation may result from a lack of time scale on the measure of rooting compared to that of dung which accumulated over a defined time period, or simply reflect the suggestion of Cherrett et al. (1971) and Norton (1976) that the extent of damage by a pest is determined by many variables, as noted in Chapter 1.

In contrast the monthly change in the extent or frequency of rooting was highly positively correlated with the abundance of pig dung in a curvilinear manner. The results support the third hypothesis described at the start of this Section. The curvilinear relationship may be associated with behavioural changes in feeding, and hence rooting, at varying pig densities, or "nested" rooting in which pigs root over an area before it has revegetated, and such rooting varied with pig density. This is a more sensitive analysis than the relationship between the extent or frequency of rooting and the abundance of pig dung, as both variables (monthly changes) were calculated over the same time period. In contrast there were significant negative correlations between the monthly changes in the extent or frequency of rooting and the climatic index (the product of rainfall and average temperature). The results show a need for further research to clarify the relative importance of pig abundance and climate in determining trends in the extent or frequency of pig rooting. In the present study the effects were confounded, as a summer decrease in dung counts corresponded to a seasonal increase in the climatic index because of higher temperatures.

The observed population density (0.9/km^2) of feral pigs in Namadgi National Park (NNP) was lower than that reported for mountain forests (2-9/km^2) in Tennessee and for forests (19-79/km^2) in Hawaii (Singer 1981). The observed density was similar to that reported (1.0/km^2) in the earlier study (Section 3.1). The coefficient of variation of the population density was 23%, compared to 50% in the earlier study. The departures of the frequency distributions of pig counts and dung counts from Poisson distributions were expected as the distribution pattern of feral pigs is probably more clumped then the random distribution assumed by the Poisson distribution.

The counts of dung in the present study were on average much lower than those reported in Hawaiian forests. Average dung pellets/20m^2 plot were 0.13 in NNP and 0.47-1.65 (Ralph and Maxwell 1984) and 83.3-150 in Hawaii (Cooray and Mueller-Dombois 1981). The latter counts have been corrected to the same plot size as used in in the present study. The precision of the NNP dung counts was variable with the ratio of the standard error over the average varying from 14%-50%, compared to the results of Ralph and Maxwell (1984) where the ratio varied from 9%-26% between sites. The percentage of plots with pig dung in NNP ranged from 1.0%-8.3% in NNP compared to 4.0%-17.5% in Hawaii (Cooray and Mueller-Dombois (1981).

The regression between the means and variances of corrected number of dung pellets per month had a slope of 2.1. This is similar to the slopes (1.0-3.0) of regressions for many plant and animal populations reported by Taylor (1961), Anderson et al. (1982) and Taylor et al. (1983).

The number of dung counted declined over summer even when corrected for decay. This suggests that pig density declined seasonally. A possible explanation is that the pigs moved to higher altitude in summer as was suggested by Boreham (1981) and reported for feral pigs in the USA (Belden and Pelton 1975, Singer et al. 1981).

Comparison of the population density and dung counts in NNP strongly suggests that the pig counts were negatively biased. The average count of dung was $0.13/20m^2$/month which is equivalent to 217 pellets/km^2/day. As the observed population density was $0.93/km^2$ then those pigs must produce 233 pellets/pig/day. This is considered unrealistically high, though no estimates of the defecation rates of feral pigs have been published. The significant regressions between dung counts and counts of pigs indicate that even when no feral pigs were seen then dung pellets were still counted.

The rates of decay of dung pellets in NNP were lower than those reported for Hawaii (Ralph and Maxwell 1984). This may have been associated with lower temperatures and rainfall in NNP. The modified exponential function had a better fit to the decay data more frequently than the simple exponential function.

The significant regressions between the extent of rooting and percentage of plots with rooting, and the abundance of dung and the percentage of plots with dung, suggest that detailed measurement or counting of either variable may not be necessary. Only the percentage of plots with rooting or with dung need be recorded. Such a recording system reduced field time from 4hrs per site to 1.5hrs per site when used in July 1986. The varying slopes of the regressions indicate each may be specific for a time period. Some of the variation may have been associated with seasonal changes in diet and defecation rates such as those reported for coyotes (Canis latrans) by Andelt and Andelt (1984), and elk (Cervus canadensis) by Collins and Urness (1979). Other sources of variation could be changes in age structure, which in mule deer (Odocoileus hemionus) can influence defecation rates (Smith 1964).

The experimental analyses of survey methods described in this and the previous Chapter have shown that some methods have potential for use in evaluation of control of feral pigs. In open habitats feral pigs can be surveyed from a helicopter and the Fourier series estimator appears to be the most accurate for estimating density. In forest habitats the extent of rooting and the abundance of dung can be measured on marked plots. In the next Chapter the aerial survey method is applied to the evaluation of the effectiveness of shooting from a helicopter. In Chapter 5 the methods for measuring rooting and counting dung are applied to the evaluation of the short and long-term effects of poisoning with warfarin. In both Chapters the development and evaluation of models of the control processes are also described.

Table 3-2: The frequency distributions of length of rooting per 10m plot in each month.The midpoint of each rooting class is shown (e.g. 0.5=0.01-1.00m). The total number of plots was 600 in May 1985 and 700 in all other months. The mean data were averaged over months from June 1985 to December 1986.

MONTH & YEAR	LENGTH OF ROOTING (m) PER 10m PLOT										
	0	0.5	1.5	2.5	3.5	4.5	5.5	6.5	7.5	8.5	9.5
1985											
May	480	75	21	12	4	5	2	1	0	0	0
June	566	93	16	10	5	6	2	0	1	1	0
July	563	88	17	16	3	7	3	2	1	0	0
Aug.	551	95	22	13	5	7	3	2	1	1	0
Sept.	522	123	16	17	6	6	4	4	1	1	0
Oct.	514	111	34	20	5	5	5	3	2	1	0
Nov.	549	95	30	10	6	4	5	0	0	1	0
Dec.	566	82	25	11	5	3	6	1	1	0	0
1986											
Jan.	573	83	19	12	3	3	5	2	0	0	0
Feb.	567	81	23	12	6	4	4	2	1	0	0
March	563	80	23	21	2	4	5	1	1	0	0
April	545	94	28	14	8	4	3	2	1	1	0
May	533	106	28	15	5	6	2	2	2	1	0
June	522	112	37	11	6	4	3	4	1	0	0
Sept.	504	125	34	12	9	9	2	2	2	1	0
Oct.	508	103	45	13	8	11	3	2	4	1	2
Nov.	519	105	37	13	11	3	5	2	2	3	0
Dec.	539	101	22	15	12	3	5	0	3	0	0
Mean	541	99	27	14	6	5	4	2	1	1	0

Table 3-3: The intercepts, slopes and correlation coefficients of a negative exponential equation fitted to the frequency distribution of rooting per plot for each month (data in Table 3.2). Degrees of freedom vary between months as a zero occurrence could not be included in the regression ($\ln 0 = -\infty$). All correlations were significant at the 0.01 level.

MONTH & YEAR	INTERCEPT (a)	SLOPE (b)	CORRELATION COEFFICIENT	DF
1985				
May	142.58	-0.81	-0.947	6
June	105.57	-0.64	-0.915	7
July	125.25	-0.69	-0.914	7
August	120.78	-0.64	-0.936	8
September	124.59	-0.62	-0.927	8
October	136.55	-0.62	-0.939	8
November	123.52	-0.65	-0.914	6
December	133.74	-0.72	-0.927	7
1986				
January	126.10	-0.73	-0.885	6
February	133.11	-0.70	-0.935	7
March	133.41	-0.73	-0.911	7
April	130.89	-0.66	-0.949	8
May	123.97	-0.64	-0.931	8
June	148.08	-0.70	-0.932	7
September	146.35	-0.64	-0.945	8
October	119.32	-0.54	-0.915	9
November	121.03	-0.57	-0.903	8
December	131.72	-0.62	-0.888	6
Mean	152.66	-0.70	-0.963	9

Table 3-4: The percentage of ground rooted by pigs at each site in each month of study. Note that the percentage refers to the extent of existing rooting at the time of measurement not the increment since the previous measurement. One site (BF) was not sampled in May 1985. The names of sites are abbreviated; HC Honeysuckle Creek, NS Nursery Swamp, PI Pine Forest, SH Shanahans Falls Creek, BO Boboyan, CG Cotter Gap, BF Brandy Flat.

	SITES							
MONTH & YEAR	HC	NS	PI	SH	BO	CG	BF	MEAN
1985								
May	3.52	1.07	5.30	1.94	1.44	1.12	–	2.40
June	4.19	0.87	6.08	2.40	0.81	0.43	0.75	2.22
July	4.69	0.89	6.75	3.34	0.99	0.52	0.14	2.47
August	4.92	1.17	7.91	3.32	1.11	1.46	0.03	2.84
September	5.83	1.19	9.83	3.77	1.26	1.08	0.09	3.29
October	6.93	1.86	10.48	3.60	1.11	1.13	0.14	3.60
November	5.79	1.42	7.08	1.67	1.01	1.01	0.13	2.59
December	6.70	1.43	6.78	0.87	0.87	0.77	0.08	2.50
1986								
January	5.35	1.50	5.90	0.58	1.13	1.19	0.02	2.23
February	6.53	1.23	6.71	0.82	1.40	1.19	0.00	2.55
March	6.54	1.31	6.45	1.50	1.93	1.43	0.01	2.74
April	7.11	1.36	7.99	0.81	1.31	2.15	0.09	2.97
May	7.58	1.57	7.18	1.75	0.83	1.54	0.02	2.92
June	7.73	1.70	5.89	2.03	1.27	2.29	0.45	3.05
September	9.04	1.78	4.79	6.51	0.77	2.28	0.08	3.61
October	10.22	1.53	6.54	7.71	0.75	4.20	0.05	4.43
November	8.76	1.27	5.70	5.84	0.69	3.64	0.16	3.72
December	7.74	0.88	4.26	5.11	0.57	3.10	0.08	3.10
Mean	6.61	1.33	6.75	2.97	1.07	1.69	0.14	

Table 3-5: The slopes, associated standard errors (SE) and Student's t statistics of regressions forced through the origin between the percentage of ground rooted by pigs at each site and an index of rooting extent. The index was calculated from the first term of a Poisson series using the percentage of plots with rooting at each site. One site (BF) was not measured in May 1985. *P<0.05, **P<0.01.

MONTH & YEAR	SLOPE	SE	t	DF	SIGNIF.
1985					
May	9.81	1.70	5.77	5	**
June	8.85	2.38	3.72	6	**
July	8.61	1.89	4.56	6	**
August	8.83	1.73	5.10	6	**
September	8.13	1.50	5.42	6	**
October	7.98	1.73	4.61	6	**
November	8.03	1.46	5.50	6	**
December	8.22	1.89	4.35	6	**
1986					
January	8.12	1.65	4.92	6	**
February	9.88	1.60	6.18	6	**
March	9.52	2.18	4.37	6	**
April	9.08	2.22	4.09	6	**
May	8.31	2.55	3.26	6	*
June	9.24	1.85	5.00	6	**
September	8.44	1.78	4.74	6	**
October	10.90	2.72	4.01	6	**
November	10.07	2.12	4.75	6	**
December	8.64	1.82	4.75	6	**
Mean	9.16	1.82	5.03	6	**

Table 3-6: The slopes, associated standard errors (SE) and Student's t statistics of regressions forced through the origin between the percentage of ground rooted by pigs at each site and the percentage of plots with rooting at each site. *P<0.05, **P<0.01.

MONTH & YEAR	SLOPE	SE	t	DF	SIGNIF.
1985					
May	0.11	0.02	5.50	5	**
June	0.10	0.03	3.33	6	*
July	0.10	0.02	5.00	6	**
August	0.10	0.02	5.00	6	**
September	0.10	0.02	5.00	6	**
October	0.10	0.02	5.00	6	**
November	0.09	0.02	4.50	6	**
December	0.10	0.03	3.33	6	*
1986					
January	0.09	0.02	4.50	6	**
February	0.12	0.02	6.00	5	**
March	0.11	0.03	3.67	6	*
April	0.11	0.03	3.67	6	*
May	0.10	0.03	3.33	6	*
June	0.11	0.02	5.50	6	**
September	0.10	0.02	5.50	6	**
October	0.13	0.03	4.33	6	**
November	0.12	0.03	4.00	6	**
December	0.12	0.03	4.00	6	**
Mean	0.11	0.02	5.50	6	**

Table 3-7: The frequency distributions of number of dung pellets per plot for each month of study. The results of the Chi-square goodness-of-fit test to a Poisson distribution and degrees of freedom are also shown. All frequency distributions were significantly different (P<0.01) from a Poisson distribution. The number of plots measured in June 1985 was 600 and in in all other months was 700.

MONTH	NUMBER OF DUNG PELLETS PER PLOT													
& YEAR	0	1	2	3	4	5	6	7	8	9	10	>10	X^2	DF
1985														
June	557	17	8	3	2	2	3	1	1	1	2	3	249.00	2
July	659	14	13	3	3	1	2	0	2	0	0	3	118.40	1
Aug.	642	16	12	10	8	1	3	1	3	3	1	0	536.64	2
Sept.	652	16	9	4	6	7	3	1	1	1	0	0	127.57	1
Oct.	678	7	2	5	1	1	2	0	1	1	1	1	89.51	1
Nov.	686	4	6	1	1	1	0	0	0	1	0	0	115.02	1
Dec.	690	7	2	0	1	0	0	0	0	0	0	0	123.48	1
1986														
Jan.	681	9	4	2	2	1	0	0	0	1	0	0	80.55	1
Feb.	687	5	3	2	1	2	0	0	0	0	0	0	101.15	1
March	668	15	8	6	0	1	1	0	1	0	0	0	86.55	1
April	661	20	8	3	1	1	0	3	0	0	0	3	84.16	1
May	673	12	8	3	1	1	1	0	0	0	0	1	93.20	1
June	680	8	3	2	2	1	0	2	1	1	0	0	77.22	1
July	691	1	3	1	0	1	0	1	0	0	1	1	69.32	1
Oct.	678	11	5	1	1	0	1	0	0	0	1	2	74.96	1
Nov.	688	2	5	3	1	0	0	0	1	0	0	0	144.10	1
Dec.	693	2	1	3	0	1	0	0	0	0	0	0	129.10	1

Table 3-8: The slopes, associated standard errors (SE) and Student's t statistics of regressions forced through the origin between the number of dung pellets at each site and an index of dung abundance. The index was calculated from the first term of a Poisson series using the percentage of plots with dung at each site. * P<0.05, ** P<0.01, NS not significant.

MONTH & YEAR	SLOPE	SE	t	DF	SIGNIF.
1985					
June	268.9	58.1	4.63	4	**
July	320.7	47.3	6.78	6	**
August	263.1	33.2	7.93	5	**
September	295.8	80.1	3.69	5	*
October	366.9	132.2	2.78	4	*
November	281.9	65.6	4.30	5	**
December	130.0	20.0	6.50	4	**
1986					
January	197.2	36.6	5.39	5	**
February	276.7	63.6	4.35	4	*
March	186.3	25.9	7.19	5	**
April	183.8	51.3	3.58	5	*
May	239.7	41.1	5.83	4	**
June	351.1	46.9	7.49	4	**
July	420.8	115.3	3.65	3	*
October	354.3	161.8	2.19	4	NS
November	290.0	55.7	5.21	4	**
December	254.2	20.8	12.22	1	NS
Mean	253.9	26.8	9.47	6	**

Table 3-9: The slopes, associated standard errors (SE) and Student's t statistics of regressions forced through the origin between the number of dung pellets at each site and the percentage of plots with dung at each site. * P<0.05,** P<0.01, NS not significant.

MONTH & YEAR	SLOPE	SE	t	DF	SIGNIF.
1985					
June	2.84	0.72	3.94	4	*
July	3.25	0.47	6.92	6	**
August	2.75	0.39	7.05	5	**
September	3.07	0.80	3.84	5	*
October	3.67	1.32	2.78	4	*
November	2.82	0.66	4.27	5	**
December	1.30	0.20	2.60	4	NS
1986					
January	1.97	0.37	5.32	5	**
February	2.77	0.64	4.33	4	*
March	1.89	0.27	7.00	5	**
April	1.91	0.59	3.24	5	*
May	2.43	0.41	5.93	4	**
June	3.51	0.47	7.47	4	**
July	4.21	1.15	3.66	3	*
October	3.54	1.62	2.19	4	NS
November	2.90	0.56	5.18	4	**
December	2.54	0.21	12.10	1	NS
Mean	2.81	0.24	11.71	6	**

Table 3-10: The percentage of reference dung pellets remaining over the months of the study. Reference dung pellets were not established in May 1985, or August 1986 or checked in August 1986. Sample sizes are also shown.

MONTH DUNG CHECKED	MONTH DUNG ESTABLISHED 1985									
	M	A	J	J	A	S	O	N	D	J
Sample Size	41	17	82	50	83	59	30	18	14	46
1985										
April	85.4									
May	82.9	94.1								
June	78.1	88.2								
July	70.7	88.2	97.6							
August	65.9	88.2	86.6	90.0						
Sept.	58.5	82.4	75.6	74.0	97.6					
Oct.	51.2	82.4	31.7	64.0	77.1	71.2				
Nov.	43.9	41.2	23.2	36.0	50.6	55.9	33.3			
Dec.	41.5	35.3	14.6	28.0	31.3	30.5	10.0	77.8		
1986										
Jan.	34.2	23.5	4.9	16.0	8.4	15.3	6.7	5.6	35.7	
Feb.	31.7	23.5	3.7	16.0	8.4	13.6	6.7	5.6	7.1	82.6
March	19.5	23.5	2.4	10.0	8.4	10.2	6.7	5.6	7.1	69.6
April	12.2	23.5	2.4	8.0	8.4	8.5	6.7	5.6	7.1	63.0
May	9.8	17.6	2.4	6.0	8.4	6.8	6.7	5.6	7.1	63.0
June	7.3	17.6	2.4	6.0	7.2	6.8	6.7	5.6	7.1	50.0
July	2.4	17.6	0.0	4.0	7.2	6.8	3.3	5.6	7.1	47.8
Sept.	2.4	17.6	0.0	2.0	7.2	6.8	3.3	5.6	0.0	34.8
Oct.	2.4	17.6	0.0	2.0	6.0	3.4	0.0	5.6	0.0	23.9
Nov.	2.4	17.6	0.0	2.0	6.0	3.4	0.0	5.6	0.0	15.2
Dec.	0.0	17.6	0.0	0.0	3.6	3.4	0.0	5.6	0.0	10.9

	1986								
	F	M	A	M	J	J	S	O	N
Sample Size	27	77	80	36	45	20	46	99	26
March	59.3								
April	44.4	79.2							
May	37.0	59.7	77.5						
June	29.6	50.7	68.8	88.9					
July	29.6	41.6	51.3	55.6	88.9				
Sept.	25.9	24.7	35.0	36.1	53.3	15.0			
Oct.	18.5	19.5	31.3	27.8	35.6	10.0	89.1		
Nov.	3.7	19.5	26.3	13.9	24.4	10.0	50.0	38.4	
Dec.	0.0	13.0	8.8	2.8	17.8	0.0	23.9	28.3	65.4

Table 3-11: The intercepts, slopes and correlation coefficients of negative exponential regressions between the arcsine of the percentage of dung pellets remaining and the months since reference dung pellets were established. * $P<0.05$, ** $P<0.01$, NS not significant.

MONTH & YEAR	INTERCEPT (a)	SLOPE (b)	CORRELATION COEFFICIENT	DF	SIGNIF.
1985					
March	96.88	−0.12	−0.974	18	**
April	77.85	−0.07	−0.919	18	**
June	92.78	−0.23	−0.970	11	**
July	74.83	−0.16	−0.985	14	**
August	57.14	−0.12	−0.864	14	**
September	52.31	−0.12	−0.919	13	**
October	36.86	−0.14	−0.779	9	**
November	31.38	−0.09	−0.602	11	*
December	42.99	−0.20	−0.743	6	*
1986					
January	80.74	−0.12	−0.977	9	**
February	68.44	−0.16	−0.899	7	**
March	74.77	−0.15	−0.981	7	**
April	80.97	−0.17	−0.962	6	**
May	94.74	−0.27	−0.956	5	**
June	88.57	−0.22	−0.999	4	**
July	73.34	−0.41	−0.925	2	NS
September	95.43	−0.38	−0.992	2	**
October	80.39	−0.52	−0.935	1	NS

Table 3-12: The intercepts, slopes and correlation coefficients of modified exponential regressions between the percentage of dung pellets remaining and the months since reference dung were established. *P<0.05, **P<0.01, NS not significant.

MONTH & YEAR	INTERCEPT (a)	SLOPE (b)	CORRELATION COEFFICIENT	DF	SIGNIF.
1985					
March	11.15	0.76	0.988	17	**
April	4.74	1.06	0.936	17	**
June	4.71	1.43	0.935	10	**
July	15.43	0.78	0.940	13	**
August	8.62	1.06	0.849	13	**
September	36.71	0.43	0.917	12	**
October	74.44	0.13	0.836	8	**
November	44.56	0.39	0.695	10	*
December	72.97	0.16	0.783	5	*
1986					
January	16.98	0.69	0.985	8	**
February	41.90	0.36	0.978	6	**
March	22.54	0.68	0.987	6	**
April	21.28	0.73	0.989	5	**
May	14.64	1.16	0.960	4	**
June	14.21	1.23	0.954	3	*
July	85.48	0.04	0.929	1	NS
September	11.83	1.80	0.985	1	NS

Table 3-13: The corrected number of dung pellets at each site in each month. Counts of dung were corrected for decay using the equation of Hill (1981). Symbols for sites are listed in Table 3.4.

MONTH & YEAR	HC	NS	PI	SITE SH	BO	CG	BF	MEAN
1985								
June	18.2	4.1	15.2	145.7	0.0	3.0	-	31.0
July	27.4	7.4	7.4	54.8	7.4	3.2	37.9	20.8
Aug.	9.1	4.1	23.3	84.0	0.0	5.1	69.8	27.9
Sept.	11.8	0.0	51.9	64.9	15.3	1.2	28.3	24.8
Oct.	37.9	1.7	8.2	29.7	0.0	0.0	67.6	20.7
Nov.	15.8	0.0	3.4	3.4	5.7	5.7	7.9	6.0
Dec.	9.6	0.0	1.6	0.0	1.6	1.6	9.6	3.4
1986								
Jan.	1.1	1.1	17.6	22.0	5.5	0.0	2.2	7.1
Feb.	6.4	0.0	7.7	12.8	2.6	0.0	10.3	5.7
March	22.4	0.0	13.5	31.4	1.1	2.2	5.6	10.9
April	7.9	0.0	14.7	103.1	2.3	1.1	6.8	19.4
May	11.7	0.0	12.7	29.7	3.2	0.0	10.6	9.7
June	14.8	10.6	0.0	12.7	0.0	5.3	24.4	9.7
July	21.2	0.0	0.0	18.0	0.0	5.3	6.4	7.3
Oct.	14.8	1.1	18.0	5.3	0.0	0.0	62.5	14.5
Nov.	4.7	0.0	12.4	15.5	0.0	3.1	15.5	7.3
Dec.	0.0	0.0	0.0	8.6	0.0	0.0	13.5	3.2
Mean	13.8	1.8	12.2	37.7	2.6	2.2	23.7	13.3

Chapter 4

Shooting from a helicopter

To date there has been only one assessment of the short-term effect of shooting from a helicopter on populations of feral pigs (Saunders and Bryant in press). An estimated 80% of feral pigs were killed by shooting. Hone (1983) and Bryant et al. (1984) reported levels of inputs and kill rates but did not estimate the percentage effects on populations and nor did O'Brien (1985). Given the potentially high costs involved in shooting from helicopters, the limited evaluation of this method is surprising. Hone and Bryant (1981) based a plan for eradication of feral pigs in a hypothetical outbreak of foot and mouth disease on the use of shooting from helicopters and trapping. The duration of shooting during such eradication was assumed to be $0.5h/km^2$, which was recognised as a planning guess in the absence of other information. Clearly, such an approach needs to be improved and the development and use of models of the shooting process could assist.

Predator-prey interactions have been modelled extensively with key components being the functional and numerical responses (Krebs 1985). The functional response describes the change in the number of prey eaten relative to changes in prey density and the duration of time available to search and eat. Control of vertebrate pests such as feral pigs by shooting is analogous to a predator searching for, chasing and eating prey. The prey are the feral pigs, the predator is the shooter and the time for searching, chasing and eating prey is the time for searching, chasing and shooting feral pigs.

The present study was designed to evaluate the effect of shooting from a helicopter on the population density of feral pigs and to develop and apply predator-prey models to this shooting. Such models could then be used to evaluate the economics of such control of feral pigs and make some comparisons between the results in different studies.

4.1. Modelling

The relationships between the number of feral pigs shot (n), initial density (N) and the duration of shooting (T) were examined using the number of pigs shot as the dependent variable. In theory both N and T could have linear or curvilinear relationships with the number shot and could act in an additive or multiplicative manner with respect to each other. This defines a total of eight possible models. Each must satisfy two initial assumptions; when no shooting is conducted (T=0) the number shot (n) must equal zero and when no pigs (N=0) occur in an area then the number shot must be zero. The assumptions need not apply simultaneously.

Additive models are of the general type;

$$n = a + f(T) + g(N)$$

where a is a constant estimated by regression, f(T) is some function for the effect of time and g(N) is some function for initial density. Such additive models do not satisfy the assumptions unless they are applied simultaneously and a=0. For example when T=0 the equation predicts a value for n>0 (= a + g(N)). Therefore additive models were not examined further.

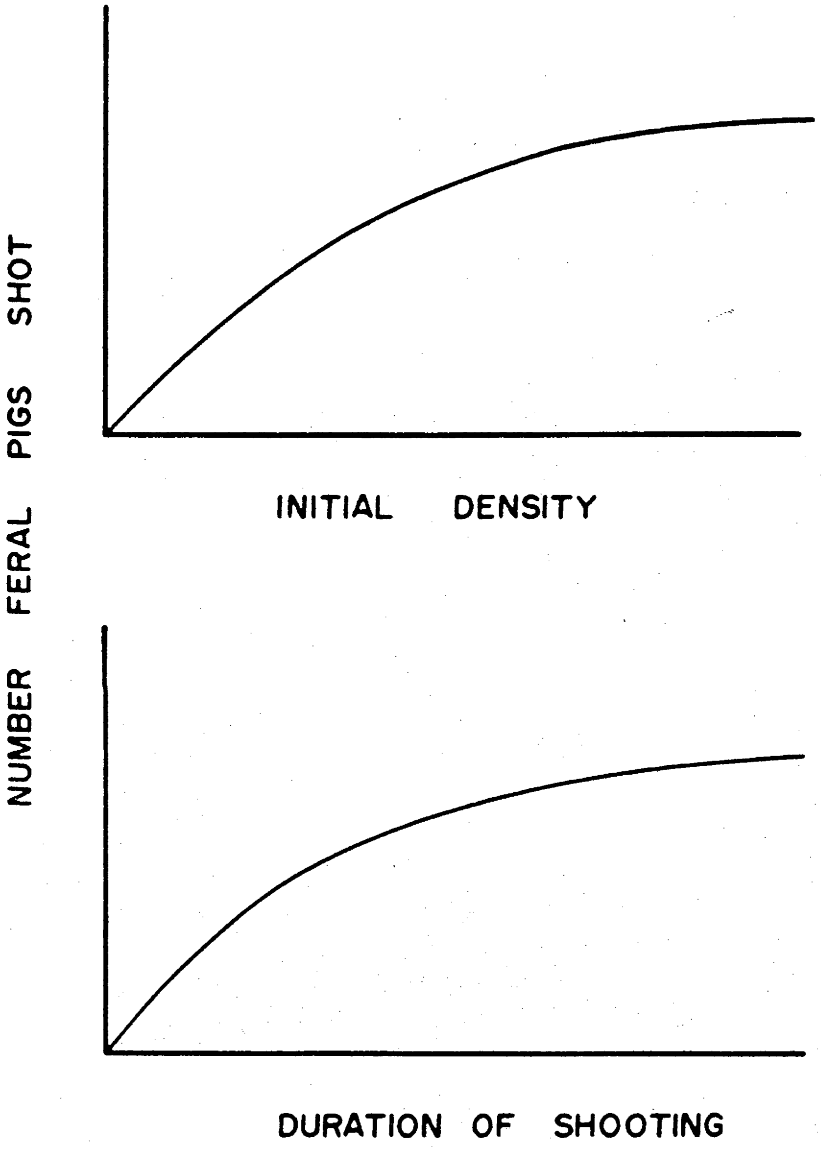
Multiplicative models are of the general type;

$$n = a\ f(T)\ g(N)$$

where terms are as above. The same assumptions apply as for additive models but now the models are robust to the non-simultaneous application of assumptions. The effects of time and initial density could act in a linear or curvilinear manner. It would be expected that with increasing duration of shooting the number of animals shot would increase but at a decreasing rate as density is lowered and animals become harder to find. Hence the effect of time should be curvilinear (Figure 4.1). As density increases the number shot should increase unless shooters get to shooting saturation where more animals are seen than can be shot and hence the effect of initial density should be curvilinear (Figure 4.1). If this true then the use of kill rate statistics (kills/h) as a linear index of pig density, as used by O'Brien (1985), may not be appropriate.

Components of predator-prey relationships have been modelled extensively starting with the linear functional response (Nicholson 1933), disc equation (Holling 1959), random predator equation (Rogers 1972) and the general model (Fujii et al. 1986).

Figure 4-1: Predicted relationships between initial density and the duration of shooting, and the number of feral pigs shot from a helicopter.



Each of the equations reported in those studies was an example of a multiplicative model. The early Nicholson model (and that of Lotka and Volterra) assumed linear effects of time and initial density, the disc equation assumed linear effects of time and the random predator equation assumed curvilinear effects of both variables. From the previous discussion, if shooting removes a substantial proportion of an animal population then the models assuming linear effects of time, such as the disc equation, are not appropriate.

The random predator equation (Rogers 1972) is;

$$n = N\ (1 - e^{-a(T - nh)})$$

where a is a measure of shooting efficiency and h is the handling time for each pig shot. The parameters were estimated by least squares regression where $y=\ln(1-(n/N))$, $x=n$, the slope of the regression was ah and the intercept was aT. As the total duration of the shooting (T) was known, the parameters a and h could be estimated.

The random predator equation describes predation when the prey population is depleted by the killing, compared to the disc and general equations which assume prey density is constant (Fujii et al. 1986, Juliano and Williams 1987). The random predator equation has the mathematical limitation that n, the number of prey killed, occurs on both sides of the equation. To avoid that problem I used a modified version of the equation.

A variation of Rogers' (1972) random predator equation was generated by assuming that the total time available for the shooting process (T) was reduced by shooting. If the time involved in shooting (chasing and shooting) was b (h/km^2) the model is;

$$n = N\ (1 - e^{-a(T - b)})$$

The model was fitted by linear least squares regression where $y=\ln(1-(n/N))$, $x=T$, the slope of the regression was a, and the intercept was ab. This model assumes curvilinear effects of T and N (if b was a function of N). The coefficient a was equivalent to the efficiency of the shooter. The model assumed that a threshold duration, b, occurs, before which no pigs were shot. Iterative least squares (Glass 1970) was not used to fit the regression as the value of N was estimated prior to calculating the regression equation.

If some feral pigs hide and hence can not be shot from a helicopter, as reported by Saunders and Bryant (in press), and if the proportion of pigs that can be shot is j, then Nj is the total number of pigs that can be shot. Hughes (1979) described a similar approach to analyse the effect of cryptic prey in predator-prey models.

4.2. Field evaluation

The aim of this study was to estimate the effect of a shooting program on population density of feral pigs and to apply the models of shooting to the results.

4.2.1. Methods

Site

The study was conducted on Woolner Station on part of the floodplain of the Adelaide and Mary Rivers in the Northern Territory as described in Chapter 2. The area has broad treeless floodplains surrounded by a strip of Eucalyptus woodland which varies in width from 2 to 10km. At the time of the study (March and April 1986) most of the floodplain areas were covered with 1-2m of water. The total area of the study site was 295km^2.

Survey Methods

The survey methods were described in detail in Chapter 2. The population density of feral pigs in the area was estimated from an aerial survey using one observer in a Jet Ranger helicopter. Feral pigs were counted on east-west transects which were selected with replacement. Transects were of irregular length, and four strip widths for estimating density were used, each of 25m with the inner boundary at the bottom of the observer's field of view. During surveying the helicopter flew at 46m (150 ft) and at a speed of 50 knots.

Shooting method

Feral pigs were shot from a Bell 47 helicopter. The helicopter had one shooter and the pilot. The area was searched completely at least once. The search pattern was pseudo-systematic. Encounters with pigs resulted in departures from a systematic search path. The pre-shoot survey showed no feral pigs were present in flooded areas, so those areas were not searched. Shooting was initially concentrated on the perimeter of the site and then towards the centre. As the western and eastern boundaries were flooded and the northern boundary was the ocean, no immigration or emigration could occur in those directions. The southern boundary was a fence (non-pig proof) in woodland. The pre-shoot survey indicated very few pigs were near this boundary so if immigration occurred it was assumed to be negligible. Shooting occurred in 65 sessions over 39.26h, for an average duration of 36 minutes per session. This time included ferrying, searching, chasing and shooting. Two shooters were used alternately. Shooters used an M14 .308 rifle and a shotgun which used BB and SG shot. Shooters averaged 2.04 shots/pig. The duration of searching, ferrying, chasing and shooting averaged 0.13h/km^2. Efforts were made to shoot pigs as humanely as possible and no wounded pigs were left. The shooting started on March 21 and finished on April 16, with intensive periods from March 21-23 and April 5, 10-12 and 15-16, 1986.

Analysis

The population density of feral pigs in the area prior to shooting was estimated by the Fourier series estimator (Burnham et al. 1980). The percentage reduction of feral pigs was calculated from the estimate of density obtained from the pre-shoot survey and the number of pigs shot/km^2 (the removal density). A post-shooting survey after the first three days of shooting showed a negative bias in the counts, presumably associated with the repeated disturbance from the shooting and hence no final post-shoot survey was flown. The pre-shoot population density was not estimated by Leslie's removal method (Caughley 1980), as the calculated regression was not significant, or by the generalized removal method (Otis et al. 1978) as hunting effort was not constant on each day. To apply the models to the shooting results, data from successive days were used to estimate n (pigs shot/km^2) and T (duration of shooting/km^2).

4.2.2. Results

The percentage reduction of feral pigs was estimated to be 79%. Pre-shoot density was estimated at 6.13 pigs/km^2 (+/- 0.50 SE). The number of pigs shot (removal density) was 4.86 pigs/km^2. A total of 1434 feral pigs was shot in the area however 60 pigs were seen that escaped.

The random predator equation fitted to the data was;

$$n = N\ (1 - e^{-2.217(T - 0.161n)})$$

The coefficient of determination (r^2) was 0.968. The estimated handling time/pig shot was 0.161h or 9.7 mins/pig.

The modified model when fitted to the data (Figure 4.2) was;

$$n = N\left(1 - e^{-13.127(T - 0.014)}\right)$$

The coefficient of determination (r^2) was 0.969. The standard error of the efficiency coefficient (13.127) was 0.890. The coefficient was significantly different from zero ($t=14.75$, $df=8$, $P<0.01$). The time involved in shooting was 0.014h/km^2 and as the removal density was 4.86 pigs/km^2 the estimated handling time/pig was 10.4secs. The handling time also estimated the threshold duration of shooting (0.014h/km^2) needed before any pigs were shot.

The modified equation was used to estimate the time (h/km^2) needed to kill 95% and 99% of pigs in the whole 295km^2 site. The estimates were 0.24 (95%) and 0.36 (99%)h/km^2. The 95% confidence intervals on the estimates were 0.21-0.27h/km^2 (95% kill) and 0.32-0.41h/km^2 (99% kill). The actual duration of searching, ferrying, chasing and shooting in the study was 0.13h/km^2 over the total site.

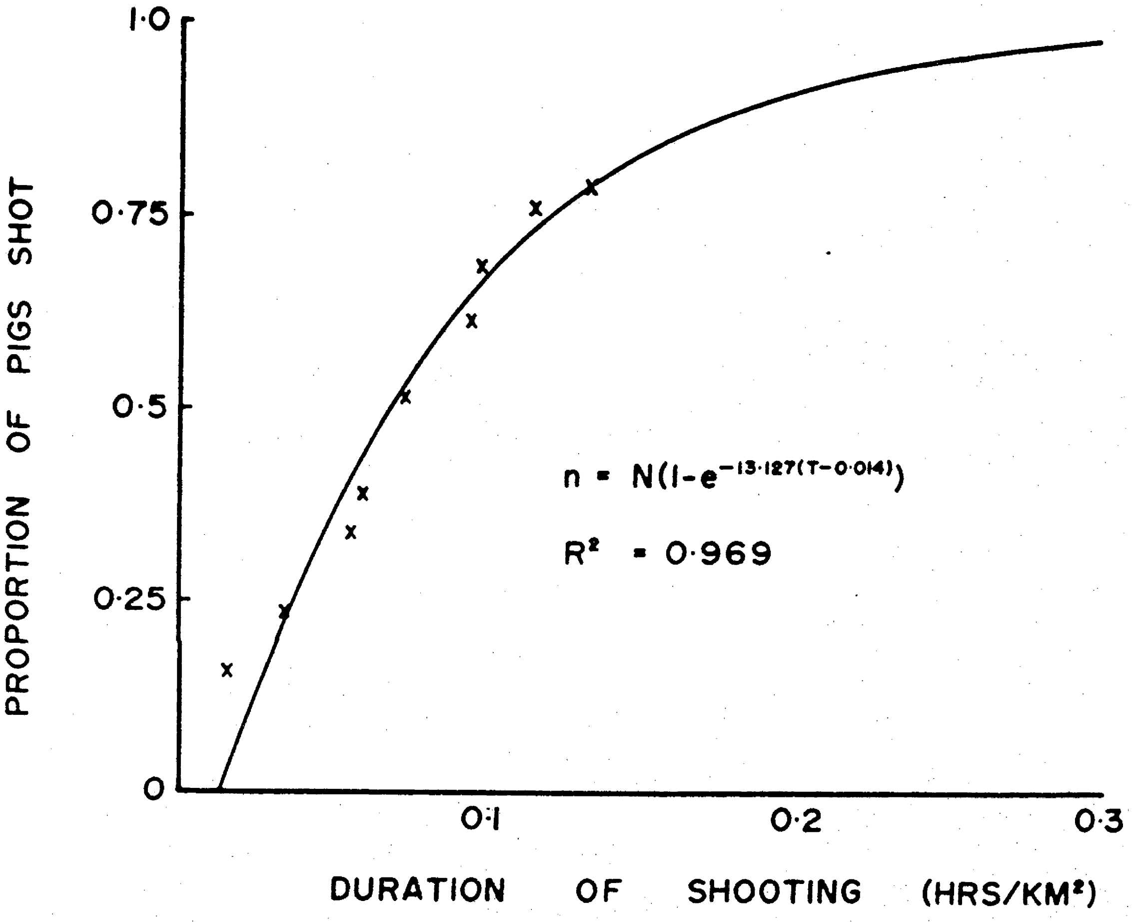
The cost/pig shot was A$7.31 (Table 4.1) which included helicopter charter, fuel and ammunition. The cost/km^2 was A$35.53 (Table 4.1).

4.2.3. Discussion

Predator-prey models have been used to evaluate control of insect pests in the laboratory and in the field. This study shows that such models can be applied to describe the effectiveness of control of feral pig populations. Nearly 97% of the variation in the number of feral pigs shot was accounted for by the predator-prey equations. The models assumed a random search pattern but the close fit of the data to the models suggests that the search pattern was more random than the shooters planned.

The two models gave very different estimates of the handling time/pig shot and of shooter efficiency. Juliano and Williams (1987) showed that the least squares method of estimating the parameters of the random predator equation gave biased results. Both parameters were usually underestimated. In the present study the efficiency coefficient was less for the random predator equation than for the modified equation, but the estimates of the handling time were the reverse. There is no independent way of determining which estimate of the shooter efficiency was biased. In contrast the estimates of the handling time/pig shot can be more easily compared. The random predator equation estimated 9.7mins/pig and the modified equation estimated 10secs. My own experience strongly supports the latter estimate as more accurate.

Figure 4-2: The relationship between the duration of shooting ($T = h/km^2$) and the proportion of pigs shot. The solid line is the predicted trend and the crosses are the data. The fitted equation has been rearranged to estimate the number of pigs shot (n/km^2), as a function of pig density (N) and the time (T).



The method of estimating pre-shoot density of feral pigs gave a precise estimate. The coefficient of variation was 8%. This was higher than the precision of the aerial survey results (coefficient of variation 31%-54%) reported by Hone (1983) or Wilson et al. (in press) (coefficient of variation of 25%).

The estimated effect of the shooting in the present study (79% kill) was nearly identical (80%) to that reported by Saunders and Bryant (in press). Both estimates were higher than the estimated 70% instantaneous kill (Giles 1980) needed to depress population density for at least a year.

There is potential for research to determine the duration of shooting in an area. Green (1984) examined the stopping rules for predators feeding in patches of prey. At present no stopping rule is used when shooting from a helicopter, and only the curvilinear nature of the catch-effort relationship has been suggested for use. The strategy of a predator staying in an area (patch) for a fixed time, such as suggested by Hone and Bryant (1981), was the best rule only if prey were randomly distributed. Such a distribution pattern is unlikely for feral pigs. An alternative approach often used in shooting from a helicopter is to stay in an area until a certain time period has elapsed since shooting the previous pig. This is the giving-up time (GUT) rule of optimal foraging. Iwasa et al. (1981) concluded that the GUT rule was the best strategy to maximise kills when the prey had a clumped distribution. Feral pigs usually have a clumped distribution pattern. Green (1984) reported that the GUT rule was fairly efficient and robust to changes in environmental conditions however an iterative assessment rule was more efficient. This rule has not been used for shooting feral pigs. The analyses of Iwasa et al. (1981) and Green (1984) are relevant to the use of shooting to control agricultural, forestry and environmental impacts, as the analyses involve estimating the benefits and costs of predation or shooting. If the objective is to eradicate feral pigs then the stopping rules will be less relevant as the primary consideration is the number of pigs killed, and the cost of doing so will be less relevant especially in an exotic disease outbreak.

The modified model has two main uses, first to estimate in a shoot how much more time is required to remove a certain percentage of animals (ie n and N are known and an equation solved for T) and second to obtain estimates of initial density when shooting conditions and personnel are similar to those in this study (ie n and T known and an equation solved for N). An example of the first use was given in the Results (Section 4.2.2). An example of the second use is to apply the fitted equation to data shown here in Table 4.1 from Hone (1983), Bryant et al. (1984) and Saunders and Bryant (in press). The study site reported by Hone (1983) was similar to that in the present study - open treeless plain adjacent to woodland. The sites reported by Bryant et al. (1984) and Saunders and Bryant (in press) were mostly open swamp with scattered trees. The data from Hone (1983) gave density estimates of 2 pigs/km^2, from Bryant et al. (1984) gave density estimates of 35.3 pigs/km^2 and from Saunders and Bryant (in press) 9.6 pigs/km^2. Each estimate was similar to or slightly higher than the number of kills/km^2.

The results and the levels of control inputs of this study can be compared with those reported in the literature (Table 4.1). Shooting time/km^2 and costs/km^2 were less in this than the other studies. However costs/kill, kills/h and kills/km^2 were intermediate between the other studies. Costs/kill were lowest (A\$3) and kills/h highest (93) when kills/km^2 were highest (35). Costs/km^2 (A\$114) were obviously highest when time (h/km^2) (0.38) was highest. Similar general trends in the costs of pig control by trapping and poisoning were reported by Turvey (1978), that is, cost/animal killed declined exponentially as pre-control density increased or the number of animals killed increased.

Combining data from each study showed that there was a significant negative exponential regression between the costs/kill (y) and kills/h (x) ($r=-0.970$, $df=2$, $P<0.05$). For kills/h greater than zero, the regression was;

$$\text{costs (\$)/kill} = 28.51\ e^{-0.03\ \text{kills/h}}$$

The negative exponential regression of cost/kill (y) and kills/km^2 (x) was not significant ($r=-0.917$, $df=2$, $P>0.05$), though the correlation was high.

The estimate from the modified equation of the handling time/pig of 10 seconds was biased as an estimate of handling time/kill, as it included the time spent chasing and shooting at feral pigs that eventually escaped. The results indicate that shooting saturation should rarely be a problem except possibly for large groups of pigs in thick vegetation. Low kills were caused by limited total time spent searching and shooting.

The efficiency coefficient (13.127) estimated in this study is a relative measure of the shooter's efficiency at spotting and shooting feral pigs. In predator-prey studies it has been shown that the rate of capture (equivalent to the efficiency coefficient) varies with predator density (Hassell 1981). That could not have occurred in the present study as there was only one predator (shooter).

The estimated time needed to kill 95% of pigs in the present study was

$0.24h/km^2$. This was longer than the time reported by Hone (1983) and less than the time used by Bryant et al. (1984) and that suggested by Hone and Bryant (1981), though the latter study assumed that $0.5h/km^2$ searching and shooting was sufficient to achieve eradication. The confidence intervals for the times needed to kill 95% and 99% of feral pigs may be biased. The regression analysis assumed a constant variance in the number of pigs shot across levels of duration of shooting. The variance may actually have increased with increasing duration of shooting. Replication of the present study would be needed to determine this.

The estimated duration of shooting ($0.36h/km^2$) needed to kill 99% of pigs would cost approximately $\$86/km^2$ or $25,488 over the total study area. Such costs will be beyond most graziers and would probably only be spent by government in an outbreak of an exotic livestock disease such as foot and mouth disease.

The application of predator-prey models to vertebrate pest control probably has much wider relevance to the control of other large mammals such as buffalo and donkeys. The general shooting process would be the same but the regression constants may be different for each species, habitat and possibly shooters and helicopter type.

This Chapter has reported studies of the effect of shooting from a helicopter on the abundance of feral pigs. An evaluation of the theory and practice of poisoning of feral pigs is described in the next Chapter.

Table 4-1: Inputs and costs of control of feral pigs when shooting from helicopters in the present study and those reported by Hone (1983), Bryant et al. (1984) and Saunders and Bryant (in press). Costs (A$) cover helicopter flying and ammunition and for the earlier studies have been corrected for inflation by assuming an annual inflation rate of 7%.

CONTROL VARIABLE	THIS STUDY	HONE (1983)	BRYANT et al. (1984)	SAUNDERS & BRYANT (in press)
Total Hours /km^2	0.13	0.16	0.38	0.21
Costs ($) /km^2	36	71	114	93
Costs ($) /kill	7	38	3	12
Kills/h	37	11	93	39
Kills/km^2	5	2	35	8

Chapter 5

Poisoning

Use of 1080 poison in the field reduced population density of feral pigs by an estimated 58%-73% (Hone and Pedersen 1980, Hone 1983), but lower mortality (11%) was reported in pen experiments (Hone and Kleba 1984). In the latter study warfarin was found to be highly acceptable and toxic (92% deaths) to penned feral pigs which were fed warfarin in wheat, in a no-choice experiment. To date the effect of warfarin on field populations of feral pigs has not been reported.

The aim of this Chapter is to report an evaluation of the short and long-term effects of warfarin on both the abundance of feral pigs and the extent of rooting by feral pigs. In addition the results are compared to the percentage reduction of feral pigs as indicated by independent estimates obtained by radio-tracking, and the predictions of a deterministic model of poisoning.

5.1. Modelling

The evaluation of poisoning for control of feral pigs has been done largely in the absence of any theoretical framework of the poisoning process or the factors influencing percentage kills. Hone (1986a) developed probabilistic models of poisoning of vertebrate pests that indicated what factors influence the probability of an animal dying and how those factors relate to each other as described in mathematical equations. Those models prescribed relationships such as the dose-response curve, between factors. A copy of the paper containing those models is included as an Appendix. In this Chapter an alternative approach is used. A model is developed which describes temporal changes in a pest population during poisoning.

The model was formulated by examining the similarities and differences between an infectious disease spreading through an initially susceptible population and the introduction and spread of poison through a pest population. A population can be divided into segments or compartments (Anderson 1981) and the rates of change of individuals between compartments may then be described by differential or finite difference equations. Such an approach has been used widely in epidemiology (Bailey 1975, Anderson 1981, Jones and Sleeman 1983). A susceptible population can become infected, then infectious and later it may develop into an immune population. Each of these compartments is analogous to susceptible, poisoned and recovered individuals of a vertebrate pest population. The obvious difference between the spread of infection or poison through a population is that in the simplest case, poisoning is analogous to a non-infectious disease. Individuals contract the disease (poison) by contact with poisoned bait, not by contact with infectious (poisoned) individuals. Hence some of the basic assumptions of disease models need to be changed.

The aim here is to develop a model of poisoning. The application of the model to a poisoning program in the field will be described later in this Chapter and predictions of the model tested by comparison with field data.

The process of poisoning of feral pig populations usually occurs in two steps. Initially feral pigs are offered non-poisoned bait. This step is usually called free-feeding or pre-baiting. The bait is placed in trails or in heaps called bait stations. When removal of bait by feral pigs has reached a high and stable level, then the second step is instigated which involves switching poisoned for the non-poisoned bait.

During free-feeding (Figure 5.1), feral pigs may be isolated (I) if they cannot find or eat the bait, susceptible (S) if they eat the bait when they find it, or they eat the non-poisoned bait (E). Obviously feral pigs can change from one compartment (I to S to E) to another over the duration of free-feeding, and must do so at certain rates. Assume that the per capita rate of change from isolated to susceptible is π, and the per capita rate of change from susceptible to eating is β. Births and natural deaths could occur for feral pigs in each compartment at per capita rates a and b respectively.

When poisoned bait is offered some animals may be isolated (I) by geographical (rivers, mountains) or behavioural (neophobic) factors (Figure 5.1). Isolated animals can become susceptible (S) at a per capita rate π. Susceptible animals can become poisoned (P) at a per capita rate β, and after a latent period ($1/\sigma$), during which poison symptoms are not apparent, they show symptoms and are then in the fourth and final compartment (Y) (Figure 5.1). Animals which show symptoms die at a per capita rate α, or recover at a per capita rate γ, and again become susceptible, or recover at a per capita rate λ and become isolated. During poisoning, animals in each compartment can die naturally at a per capita rate b or births can occur at a per capita rate a.

Finally it is assumed that the sex ratio in the population is equal and the total population (N) is the sum of each segment;

$$N = I + S + P + Y$$

In a classic disease model the rate of change of the infected population is assumed to be proportional to the product of the number of susceptible animals and the number of infected animals (Bailey 1975, Anderson 1981). The latter occurs because infected individuals are infectious; they can spread the pathogen from one infected individual to an uninfected individual without going back to the source of infection. An analogous situation occurs in poisoning vertebrate pests when individuals are poisoned by ingesting poison bait or part or all of another individual that has been poisoned and died. The latter is usually called secondary poisoning, and is mostly of concern when the second individual is of a different and/or native species from that initially poisoned. Where secondary poisoning does not occur, the initial assumption needs modifying. The change in the number of poisoned animals (P) is related to the number of susceptibles (S) but independent of how many individuals have been poisoned or are dead.

The flow of individuals between compartments in a feral pig population can be described by a series of equations. In the models developed here finite difference equations are used for computational simplicity.

Free-feed period

$$I = -\pi I + aI - bI$$

$$S = \pi I + aS - bS - \beta S$$

$$E = \beta S + aE - bE$$

Poisoning period

$$I = aI + \lambda Y - bI - \pi I$$

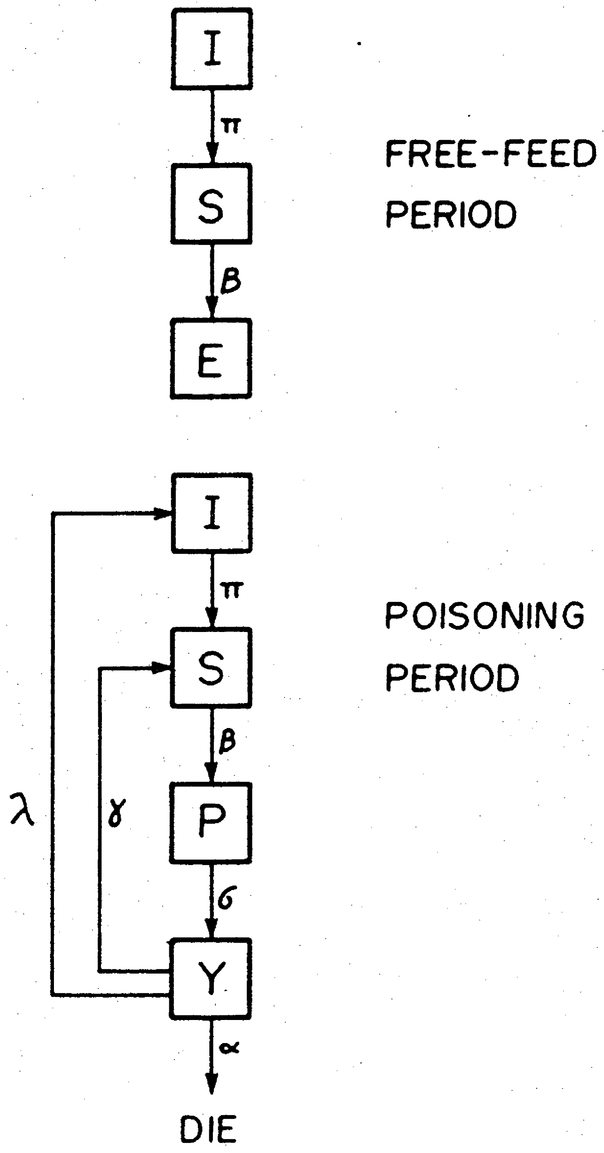
$$S = aS + \pi I + \gamma Y - bS - \beta S$$

$$P = aP + \beta S - bP - \sigma P$$

$$Y = aY + \sigma P - bY - \alpha Y - \gamma Y - \lambda Y$$

Application

Figure 5-1: Compartment model of poisoning of a feral pig population. Arrows show direction of transfer and associated Greek symbols indicate rates of transfer per unit time. Symbols in boxes show actual numbers of animals, and are those animals, isolated (I), susceptible (S), eating non-poisoned bait (E), eating poisoned bait (P) and showing symptoms of poisoning (Y).



The model can be applied in different field situations. If the free-feed period is not used then obviously only the second part of the model is appropriate. If a latent period is absent, such as with cyanide, then $\sigma=0$ and P=0. If poison bait is left available to pest animals then the existing model can be used. If however the poisoned bait is removed after several days then for time periods after that, $\beta=0$. If bait shyness (that is an aversion to eat the poisoned bait) occurs then γ approaches or equals zero. If births and natural deaths are absent then a=b=0. Inhibition of reproduction by a poison results in no births for that segment (Y) of the population and so a=0 for that segment. If there is no isolated segment of the population then $I=0=\pi=\lambda$. If pesticide resistance occurs then π approaches 0 and α is a negative function of time.

Estimation of parameters

The method of calculating the model parameters is now described. It was assumed that free-feeding occurred for at least three days, bait shyness was absent, natural deaths and births were zero and resistance to warfarin did not occur. Density of the pig population was assumed to be 5 pigs/km^2 and all pigs were susceptible (S=5, I=0).

As no portion of the population was isolated then $I=0=\pi=\lambda$. The rate of change from susceptible to eating the bait, either non-poisoned or poisoned, (β) was assumed to be the inverse of the contact frequency, which was assumed to be the average number of days till the bait (either non-poisoned or poisoned) was eaten. It was assumed that bait removal was rapid and that the time was 1.1 days. Hence $\beta = 1/1.1=0.909$ days^{-1}. The inverse of the time from ingestion of poisoned bait to development of symptoms was σ. For warfarin poisoning of feral pigs the average time for development of symptoms was assumed to be 3 days based on the results of Hone and Kleba (1984). Hence $\sigma=1/3=0.333$ days^{-1}. The rate at which feral pigs died (α) was estimated as the product of the inverse of the average time from dosing till death and the proportion of feral pigs killed by the poison at the concentration to be used. The average time till death was assumed to be 7 days and the proportion dying 0.92 (Hone and Kleba 1984). Hence $\alpha = (1/7)\mathrm{x}0.92=0.131$ days^{-1}. The mortality for both sexes is combined though Hone and Kleba (1984) reported males were significantly more tolerant of warfarin than females. Hone and Kleba (1984) reported the days till death, measured from the end of the poisoning, not from the start, as estimated here. The rate at which pigs recovered and became susceptible (γ) was the product of the inverse of the duration of symptoms and the proportion of pigs that survive and become susceptible. The duration of symptoms was assumed to be 10 days and the proportion surviving and becoming susceptible was 0.08 (=1-0.92). Hone (1983) estimated that some pigs ate 1080 bait and survived in the field so a small proportion of feral pigs were assumed to survive here. Hence the rate was γ =0.008 (=0.08/10) days^{-1}.

The model for free-feeding was;

$S = -0.909\ S$

$E = 0.909\ S$

The model for the poisoning period was;

$S = 0.008\ Y - 0.909\ S$

$P = 0.909\ S - 0.333\ P$

$Y = 0.333\ P - 0.131\ Y - 0.008\ Y$

5.2. Field evaluation

5.2.1. Methods

Site

The study was conducted in Namadgi National Park (Figure 3.2). The topography, vegetation and climate were described in Chapter 3, Section 1.

Design

There were two evaluations: short-term (April 1986 to July 1986) and long-term (May 1985 to May 1986). In the short-term evaluation feral pigs at two sites were poisoned and at five were not poisoned, but all seven sites were monitored. In the long-term evaluation, poisoning and monitoring occurred at three sites and four sites were monitored but not poisoned. In both evaluations, the sites poisoned and monitored were a sample from a large number of sites which were being poisoned. Sites to be poisoned were selected by park staff on the basis of access and perceived damage by feral pigs. The selection was not made on the basis of any estimates I had of the extent of pig rooting or pig density. Sites monitored were those described earlier in Chapter 3, Section 2.

Survey methods

For the short-term evaluation, the frequency of pig rooting on plots was measured and the abundance of feral pigs was estimated by dung counts on randomly selected plots as described in Chapter 3, Section 2. Dung were cleared off the plots monthly, and fresh dung were marked each month to estimate decay rates. For the short-term evaluation the total number of plots on which rooting and dung were measured was 500 at the poisoned sites and 450 at the non-poisoned sites. Monthly monitoring started in April 1986 and ended in July 1986. Poisoning occurred at the Pine Forest and Boboyan (Figure 3.2) in May 1986.

For the longer-term evaluation, the variables measured were the extent of rooting, the frequency of plots with rooting, the number of dung pellets per site and the frequency of plots with pig dung as described in Chapter 3, Section 2. For the evaluation, 100 plots were measured monthly at each of seven sites from May 1985 to May 1986. The sites (Figure 3.2) at which poison was applied and the dates of poisoning were; Nursery Swamp in July 1985, Shanahans Falls Creek in August 1985 and Boboyan in September 1985. Additional measurements were made at each of the seven sites from June to December 1986, except for August 1986, and were used in part of the evaluation to estimate rates of increase of pig populations.

In both the short and longer-term evaluations there were insufficient observations of feral pigs to directly analyse the effect of poisoning on their population density.

Poisoning

At sites to be poisoned, feral pigs were offered non-poisoned bread and wheat for several days prior to the introduction of wheat poisoned with warfarin at 0.13% concentration (w/w). The poisoned bait was prepared in a 2% sodium hydroxide solution to dissolve the warfarin. Poisoned bait was usually placed under tussocks or soil and poisoned bait not eaten by feral pigs was not removed. The free-feed and poisoned bait were distributed at several hundred small bait stations, each with 1-2kg of bait. The bait stations were placed at random with respect to the plots for monitoring. A similar method of distributing 1080-poisoned bait was described for control work in Namadgi National Park (then Gudgenby Nature Reserve) (McIlroy 1982).

Analysis

The short-term effects of poisoning on the frequency of occurrence of pig rooting and dung, and the abundance of dung pellets were tested by Chi-square analysis (Snedecor and Cochran 1967). The percentage reduction was estimated from the pre- and post-poisoning counts. For analysis, the number of plots with rooting, the number of plots with dung, and the number of dung pellets of the first post-poisoning month were corrected to allow for the latent period of 7 days, from the ingestion of warfarin-poisoned bait till death in pigs (Hone and Kleba 1984). This was based on the results of poisoning pigs with warfarin in wheat at a 0.1% concentration (w/w) for 2 days where the average time till death was 5 days, from the end of poisoning. The correction was necessary as the percentage reduction, especially of the abundance of dung, would otherwise have been underestimated.

The longer-term effects of poisoning, months and their interaction, on each of; the percentage of ground rooted, the percentage of plots with rooting, the corrected number of dung pellets, counts of dung pellets and the percentage of plots with dung, were tested by analyses of variance (Snedecor and Cochran 1967). Both treatments (poisoning and months) were analysed as random factors since they were a random sample from a larger population. Percentage data were arcsine transformed prior to analysis and other data transformed to common logarithms, after adding one, to obtain homogeneity of variances. Counts of dung pellets were corrected for decay as described in Chapter 3, Section 2. Differences between treatment means were compared by least significant differences if the initial analysis of variance test was significant (Snedecor and Cochran 1967).

The analysis of variance assumed independence of observations at the poisoned and non-poisoned sites. If some pigs moved between sites over the year then the analysis would not accurately estimate the effect of poisoning. To overcome this, paired Student's t tests (Snedecor and Cochran 1967) were used to test if the average difference between poisoned and non-poisoned sites was different from zero. Months were used as replicates and data were not transformed prior to analysis. Tests were applied to the same five variables as analysed by analysis of variance.

The long-term effects of poisoning were also analysed by calculating the observed instantaneous rate of increase over the duration of the study at the poisoned (May 1985 to December 1986) and non-poisoned (June 1985 to December 1986) sites. Rates of increase were estimated as the slopes of the regressions of months and the transformed corrected counts of dung pellets. Pellet counts were transformed to natural logarithms (Caughley 1980). The significance of the regression slopes were analysed by Student's t test (Snedecor and Cochran 1967).

Differences between poisoned and non-poisoned sites, and between months, in the average number of dung pellets per plot where dung occurred, were analysed by one-way analyses of variance.

5.2.2. Results

Short-term evaluation

The uncorrected percentage reduction at the poisoned sites in the number of plots with pig rooting was 2% after 1 month and 3% after 2 months (Table 5.1). There was significant heterogeneity in the number of plots with rooting between the poisoned and non-poisoned sites ($X^2=12.67$, df=3, $P<0.01$). The significance of the Chi-square analysis was associated with the reduction in the number of plots with rooting from April to May which was before the poisoning. The corrected reduction was 25% after 1 month. The number of plots with rooting increased at the non-poisoned sites and decreased at the poisoned sites (Table 5.1).

The uncorrected percentage reduction at the poisoned sites in the number of dung pellets was 83% after 1 month and 94% after 2 months (Table 5.2). There was significant heterogeneity in the number of dung pellets between the poisoned and non-poisoned sites ($X^2=22.27$, df=2, $P<0.01$). The corrected reduction was 87% after 1 month.

The uncorrected percentage reduction at the poisoned sites in the frequency of occurrence of plots with dung was 88% after both 1 and 2 months (Table 5.3). There was no significant heterogeneity in the number of plots with dung ($X^2=4.26$, df=2, $P>0.05$). The corrected reduction was 90% after 1 month.

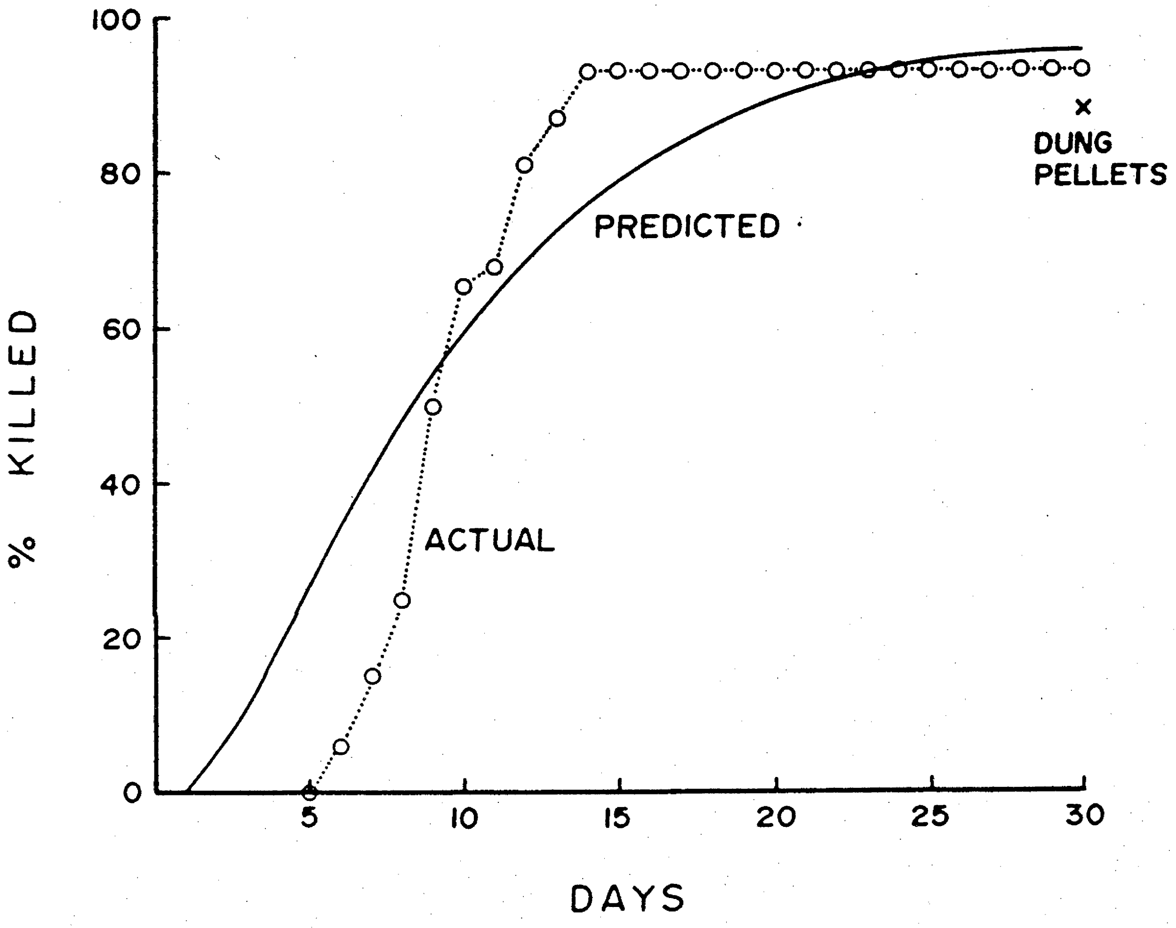
The percentage reduction of radio-tagged pigs was 94% (30/32) after 14 days (Saunders pers. comm., McIlroy pers. comm.). The deterministic model predicted a reduction of 76% after 14 days and 97% after 1 month (Figure 5.2).

Long-term evaluation

The effects of poisoning were estimated firstly by analysis of variance. The monthly average (+/- SE) percentage of ground that had been rooted by feral pigs at the poisoned sites was 1.50% (+/- 0.01) which was significantly ($P<0.01$) lower than that at the non-poisoned sites (3.66% +/- 0.01) ($F=105.303$, df=1,12). There were no significant effects of months ($F=2.189$, df=12,12) or the interaction of poisoning and months ($F=0.047$, df=12,64) on the percentage of ground that had been rooted by feral pigs.

The monthly average (+/- SE) percentage of plots with rooting at the poisoned sites (18.4% +/- 0.01) was significantly ($P<0.01$) lower ($F=10.494$, df=1,12) than that at the non-poisoned sites (23.6% +/- 0.01) (Figure 5.3). There was a

Figure 5-2: A comparison of the actual (dashed line) and predicted (solid line) percentage reductions of feral pigs after poisoning with warfarin in Namadgi National Park. The corrected reduction estimated from the counts of dung pellets is indicated by the cross.



significant ($P<0.01$) difference in the percentage of plots with feral pig rooting between months ($F=4.164$, df=12,12) with the highest in October and the lowest in February (Table 5.4). The interaction of poisoning and months was not significant ($F=0.057$, df=12,64).

Both of the above analyses refer to the spatial extent or frequency of rooting at the time of measurement, not the increment from month to month.

The monthly average (+/- SE) percentage of plots with dung was 4.09% (+/- 0.01) at the poisoned sites, which was significantly ($P<0.05$) lower ($F=5.275$, df=1,10) than that at the non-poisoned sites (4.27% +/- 0.01) (Figure 5.4). The percentage of plots with dung was significantly ($P<0.05$) different ($F=4.236$, df=10,10) between months and was highest in August and lowest in December (Table 5.5). There was no significant interaction between poisoning and months ($F=0.251$, df=10,55).

There was no significant effect of poisoning on the corrected number of dung pellets ($F=3.671$, df=1,10), months ($F=2.081$, df=10,10) or their interaction ($F=0.518$, df=10,55).

The monthly average (+/- SE) number of dung pellets (not corrected for decay) per 100 plots at the poisoned sites (13.3 +/- 0.2) was significantly ($P<0.05$) higher than at the non-poisoned sites (11.5 +/- 0.2) ($F=9.163$, df=1,10). There was a significant ($P<0.05$) effect of months ($F=4.349$, df=10,10) with the number of dung pellets being highest in July and lowest in December (Table 5.6). The interaction ($F=0.262$, df=10,55) of poisoning and months on the average number of dung pellets was not significant.

A complementary analysis of the effects of poisoning was done by paired Student's t test. The t test analysis found significant differences in the extent of rooting ($t=15.07$, df=12, $P<0.001$) and the percentage of plots with rooting ($t=6.02$, df=12, $P<0.001$) between the poisoned and non-poisoned sites. In both cases the rooting was less at the poisoned sites. There were no significant differences between poisoned and non-poisoned sites in the corrected number of dung pellets ($t=1.12$, df=10, $P>0.05$), the number of dung pellets ($t=0.70$, df=10, $P>0.05$) and the percentage of plots with dung ($t=0.35$, df=10, $P>0.05$).

Over the duration of the study (May 1985 to December 1986 at the poisoned sites and June 1985 to December 1986 at the non-poisoned sites) poison was placed at five sites (NS, SH, BO, PI, HC) and not at two sites (CG, BF). The observed instantaneous rate of change of corrected dung pellets at the poisoned sites was

Figure 5-3: The percentage of plots with rooting at poisoned and non-poisoned sites from June 1985 to May 1986 in Namadgi National Park. Poisoning with warfarin was applied at one site in each month from July to September inclusive, and each poisoning is indicated by an arrow.

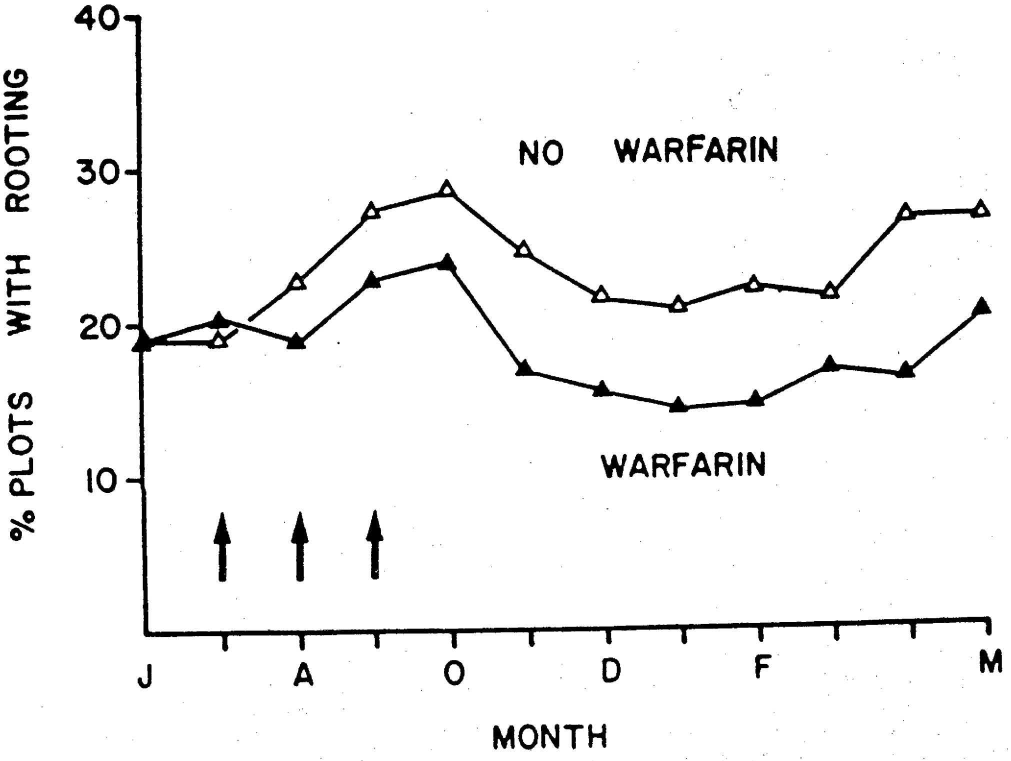
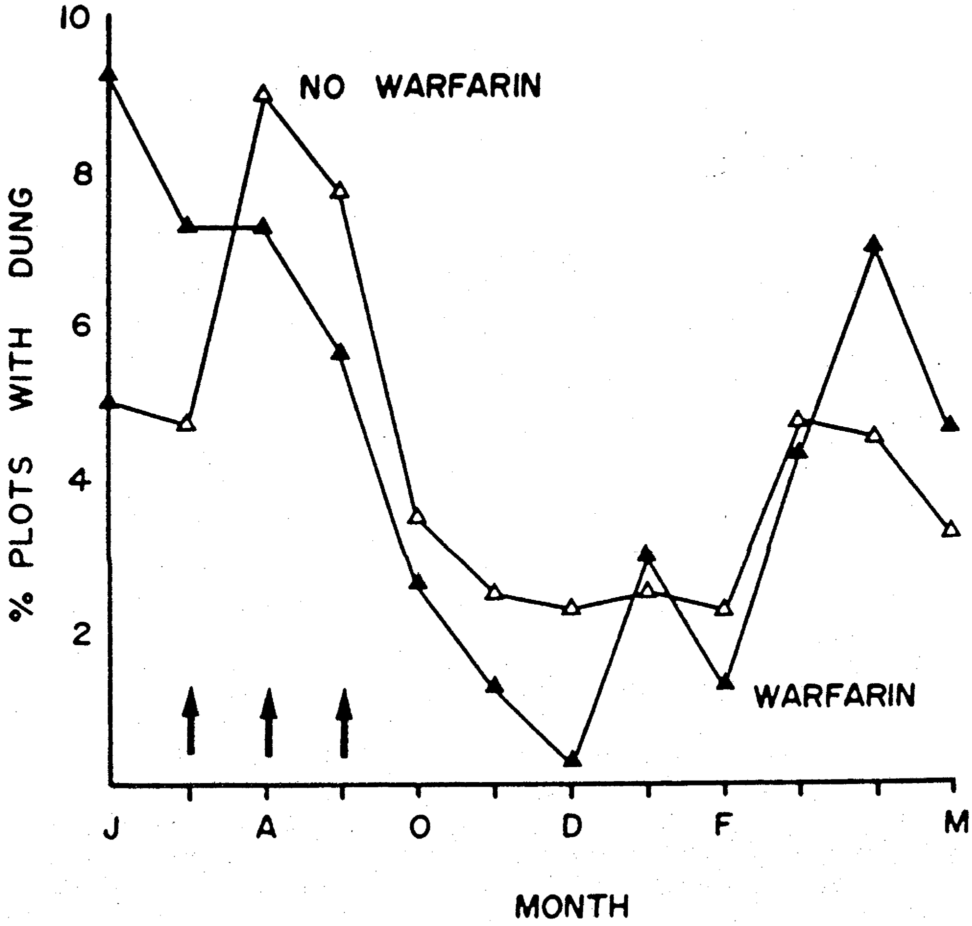


Figure 5-4: The percentage of plots with pig dung at poisoned and non-poisoned sites from June 1985 to May 1986 in Namadgi National Park. Poisoning with warfarin was applied at one site in each month from July to September inclusive, and each poisoning is indicated by an arrow.



-1.12/yr (+/- 0.36 SE) which was significantly different from zero (t=3.11, df=15, P<0.01). At the non-poisoned sites the rate of change was -0.41/yr (+/- 0.56 SE) which was not significantly different from zero (t=0.73, df=14, P>0.05). Over all sites the rate of change was -0.86/yr (+/- 0.33 SE) which was significantly different from zero (t=2.62, df=15, P<0.05). The overall regression was solved for y=0 (no pigs) to estimate the duration of the presence of feral pigs in the park if the present rate of poisoning continued and no immigration of pigs occurred. The predicted duration was 3.5 years which corresponds to December 1988. Note that this evaluation was over a slightly longer time period and had more sites poisoned than the earlier analyses.

On plots where dung occurred, the average number of dung pellets at poisoned and non-poisoned sites (2.52 v 2.54) were not significantly different (F=0.004, df=1,61, P>0.05). There were no significant differences between months (F=1.265, df=10,52, P>0.05) in the average number of dung pellets on plots where dung occurred.

5.2.3. Discussion

The results show that in the longer term, warfarin poisoning of feral pigs significantly changed the extent and frequency of occurrence of rooting and the frequency of occurrence of dung pellets. The extent of rooting and the frequencies of occurrence of rooting and of dung on plots were less at the poisoned than non-poisoned sites. At the poisoned sites the observed instantaneous rate of change of counts of corrected dung pellets was negative, but at the non-poisoned sites it was not significantly different from zero. In contrast, the uncorrected abundance of dung was higher at the poisoned than non-poisoned sites. This may have been associated with differences in the initial abundance of dung pellets or different decay rates between sites. The results reported here are the first long-term evaluation of poisoning for control of feral pigs or their sign.

In the short term there were significant reductions in the population density of feral pigs, but no change in the frequency of rooting. As areas of rooting may take months or years to revegetate, the lack of response of rooting, especially in winter (June, July and August) was expected. The corrected percentage reduction in the number of plots with rooting (25%) was an overestimate. This must have been associated with very little rooting activity in May 1986 at the poisoned sites. In contrast, at the non-poisoned sites rooting was more frequent. This difference may have been associated with the free-feeding of feral pigs. Large amounts of non-poisoned bait were distributed and it was eaten rapidly by the feral pigs. The estimated percentage reduction in pig abundance (87%-90%) was nearly identical to that reported (92%) for penned feral pigs fed warfarin (Hone and Kleba 1984). The independent estimate from radio-tracked pigs (94%) was also similar. That closeness of the estimates from the counts of dung pellets and from radio-tagged pigs is notable. The pigs with radio-transmitters were trapped in the area using wheat, the same bait as used for the poisoning. Hence there was potential for bias in the estimate from the radio-tagged pigs, but any bias appears to be minimal. Each estimate was higher than those reported (58%-73%) for 1080 poison use in the field (Hone and Pedersen 1980, Hone 1983).

As the long-term evaluation was conducted over a year there was potential for feral pigs to move between poisoned and non-poisoned sites. This may limit interpretation of the analyses of variance tests of the effects of poisoning, but will not influence the paired t tests. There were no significant interactions of poison and months in any of the analyses of variance. That may indicate that each variable measured was inherently too variable for the analysis to give a significant result as this variability led to a large residual variance in each analysis of variance.

The trends in the extent of rooting and of dung show that the effects of season were as large as, or larger than, the effect of poisoning. The rooting and dung counts were lowest in summer (December to February) and highest in winter (June to August). This could be associated with seasonal movement of feral pigs to higher altitudes in summer and their return in winter. Such seasonal movements have been reported for feral pigs in Tennessee (Belden and Pelton 1975, Singer et al. 1981) and suggested for pigs in Namadgi National Park by Boreham (1981).

The agreement between the predictions of the deterministic model and the field results suggests that the model describes the essential features of poisoning feral pigs. The model is of strategic and predictive use in the evaluation of warfarin. The analogy between the spread of infection through a susceptible population (Anderson 1981) and the spread of poison through a population of feral pigs appears to be useful. The model also indicates which data would be useful to collect in preliminary pen and field experiments in the process of pesticide evaluation. The relevant data are the average number of days till the bait is eaten, time from ingestion of poison to development of symptoms, time from ingestion of poison to death, percentage kill at a specified poison concentration and the duration of symptoms.

The accuracy of the model's predictions depends on the robustness of the model, the assumptions and the accuracy of the data used in the model. The results here suggest that each of these criteria needs more research. Some caution may be needed in the application of the model. For example, deaths began occurring later in the field than predicted, but once started the deaths occurred over a short time period. Hence after 14 days the predicted percentage kill was 76% and the actual percentage kill was 94%. Deaths may occur over a longer time in pen experiments than they do in the field. Alternatively the feral pigs may have been slower to start eating the poisoned bait than assumed in the model. Two general cautions need to be applied to the results of the modelling. Agreement between predictions and results does not prove the model is correct, as the results may be explained by an alternative model some time in the future. This is the fallacy of affirming the consequent of logic (Hempel 1966). Secondly the predictions describe average results and the actual data describes one unreplicated result. Hence some difference between the two results is to be expected.

The predictions of the model were examined by sensitivity analysis. The predictions of percentage kill are density-independent. The model was run at different initial pig densities and identical trends in percentage kill were obtained. The inclusion of isolated pigs in the model lowered the predicted percentage kill. For example, if 6% of feral pigs were initially isolated, but gradually lost isolation, the predicted percentage kill was 71% after 14 days and 91% after 30 days. When the time till bait was eaten was increased to 5 days, the predicted percentage kill was 64% after 14 days and 93% after 30 days.

The probabilistic model (Hone 1986a) discussed in Chapter 1 was not tested in this experiment. However the results of the field poisoning suggest that several control parameters identified by that model were relevant. The maximum value of the probability of a pig eating the bait was apparently high, and the pigs apparently found the bait frequently. The maximum value of the probability of a pig dying given that it had eaten the poisoned bait was apparently high. The weight of bait available was high and the bait was available for a long time. For wheat, the handling time per unit (wheat grain) of bait was low. It appears that behavioural interactions between pigs at bait stations were either neutral or facilitatory and that the poison appears to have been applied when there was low intake of alternative food.

The results in this and previous Chapters of the thesis are reviewed in the Discussion (Chapter 6), with review of their broader scientific interest and relevance to control of feral pigs and their impacts.

Table 5-1: The number of plots with rooting by feral pigs at the poisoned and non-poisoned sites in each month of study. Poison was applied in May after the plots were measured.

MONTH	POISONED	NON–POISONED
April	141	119
May	117	137
June	115	143
July	114	175

Table 5-2: The number of dung pellets at the poisoned and non-poisoned sites in each month of study. Poison was applied in May after the pellets were counted.

MONTH	POISONED	NON-POISONED
May	18	55
June	3	66
July	1	52

Table 5-3: The number of plots with dung pellets at the poisoned and non-poisoned sites in each month of study. Poison was applied in May after the pellets were counted.

MONTH	POISONED	NON-POISONED
May	8	26
June	1	20
July	1	12

Table 5-4: The average percentage of plots with rooting by feral pigs in each month from May 1985 to May 1986 inclusive. Percentages not significantly different are underlined. Averages are expressed as the arcsine of the percentage. The least significant difference was 3.0.

Feb	Jan	Dec	Mar	May85	Jun	Jul	Aug	Nov	Apr	May86	Sep	Oct
23.4	23.7	24.9	25.1	25.3	25.3	25.3	26.1	26.7	27.0	28.0	29.3	30.1
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	—	—	—	—	—	—	—	—				
		—	—	—	—	—	—	—	—			
			—	—	—	—	—	—	—	—		
								—	—	—	—	
										—	—	—

Table 5-5: The average percentage of plots with dung of feral pigs from July 1985 to May 1986. Percentages not significantly different are underlined. Averages are expressed as the arcsine of the percentage. The least significant difference was 0.6.

Dec	Feb	Nov	Jan	Oct	May	Mar	Apr	Jul	Sep	Aug
5.7	6.6	7.4	8.0	8.3	9.1	10.4	11.7	12.9	13.0	14.3

Table 5-6: The average number of dung pellets per 100 plots each month from July to May 1986. Averages not significantly different are underlined. Data are counts transformed to common logarithms after adding one. The least significant difference was 0.35.

Dec	Feb	Jan	Nov	May	Oct	Mar	Apr	Sep	Aug	Jul
0.37	0.59	0.63	0.69	0.76	0.77	0.78	0.81	1.04	1.09	1.15
—	—	—	—							
	—	—	—	—	—	—	—			
			—	—	—	—	—	—		
				—	—	—	—	—	—	
							—	—	—	—

Chapter 6

Discussion

Control of populations of feral pigs occurs in many areas, using many methods (Tisdell 1982). The results in this thesis show that the effects of shooting from a helicopter and poisoning on populations of feral pigs can be assessed and modelled. The effects on populations can exceed the 70% instantaneous reduction needed to depress populations for at least one year (Giles 1980) and the effects of continual control were broadly similar to the hypothetical effects suggested by Hone and Robards (1980). That is, continual control each with a high percentage kill will decrease pig abundance.

The aims, methods and results will now be reviewed for each of the three components of the thesis; surveying, modelling and field evaluation.

6.1. Surveying

In the survey component of the study, repeatable and precise methods of ground surveying the population density of feral pigs and their sign were developed and applied in forests and woodlands. Precise methods of aerial surveying of populations were developed and applied in floodplains and open woodlands. The aerial survey method appears to give accurate estimates of density using the Fourier series estimator which Burnham et al. (1980), Alldredge and Gates (1985), Buckland (1985) and Seber (1986) considered was the most powerful line transect estimator currently available. The results expand the range of survey methods available for feral pigs and their sign. The analysis of the methods was more extensive than that of other evaluations and reviews (Barrett 1982), except for capture-recapture methods, some of which were evaluated well by Baber and Coblentz (1986).

Feral pig sign such as rooting or dung can be surveyed on either randomly selected unmarked or marked plots. In this study the main criterion for selecting fixed, marked plots was the increased sensitivity of measures on fixed plots to detect short-term changes in population size of feral pigs or their sign. The evaluation of survey methods in Namadgi National Park occurred with relatively low pig abundance compared to reported densities in forests in Hawaii, Tennessee and Poland (Singer 1981), and so required a large number of fixed plots to detect changes in pig abundance or rooting. The method of dung counts and measurement of rooting extent will probably have much wider application than just mountain forests and woodlands. The method could be used in any habitat, except swamps, in contrast to the aerial survey method which will be of most use in floodplain, grassland and open woodland habitats.

6.2. Modelling

The modelling work indicated that the functional response component of predator-prey theory is relevant to the evaluation of shooting and poisoning of feral pigs. Predator-prey theory seems widely applicable to the evaluation of trapping of feral pigs and shooting pigs from the ground, and to the control of other vertebrate pests. The modelling work integrated theory and data, as is necessary for any model to be useful (Stenseth 1984), and identified strategies for improving the efficiency of the evaluation of shooting from helicopters and of poisoning. The agreement between predictions and field data for poisoning is encouraging but more testing of predictions is necessary before the generality of the models can be assessed.

The effect on predator-prey systems of hiding behaviour by prey has been examined partly by Hughes (1979) but more research is needed. That this is a real problem was shown by Saunders and Bryant (in press). They reported two of six feral pigs with radio-transmitters were never seen by shooters despite intensive searching and shooting from a helicopter.

The differing susceptibility of hosts or prey is an important source of population stability in host-parasite (Hassell and Anderson 1984) or predator-prey (Murdoch and Oaten 1975) relationships. Murdoch and Oaten (1975) also identified prey refuges, limits to predator dispersal and switching by predators as important sources of population stability of prey species. Each of these factors may be important in control of feral pigs.

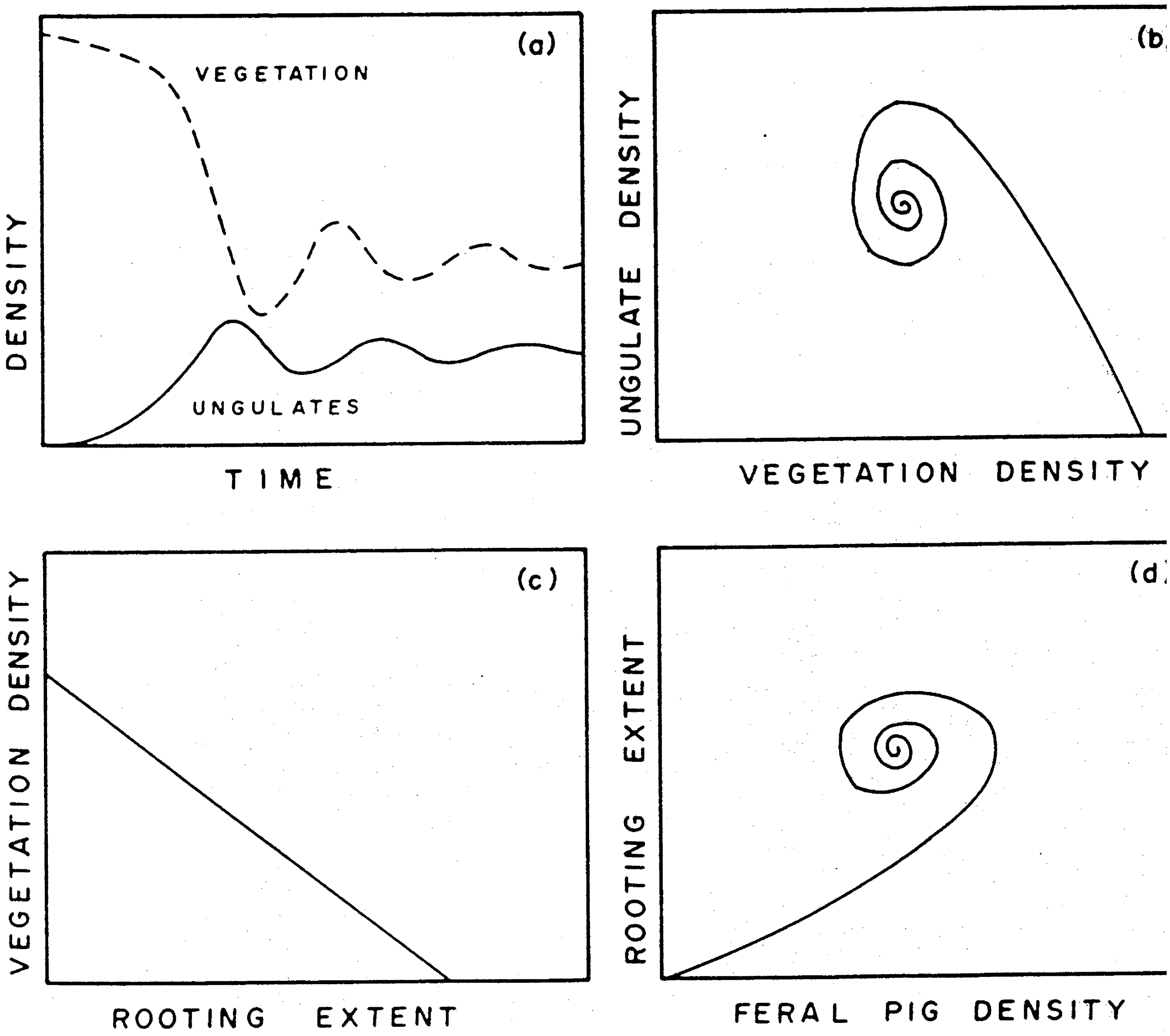
The dynamics of pig populations relative to population or damage control have been emphasised in previous work (Tipton 1977, Andrzejewski and Jezierski 1978, Giles 1980, Hone and Robards 1980, Tisdell 1982). Results reported here indicate the need to integrate theories of population dynamics and of impact and control processes. Caughley (1970) and Caughley and Lawton (1981) suggested that non-territorial ungulates exhibit an eruptive fluctuation in population size over time since introduction (Figure 6.1a). The relationship results from the interaction of ungulates with their food supply which can be shown as an inward spiral (Figure 6.1b) during the eruption. Feral pigs are non-territorial ungulates, which do reduce the abundance of their food supply (Howe et al. 1981). Challies (1975) reported that feral pigs on Auckland Island appeared to have an eruptive pattern in population size over time since introduction. Singer (1981) suggested that feral pigs in Great Smoky Mountains National Park (GSMNP) in Tennessee erupted then stabilised, the oscillations apparently being dampened by variable food supply. Such a phenomenon could amplify oscillations depending on the timing of variation in food supply. In contrast, Crawley (1983) considered that the effect of rooting by feral pigs in GSMNP was an example of amensalism. The interaction decreased the abundance of vegetation but had negligible effect on the pig population.

The pattern in Figure 6.1b suggests that a relationship may occur between the abundance of feral pigs and the extent of new rooting over the duration of an eruption. If the extent of new rooting is negatively related to vegetation (food) abundance (Figure 6.1c) then the extent of new rooting will be related to abundance of feral pigs in a curvilinear relationship (Figure 6.1d).

The predicted relationship between the extent of rooting and pig abundance suggests that the assumption of Belden and Pelton (1975), Conley (1977) and Giles (1980) of a simple positive relationship between feral pig abundance and the extent of rooting was too simplistic, as some levels of rooting correspond to more than one level of feral pig abundance. However a distinction needs to be made between the extent of new rooting and the extent of rooting. The former refers to rooting occurring in a defined time period and the latter to the extent of rooting at a particular time and does not involve any determination of the age of the rooting. The model presented here indicates how the disparate results (Section 3.1) of Cooray and Mueller-Dombois (1981) and Ralph and Maxwell (1984) differed in the relationship between rooting and the abundance of feral pigs. Each study may have been measuring rooting and pigs at different times since introduction of feral pigs.

The probabilistic models of poisoning (Hone 1986a) reviewed in Chapter 1 can be applied to results of an evaluation of rodenticides. Richards and Huson (1985) reported a response surface between the percentage reduction of rodents and five control parameters. Their analysis assumed linear relationships between the parameters and the response. However Richards and Huson (1985) identified a significant linear trend in the residual error of the response surface. The cause of that trend may be the curvilinearity of relationships described in the models of Hone (1986a).

Figure 6-1: A theoretical model of temporal changes in population density of feral pigs and the extent of new feral pig rooting. (a) Predicted trends in ungulate and vegetation density over time since introduction. (b) The same data graphed in phase space. (c) Hypothetical relationship between vegetation density and the spatial extent of new pig rooting. (d) Predicted relationship between density of feral pigs and the extent of new pig rooting during an eruption.



A general issue about the poisoning of feral pigs or other vertebrate pests follows from the modelling work reported here. Caraco and Pulliam (1984) and Clark and Mangel (1984) reported models of foraging which predicted that when animals fed in groups the variance of individual food intake, compared to feeding alone, was reduced. Feral pigs sometimes feed in groups and sometimes alone, so could be expected to have less variable food intake per pig compared to the situation where they all fed alone or in equal-sized groups. Hence, pigs would be expected to receive more variable poison doses when feeding alone. Similarly, when feeding interference occurs, the variance in poison bait intake would be expected to increase. Conway (1981) reported results of work by Comins which showed the consequences of each pest receiving an equal or unequal dose of poison. The latter situation increased the proportion of the population subject to a low dose and hence to higher selection pressure for pesticide resistance. In the context of feral pigs eating poisoned bait, feeding interference could be the mechanism producing the same result. That is, interference between pigs may result in variable poison doses and variable selection pressure for tolerance or resistance to the poison. The development of resistant rodent populations has occurred (Greaves 1971) and could occur in feral pigs.

The topics of immigration, evaluation and objectives will now be discussed in turn, relative to the field results obtained in this thesis.

6.3. Field evaluation

Immigration

Poisoning in Namadgi National Park, by applying poison once in one to two years, probably allowed immigration and breeding of pigs to reduce the effects of the poisoning on the extent of rooting. Tisdell (1982) discussed the implications for farmers of immigration of pigs. Movement would reduce the profitability of control and if immigration was high would make control unprofitable. Eradication of feral pig populations in parts of Hawaii Volcanoes National Park was based on fencing, to prevent immigration (Stone 1985). Andrzejewski and Jezierski (1978) reported that a substantial proportion of a wild boar population in a Polish forest were not resident but moved into or out of the area of study. This could have been associated with extensive movements or a very small area of reference in that study.

If immigration is a significant component of the increase in abundance of feral pigs then the term "population" is difficult to apply. Krebs (1985) defined population as a group of individuals of one species occupying a particular space at a particular time. Immigration may blur the discreteness of a population, especially one with no clear boundaries. Where feral pigs are continuously distributed then the concept of a population is hard to use, as discussed by Krebs (1985) for any species. In eastern and northern Australia feral pigs are distributed continuously (Tisdell 1982).

Stenseth (1981) and Stenseth and Hansson (1981) analysed, by modelling, the role of immigration in population dynamics and pest control. They concluded that the best control strategies varied with the dynamics of a pest population. If empty patches (no pests) occurred and methods were available to prevent immigration, then the methods should be used rather than try to increase mortality elsewhere in the population. This is the strategy used in Hawaii Volcanoes National Park (Stone 1985) and corresponds to the use of conditions identified by Soule (1983) as contributing to the extinction of species; isolation and poor dispersal.

Stenseth (1981) concluded that it was more effective to reduce reproduction if trying to control r-selected species compared to K-selected species. Stenseth (1981) also noted that the application of pesticides was unlikely to be the optimal strategy for control of r or K-selected species. In contrast, Conway (1981) considered that pesticides were the most appropriate means of control of r-selected species and that they were efficient for K-selected species. Caughley (1976) criticised as simplistic the r and K classification of species, as his modelling of ungulate dynamics showed that seven variables needed to be described to predict trends in abundance, not two - the values of r and K. Feral pigs may be more of an r-selected species because of their large litter size, but their relatively large bodysize suggests that they are a K-selected species. Such difficulties in classifying feral pigs as an r or K-selected species and the differences in opinion between authors indicate that further research is needed.

Evaluation

The evaluation of poisoning was assisted by the monitoring of the non-poisoned sites. Without the control (non-poisoned) sites the effect of poisoning could easily have been overestimated and the decline in rooting in October and November 1985 attributed solely to poisoning. Cochran and Cox (1957) described experimental situations where a treatment control may or may not be necessary. When the effect of a treatment is well known then the control (non-treatment sites) is not necessary. When the effect of a treatment is variable or not known then a control is necessary. These three situations can occur sequentially in the evaluation of a pesticide or any control method as the effect is unknown at the start of a study but well known by the end. In this study a control (no shooting) site was not used in the evaluation of shooting from a helicopter, as the effects of such shooting were better known than the effects of warfarin poisoning in the field.

In many field evaluations of the use of poisons for vertebrate pest control, experimental controls (non-poison sites) were not used (Rowley 1958, Poole 1963, Batcheler et al. 1967, Rowley 1968, Rennison 1977, Hone and Pedersen 1980, Richards 1981, Rowe et al. 1981, Tietjen and Matschke 1982, Greaves et al. 1982a, Robinson and Wheeler 1983, Buckle 1985, Rowe et al. 1985, Balasubramanyam et al. 1985, and Thomson 1986). In contrast, experimental controls were used in field evaluations of pesticides for vertebrate pest control by Cooke (1981), Oliver et al. (1982), Greaves et al. (1982b), Hone (1983), Foran et al. (1985), Crosbie et al. (1986) and McIlroy et al. (1986).

Objectives

Caughley (1981) identified four classes of "overpopulation". The first class was of animals that threaten life or livelihood. The second class was of animals that depress the density of favoured species. The third class was of animals that are too numerous for their own good and the fourth class was of animals in systems that were off their equilibrium. Caughley considered many wildlife management issues were claimed to be class four situations when they were actually one of the other classes. It has been shown that feral pigs depressed the density and biomass of some plant species in Tennessee (Bratton 1975, Singer et al. 1981, Howe et al. 1981) and Hawaii (Stone 1985) and changed the composition of plant communities in a sub-alpine area in Australia (Alexiou 1983). Examples of class one situations were reported for lamb predation by feral pigs (Pavlov et al. 1981, Pavlov and Hone 1982). I know of no situations of "overpopulation" of feral pigs in Australia that are classified as class three or four. The abundance of feral pigs in nature conservation areas in Australia has probably been incorrectly labelled as a class four situation as Caughley (1981) discussed for many mammals.

Caughley (1983) described five types of culling of mammal populations. Closer scrutiny of those types is needed to determine if control of feral pig populations is one of these, namely manipulative or idiotic culling. The former is aimed at conserving various specified plant and animal communities and the latter is not (Caughley 1983). Similarly, continuing management can be viewed as tests of scientific hypotheses (Caughley 1983, Macnab 1983), the results of which should advance scientific knowledge and understanding of management.

Any of the methods of population control or culling that are used periodically should be used at a frequency that achieves a particular objective. Occasional control will simply result in a culling operation of indefinite duration that may not achieve any objective other than satisfying some desire to kill pigs. Such control could also reduce competition between pigs and result in a high rate of recruitment into the population.

The response of feral pig populations to culling or control is influenced by the rate of increase of the populations. A variety of estimates of instantaneous rates of increase have been reported for populations of feral pigs. Hone and Pedersen (1980) reported an observed rate of increase of 0.57/yr (+/- 0.18 SE) with a range from -0.84 to 1.64/yr. Giles (1980) reported a range from -0.73 to 0.71/yr, and Bratton (1975) cited Kozlo (1970) (1.02/yr) and Kormilitsin and Dulitskii (1972) (0.41/yr).

The intrinsic rate of increase (r_m) for populations of feral pigs can be estimated from empirical relationships between the intrinsic rate of increase and bodyweight. Using an average bodyweight of 40kg for an adult feral pig, the estimated intrinsic rates of increase are 0.40/yr (Caughley and Krebs 1983), 0.31/yr (Hennemann 1983) and 0.26/yr (Robinson and Redford 1986).

Not all reported estimates of rate of increase can be interpreted as real increases. The estimates cited by Bratton (1975) and Giles (1980) and those from the bodyweight equations, have no estimates of precision so the statistical significance of the rates cannot be calculated. Hone and Pedersen (1980) reported that the overall rate of increase was not significantly different from zero ($t=3.17$, $df=2$, $P>0.05$), but at one site the rate of increase (1.09/yr +/- 0.06 SE) was significantly different from zero ($t=18.17$, $df=2$, $P<0.005$). In the field studies described in this thesis a better test of the rates of increase would have required more data. Harris (1986) showed that when counts of animals are highly variable it was necessary to obtain multiple counts each year, or some other unit of time, to ensure a precise estimate of rate of increase. The estimates from the bodyweight equations may be conservative as they were calculated for species in their natural habitats, and feral pigs in Australia may have a higher intrinsic rate of increase because of fewer predators, diseases and parasites, than in their natural habitats.

6.4. Synthesis

On the basis of the results in this thesis and relevant literature on feral pigs and other wildlife populations, new ideas were synthesised. The ideas should be treated as hypotheses, not conclusions.

The different aspects of the control of feral pig populations may be combined in a new concept of the control regime; the combined aspects of intensity, frequency, season and spatial extent of control. Intensity refers to the level of control effort (and hence percentage kill), frequency to how often control occurs, season to time of year and spatial extent to the area over which control occurs. The concept is analagous to that of a fire regime that has been developed in fire management in Australia (Gill 1981). In the assessment of control of feral pigs as in this thesis, emphasis has been placed on the intensity of control and little attention has been placed on the other components of the regime.

Research on control of feral pigs or their impact has concentrated on the effects of control methods on pig density, rather than investigating the relationship between the level of a control method (such as the amount of poisoned bait) and the response of population density - the classic dose-response relationship as discussed for pest control generally by Hillebrandt (1960). The law of diminishing returns (Hardaker et al. 1970) is central here. Each unit increase in the amount of control gives a slightly smaller increase in the response. Alternately the least cost combinations of control methods could be determined by linear programming (Gupta and Cozzolino 1975).

The frequency of control has been discussed relative to the rate of increase of feral pig populations. The rate of offtake of pigs must exceed the intrinsic rate of increase for abundance to decline (Singer 1981). The effect of season on control was not examined in this study. If bait intake or pig reproduction rates varied with season then control effectiveness will vary with season. The importance of spatial extent of control has been discussed, particularly with respect to immigration.

The control regime is part of a suggested broader planning process that is outlined in Table 6.1. The planning steps broadly follow those described by McAllister (1980). The suggested analyses and tools are also listed. They include analyses not examined in this thesis or used previously in control of feral pigs, such as decision theory (Raiffa 1968, Norton 1976) and the use of geographic information and expert systems (Davis et al. 1986). The control methods could be target-specific using the approach described by O'Brien (1986). The management planning process (Table 6.1) is an attempt to develop a planning framework for control of feral pigs, similar to the framework for fire management described by Good (1981).

Data that could be collected for monitoring in a park like Namadgi National Park should be similar to that described by Macdonald and Grimsdell (1983) for conservation areas of about 1000km^2 in the sub-humid rainfall zone. They suggested data on distribution and abundance of large herbivores should be collected on a longer than annual basis, be moderately accurate, of high to moderate precision and at a scale of resolution of 4-25km^2. In Namadgi National Park monitoring would be most useful if it occurred at about 3 monthly intervals and at a finer scale of resolution (<4km^2).

The theory of population dynamics has additional relevance to control of feral pigs. Populations have been reduced to low numbers after control in NSW (Hone 1983) and Hawaii (Stone 1985). The pattern of distribution and abundance of such populations appears similar to that described for some rare, vulnerable or endangered species (Drury 1974, Margules and Usher 1981, Ride and Wilson 1982). That is, populations show limited distribution and very low density. Such a pattern generates the hypothesis that such populations of feral pigs may become extinct naturally as a consequence of inbreeding. To test the hypothesis requires a closer look at the literature and estimation of the effective population size.

Andrzejewski and Jezierski (1978), after a study of wild boar in a Polish forest, concluded that "it would not appear possible for a wild boar population with density less than 10 individuals per 1000ha [1.0/km^2] of forest to exist continuously in time without constant immigration..". In their study area of 2500ha in Kampinos National Park this would correspond to a minimum of 25 (=2500x10/1000) wild boar.

Kimura and Crow (1963) defined the effective population size as "the size of an idealized population that would have the same amount of inbreeding or of genetic frequency drift as the population under consideration". Hill (1972) defined it as the "number of individuals entering the population each generation, where an individual must breed to enter the population." Lacava and Hughes (1984) used a model by Kimura and Crow (1963) to estimate the effective population size for several species. Reed et al. (1986) reviewed the model of Lacava and Hughes (1984) and improved it. Using the model of Reed et al. (1986) for a population with overlapping generations, and data from Giles (1980), the number of feral pigs needed to have an effective population size of 50 pigs can be estimated. Such a population size should retain its genetic diversity for decades or longer

(Schonewold-Cox 1983, Reed et al. 1986). If pigs of both sexes have peak breeding rates at 3 years old, the sex ratio of pigs at birth is 1:1, average litter size is 6 piglets, and sows produce 2 litters per year, and 80% of sows and boars breed each year, then the number of pigs needed to have an effective population size of 50 is 72 pigs.

Such calculations and theory assume that small populations of feral pigs are isolated. In many such populations of feral pigs there may be enough natural dispersal of individuals into the small populations to neutralise any effects of inbreeding depression on fecundity or mortality. This is an area for further research. However small isolated populations may be vulnerable to chance events including storms or disease outbreaks as outlined for the management of endangered species by Maguire (1986). That study suggested that to increase the chances of survival of the endangered species it was better to have several small populations than only one. In this context the management strategy should be to decrease the number of small feral pig populations so that the species is more vulnerable to the effects of chance events.

The different effects of poisoning on the extent of rooting and pig abundance in Namadgi National Park in this study indicate a need to research the ecological effects of rooting in Australia. A large body of theory on disturbance dynamics is now available (Noble and Slatyer 1977, Pickett and White 1985, Groves and Burdon 1986) which could be integrated with the theories of plant-herbivore interactions (Caughley and Lawton 1981, Crawley 1983, Edelstein-Keshet 1986).

To conclude, this thesis investigated the assessment of the results of control of feral pig populations. The assessment was in three parts; surveying, modelling and field evaluation of shooting and poisoning. The central hypothesis in the thesis was that control of feral pigs does not influence the population density of feral pigs. That hypothesis was refuted for shooting from a helicopter and poisoning with warfarin. The latter control method also reduced the frequency of pig sign, rooting. The relevance of theories of predator-prey relationships and the spread of diseases to control of feral pigs has been described. A new concept of a pest control regime was introduced. Much exciting research remains to be done.

Table 6-1: Steps in planning control of populations of feral pigs. Tools and analyses useful at each step are also shown.

STEPS	TOOLS AND ANALYSES
Establish objectives	
Measure effects of pigs on ecosystems	Experiments
Describe or predict effects of control on feral pigs and impacts	Modelling, geographic information systems (GIS)
Reformulate objectives	
Specify control regime and allocate resources	Budgeting, decision analysis
Implement control	
Record control effort and monitor results	GIS, surveying
Interpret results in long-term perspective (>10 yrs)	Modelling
Predict future control regime	GIS

Appendix A

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Appendix B

Integrative Models of Poisoning Vertebrate Pests

INTEGRATIVE MODELS OF POISONING VERTEBRATE PESTS

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ABSTRACT: Strategies for the control of vertebrate pest are identified using mathematical models of poisoning. The models integrate aspects of foraging ecology and toxicology in a probabilistic framework The structure, assumptions and control implications of the models are presented. Variables (control parameters) influencing the probability that a pest animal dies in a poison programme are identified and classified according to their degree of operator control. Control strategies suggested by the model: are identified, and practical means of applying them are discussed. The models suggest that the probability that an animal dies is a function of 15 to 17 control parameters, of which operators have direct control over a maximum of 4: poisoned bait abundance, poison bait dispersion, the time over which poisoned bait is available, and poison concentration.

INTRODUCTION

Many methods are used to control the damage or abundance of vertebrate pests. Poisoning is one of the oldest methods, with a recorded history going back to classical Greece. Today poisoning is used against many vertebrate pests around the world, such as rodents, birds, and large mammals.

The evaluation of poisoning has concentrated on either laboratory or field testing of and acceptability and toxicity to, target and nontarget species. Many of the current field practices have evolved from a combination of rigorous experiments and field experience. Not all the practices have been exhaustively tested because it is virtually impossible to do so. Experiments to evaluate three poisons, in each of three bait types with four delivery systems, in four seasons of the year become too large to conduct in the field. An alternative approach to evaluating poisoning is to develop theoretical models based on relevant field and laboratory data and evaluate the effects of different poisoning strategies. Mathematical models can be used to indicate the response of pests to different control inputs, and to describe how the control inputs interrelate.

The principal use of mathematical models in pest control is to provide guidelines for evaluating alternative control strategies (Conway 1977, Conway and Comins 1979). If the values of model parameters can be estimated then the models may also be of great predictive value. This paper is concerned with the development of models of strategic rather than predictive value. The models are developed from theoretical and empirical backgrounds in vertebrate pest control, and aspects of theoretical and applied ecology. The integration of principles from these diverse scientific fields reveals some unusual and useful patterns.

There have been surprisingly few attempts to integrate the many patterns and processes in poisoning vertebrate pests, identify control strategies and express the results in a mathematical form or model. Gentry (1971) developed a mathematical model of rat eradication programs. The model was based on a series of simultaneous integral equations, which describe changes in the number of rats of different ages. Natural changes in abundance were described, and the effects of sterilization and poisoning examined. Batcheler (1982) developed a simple probability model to estimate the number of random bait encounters required to kill a pest. This was based on the toxic loading and piece-weight distribution of baits. Modelling has been used more extensively for evaluating chemical and other control of invertebrate pests such as cattle tick (Sutherst et al. 1979).

The aim of this paper is to describe strategies suggested by four mathematical models of poisoning vertebrate pests.

Models

The models are formulated for short time periods so that natural births, deaths, immigration and emigration are approximately zero. An attempt has been made to remove from a poisoning program many minor features and describe the essential, central elements. Population parameters such as age, breeding status, sex ratio, and weather are treated as sources of random variation. The models relate to typical vertebrate pest poison programs such as those using poisonous bait stations, throw-packs, or poisoned bait trials.

Probabilistic models are developed which estimate the probability of an animal dying in a poisoning program. The probabilistic approach reflects underlying uncertainty in describing the effects of all factors and interactions that may determine how many, or what percentage of a vertebrate pest population is killed by poisoning.

The models are based on several principles. Firstly, that the total number of animals in a population (N) is equal to the sum of the number of animals that find and eat the poisoned bait (NE), that find and do not eat the poisoned bait (NDE), and that do not find the poisoned bait (NDF).

$$N = NE + NDE + NDF \qquad (1)$$

where NE, NDE or $NDF \geq 0$

Secondly, the number of animals that find and eat the poisoned bait (NE) comprises two groups: those that eat the poisoned bait and die (NED) and those that eat the poisoned bait and do not die (NEd) (Hone 1983).

$$NE = NED + NEd \qquad (2)$$

Thirdly, the number of animals that eat the poisoned bait and die (NED) is equal to the product of the number of animals (N) and the probability of an animal dying (p).

$$NED = p\ N \qquad (3)$$

The fourth principle is that the probability (p) of an animal dying is the product of the probability of an animal eating the poisoned bait (P(E)) and the probability of dying given that it has eaten the poisoned bait (P(D/E)).

$$p = P(E) \times P(D/E) \qquad (4)$$

The modelling process now concentrates on estimating the probabilities P(E) and P(D/E).

Models are developed for differing ecological and control situations (Table 1). The determinants of which model is appropriate are bait dispersion and the search pattern of the vertebrate pest(s). Models based on random search by a pest use different forms of the functional response relationship commonly described for predator-prey (Hassell 1981) and plant-herbivore interactions (Caughley and Lawton 1981).

Table 1: Ecological components of probability models of poisoning vertebrate pests for differing bait dispersion and pest search patterns. The notation in the table indicates that the probability of an animal dying (p) is partly a function of that enclosed by the brackets.

Pest search pattern	Poisoned bait dispersion	
	Random	Clumped
Random	p = f (Functional response Type III)	p = f (Functional response Type II)
Non-random	p = f (Optimal foraging)	p = f (Optimal foraging)

The functional response describes the relationship between bait (food) intake and bait (food) abundance. In poisoning programs when bait is provided <u>ad libitum</u> this response is still relevant as it is simply a special situation described by the functional response relationship. As animal search patterns are often nonrandom, other models are developed based on such searching, and these models use aspects of optimal foraging theory (Charnov 1976 a,b, Caraco and Pulliam 1984).

Discussions of functional response and optimal foraging models in the literature usually assume that once an animal found food it ate the food. The models developed here do not assume this, but generate a probability that an animal eats bait, P(E), and describe what influences that probability. Hence the models are more general than that developed by Batcheler (1982) in which random search and a linear relationship between bait abundance and bait intake were assumed. The models are simpler than that developed for mantid feeding by Charnov (1976a), as vertebrate pests feed on stationary not mobile prey (bait).

Poisoning vertebrate pests most commonly involves distributing poison bait in clumps and the pests feeding in a nonrandom manner. Such a situation is described in model (iv). The other models are described for comparative purposes. Surprisingly the control strategies suggested by each model are very similar.

(i) Random bait dispersion and random search pattern.

The probability that an animal eats the poisoned bait is assumed to be a positive saturation function of the number of times an animal finds the bait (t) and a function of behavioral interference or facilitation between animals that find the bait (α). In a simple case:

$$P(E) = \left(\frac{k_1 t}{x_1 + t}\right) \alpha \qquad \begin{array}{l} \text{for } t \geq 1 \\ 0 \leq k_1 \leq 1 \\ x_1 \geq 0 \end{array} \qquad (5)$$

where k_1 is the maximum probability or value of P(E), and x_1 is the number of times required to have k_1 at half its maximum value. Equation (5) is a saturation equation at t increases. Animals showing neophobia such as some rats (Shorten 1954, Barnett 1958) and some rabbits (Oryctolagus cuniculus) (Rowley 1963, Oliver et al. 1982) will have $k_1 = 0$ and hence $P(E) = 0$. The coefficient α equals 1 when animals do not interact, $\alpha > 1$ represents behavioral interference between animals such that others decrease the probability, and $0 \leq \alpha < 1$ represents social facilitation, where other animals increase the probability that an individual eats the poisoned bait. The value of α is assumed to be related to the weight (W) of each animal, such that larger animals experience less interference from others, and less social facilitation. This relationship is not formalized here, but will be examined elsewhere.

The probability that an animal ingests a lethal dose of poison given that it has eaten the bait (P(D/E)) is a positive saturation function of the dose of poison bait ingested (f)/ weight of animal (W)). This is based on the classic dose-response relationship when the dose is expressed on an arithmetic scale (Snyder 1984). A simple equation for this is:

$$P(D/E) = \frac{a\left(\frac{f}{W}\right)}{\left(\frac{f}{W}\right) + b} \qquad (6)$$

$$= \frac{a\,f}{f + bW}$$

where $0 \leq a \leq 1$ and $b > 0$. The maximum probability is a, and when $a = P(D/E) = 1.0$ then b is the dose/weight at which the probability (P(D/E)) is 1/2; the LD_{50}.

The weight of poisoned bait eaten (f) is the sum of the weight of bait (food) eaten (Wb) and the weight of poison eaten (Wp).

$$f = Wb + Wp \qquad (7)$$

The weight of bait eaten (Wb) is assumed to be a positive saturation function of the weight of poison bait available ($\bar{x}$), bait dispersion (i), a function of behavioral interference or facilitation among animals that find the bait (β), and the time bait is available (T).

$$Wb = \left(\frac{k_2 \quad \bar{x}^i \quad T}{1 + (k_2 t_1 \bar{x} + k_3 t_2 AF)^i}\right)^{\beta} \quad \text{for } k \geq 0 \qquad (8)$$

where k_2 is the maximum weight (kg) of bait that can be eaten, AF is the weight of alternate food, t_1 is the handling time for each bait unit, t_2 is the handling time for each alternate food unit, k_3 is a coefficient and $\beta = 1$ when there is no interference between animals. When $0 < \beta < 1$ other animals decrease an individual's intake, and when $\beta > 1$ other animals facilitate greater bait intake. Hence this incorporates the effect of social rank (Brown 1975). The value of β is, as for α, a function of body weight (W).

The part of equation (8) in the outer brackets is the multispecies equivalent of the functional response of a predator or herbivore to changes in prey abundance (Lawton et al. 1974). Real (1979) showed that random prey dispersion generated a Type III response, which occurs when $i > 1$, so this was added to the basic model. Other types of functional responses (Marten 1973) are not described here but may be incorporated later. Similarly the two-prey equivalent of the Rogers (1972) random predator equation (Lawton et al. 1974) is not discussed, other than the note that it is relevant when feeding significantly reduces bait abundance ($\bar{x}$).

The maximum weight of bait eaten by an animal (k_2) is assumed to be linearly related to its maintenance energy requirements, which is related to body weight (Kirkwood 1983) as:

$$k_2 = d\,W^{0.75} \qquad (9)$$

where d is a coefficient such that $d > 0$.

The weight of poison eaten (W_p) is related to the concentration of poison (C) in the poisoned bait.

$$C = \frac{W_p}{W_p + Wb} \qquad (10)$$

Rearranging equation (10) gives:

$$W_p = \left(\frac{C}{1 - C}\right) Wb \qquad (11)$$

Substituting for k_2 in equation (9) into equation (8), then modified equation (8) and equation (11) into equation (7), and equation (7) into equation (6) gives:

$$P(D/E) = \frac{a(dW^{0.75}\bar{x}^{i}T)^{\beta}}{(dW^{0.75}\bar{x}^{i}T)^{\beta} + b(1 + (dW^{0.75}t_1\bar{x} + k_3t_2AF)^{i})^{\beta}W(1 - C)} \tag{12}$$

We now have estimates of P(E) (equation (5)) and P(D/E) (equation (12)). Substituting for each in equation (4) gives:

$$P = \left(\frac{k_1t}{x_1 + t}\right)^{\alpha} x \frac{a(dW^{0.75}\bar{x}^{i}T)^{\beta}}{(dW^{0.75}\bar{x}^{i}T)^{\beta} + b(1 + (dW^{0.75}t_1\bar{x} + k_3t_2AF)^{i})^{\beta}W(1 - C)} \tag{13}$$

Equation (13) indicates that the probability that an animal dies is a function of 17 control parameters. As equation (13) includes two terms each with divisions, then the value of p will be determined by the relative value of parameters in the numerator and denominator of each term, rather than the absolute value of each parameter.

The strategic planning options are defined by the above relationships (Table 2). However, of all 17 parameters operators have direct control over only $\bar{x}$ (bait density), i (degrees of bait randomness or clumping), C (poison concentration) and T (time bait is available). By prebaiting (also called free-feeding) operators attempt to increase t (number of times an animal finds the bait) to increase the probability of dying. Rowley (1958) reported an increase in the number of rabbits feeding on bait, with days since start of free-feeding, indicating an increase in the probability of eating bait (P(E)). Rowley (1958) also noted the social effect of feeding on the bait, corresponding in this model to social facilitation ($0 < \alpha < 1$) increasing the probability of eating. Krebs et al. (1972) reported a similar effect of group foraging on the behavior of captive great tits (Parus major). Operators have partial control over behavioral interactions (α and β) by careful design of poison sites.

Table 2. Control parameters that influence the probability of an animal dying in a poisoning program, based on a model for random bait dispersion and random pest search pattern. Control strategies suggested by the model to increase the probability and a subjective assessment of the degree of operator control over each control parameter are also listed. Strategies for other bait dispersion, search pattern combinations are outlined in the text.

No.		Control parameter	Control strategy	Degree of operator control
1	k_1	Maximum value of P(E)	Increase	Limited
2	t	Times animal finds bait	Increase	Partial
3	x_1	Coefficient	Decrease	None
4	α	Behavioral interactions	Decrease	Partial
5	a	Maximum value of P(D/E)	Increase	Limited
6	d	Coefficient	Increase	None
7	W	Animal weight	Decrease	Limited
8	$\bar{x}$	Poisoned bait abundance	Increase	Direct
9	i	Poisoned bait dispersion	Increase	Direct
10	T	Time bait available	Increase	Direct
11	β	Behavioral interactions	Increase	Partial
12	b	Susceptibility to poison	Decrease	Limited
13	t_1	Handling time of bait	Decrease	Limited
14	k_3	Coefficient	Decrease	None
15	t_2	Handling time of other food	Decrease	None
16	AF	Alternate food abundance	Decrease	Limited
17	C	Poison concentration	Increase	Direct

There is limited or no control over the average value of each other parameter. By strategic timing f poisoning, the amount of alternate food available (AF) and animal weight (W) can be decreased. Manging poison resistance, can decrease the LD_{50} (b).

ii) Clumped bait dispersion and random search pattern.

With clumped bait dispersion the above model (equation (13)) is altered, but only by setting i = 1.0. This generates a Type II functional response (Real 1979) and simplifies the model slightly. This corresponds to the situation of extreme clumping, where all the bait is in one location. The control options are the same as for the previous model. In both models the response to an increase or decrease of a control parameter will be a curvilinear change in the value of p.

(iii) Random bait dispersion and nonrandom search.

Many models of foraging by a predator have been developed to describe how a predator forages when it responds to food abundance and depletes its own food supply. Such foraging is equivalent to nonrandom search by an animal. Mathematical description of this foraging usually assumes prey occur in patches with the patches randomly distributed. Pulliam (1974) developed a foraging model for random distribution of prey and systematic searching by the foraging animal. This will form the basis of the discussion here. Similar equations were described by Charnov (1976a), Belovsky (1984) and Persson (1985). The stopping rates are not discussed here other than to recognize they are a basic mechanism of nonrandom search.

The model developed by Pulliam (1974), described the number of prey eaten per-unit-time when two prey types were available. These correspond to the bait and alternative food which is invariably present. Pulliam's equation (9) when translated to familiar terminology and including the effect of behavior (β) is:

$$Wb + W_{AF} = \left(\frac{(\bar{x} + AF)T}{1 + t_1\bar{x} + t_2AF}\right)^{\beta} \qquad (14)$$

where W_{AF} is the weight of alternate food eaten per-unit-time, AF is the weight of alternate food available, t_1 is the handling time for each alternate food unit, and T is the time bait is available. This equation is very similar to the functional response in equation (8)--both are positive saturation equations. Differences between the equations will be discussed elsewhere.

Rearranging equation (14), and substituting as before, into equation (6) gives:

$$P(D/E) = \frac{a((\bar{x} + AF)T)^{\beta} - aW_{AF}(1 + t_1\bar{x} + t_2AF)^{\beta}}{((\bar{x} + AF)T)^{\beta} - (1 + t_1\bar{x} + t_2AF)^{\beta}(W_{AF} + bW(1 - C))} \qquad (16)$$

We now have estimates of P(D/E) (equation (16)) and P(E) (equation (5)), so substituting for each in equation (4) gives:

$$P = \left(\frac{k_1 t}{x_1 + t}\right)^{\alpha} \times \frac{a((\bar{x} + AF)T)^{\beta} - aW_{AF}(1 + t_1\bar{x} + t_2AF)^{\beta}}{((\bar{x} + AF)T)^{\beta} - (1 + t_1\bar{x} + t_2AF)^{\beta}(W_{AF} + bW(1 - C))} \qquad (17)$$

Equation (17) shows that the probability that an animal dies is a function of 16 parameters. The strategic planning options are as listed in Table 1, with the exceptions of increasing the coefficient d, and bait dispersion i. A new strategy is to decrease the value of the weight of alternate food eaten (W_{AF}), though this is under limited operator control. Of all parameters only bait density ($\bar{x}$), poison concentration (C) and the time bait is available (T) are under direct operator control.

Pulliam (1974) also developed a model for clumped prey distribution. It is not used in the next section, as it assumed that once an animal found a clump it consumed all prey in the clump before going to the next clump. Clearly this violates the marginal value theorem of Charnov (1976b), or other stopping rules (Iwasa et al. 1981, Green 1984).

(iv) Clumped bait dispersion and nonrandom search.

Most situations of poisoning vertebrate pests involve poisoned bait distributed in clumps, and pest animals searching for it, with a nonrandom search pattern.

Caraco and Pulliam (1984) outlined a model for a group of n animals exploiting food in a patchy environment. Extending the model by including alternative food the average amount of food (poisoned bait and alternate food) consumed by individuals ($W_b + W_{AF}$) in the group in a patch is given by

$$W_b + W_{AF} = \frac{\bar{x} + AF}{n}(1 - e^{-hnT}) \qquad (18)$$

where $\bar{x}$ + AF is the initial food abundance in a patch (≡ weight of poisoned bait offered + alternate food), h is a coefficient, T is the time in the patch (≡ time at a bait station), e = 2.718 and n is the number of animals that eat the bait.

Caraco and Pulliam (1984) described the situation where no interference occurred between animals feeding in a patch, i.e., $\beta = 1$ where:

$$W_b + W_{AF} = \frac{\bar{x} + AF}{n^{\beta}}(1 - e^{-hn^{\beta}T}) \qquad (19)$$

Behavioral interference occurs when $\beta > 1$, and when $o < \beta < 1$ social facilitation occurs.

Further, they assumed that when one individual had located a food patch, other members of the group immediately congregated there and started feeding. This is equivalent to the limiting value of 0 for α, because of the social facilitation.

Caraco and Pulliam (1984) assumed $P(E) = 1.0$; however, in the more general case here we will not be so restrictive. An estimate of $P(E)$ is given by equation (5). An estimate of $P(D/E)$ is given by equation (6), however, f is now estimated from equation (19).

Substituting for f from equation (19) into equation (6) gives:

$$P(D/E) = \frac{a(\bar{x} + AF)(1 - e^{-hn^{\beta}T}) - aW_{AF}n^{\beta}(\frac{1}{1-C})}{(\bar{x} + AF)(1 - e^{-hn^{\beta}T}) - n^{\beta}W_{AF}(\frac{1}{1-C}) + bW} \qquad (20)$$

Substituting for $P(E)$ and $P(D/E)$ in equation (4) gives:

$$p = \left(\frac{k_1 t}{x_1 + t}\right)^{\alpha} \times \frac{a(\bar{x} + AF)(1 - e^{-hn^{\beta}T}) - aW_{AF}n^{\beta}(\frac{1}{1-C})}{(\bar{x} + AF)(1 - e^{-hn^{\beta}T}) - n^{\beta}W_{AF}(\frac{1}{1-C}) + bW} \qquad (21)$$

Equation (21) indicates that the probability that an animal dies is a function of 15 parameters. This is only slightly simpler than the models above for random search (Equation 13). The control strategy options are again similar to those outlined in Table 1, with several exceptions and additions. The exceptions are changes to d, i, t_1, k_3 or t_2 as they do not appear in equation (21). Two new variables are included: a coefficient h and the number of pest animals that eat the poisoned bait n. In both cases the control strategy is to increase the parameter which is under limited or no operator control.

Caraco and Pulliam (1984) showed that when feeding interference within a group of n foragers did not occur ($\beta = 1$) and animals foraged optimally, the rate of food intake was the same for individuals whether they were in a group or not. Also they showed the variance on daily intake per individual was n times greater for solitary than group foragers. Clark and Mangel (1984) also reported a model that predicted a reduction in the variation in individuals feeding when in a flock. Since feeding interference is unlikely to be nonexistent, these interesting results may not be of general application, but they identify an interesting area for applied research. When feeding interference occurs, an increased variance in food intake could be expected and would have important practical consequences. Conway (1981) described a model developed by Comins, which showed the consequences of each pest receiving an equal pesticide dose or an unequal dose. The latter situation increased the proportion of the population subject to a low dose and hence to higher selection for pesticide resistance. In our example feeding interference could be the mechanism producing the same result because of the increased variability in poison intake. This possibility has not been widely discussed in managing resistance to anticoagulant pesticides in rodents or other species.

CONCLUSION

Many strategic planning options for poisoning vertebrate pests have been described. The planning options for different ecological situations are very similar. Some options are currently used, such as varying the poison concentration, and amount, location, and temporal availability of poisoned bait. Other options have had limited or no use, such as using small baits to decrease handling (eating) time per-bait-unit, poisoning when there is limited alternative food, and designing bait packets or stations to decrease behavioral interference between animals.

The modelling shows how many control parameters interact in complex, usually nonlinear relationships. The models provide a theoretical framework for explaining why particular events occur when poisoning vertebrate pests. Aspects of foraging ecology are suggested as a useful area for applied pest research. Demographic characteristics (e.g., age and sex) of pest populations influence poisoning kills in several ways, especially as determinants of pest body weight, which directly influence food intake, behavior and poison susceptibility. Pest species with a large variation in body weight, such as large mammals, should have more variable responses to poisoning than small mammals. As a consequence they may develop greater pesticide resistance independent of any contribution from different breeding rates.

The models outlined describe some of the essential features of poisoning programs and reveal interesting relationships between various factors influencing the probability that an animal is killed. The models are more than an analogy but less than a facsimile of poisoning vertebrate pests. The strategic planning uses of the models are obvious, and some agreement exists with laboratory and field data. Further development will refine the strategic and predictive applications of these models.

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