

Chapter 3

The Attraction of Free Ranging Feral Boars to Caged Oestrous and Non-oestrous Feral Sows.

3.1 Introduction

The rather loose social organisation of wild pigs in relation to other ungulates has been described in Chapter 1. To recapitulate boars are generally solitary and occupy a substantially larger home range than sows. The mooted reason for the larger home ranges in many mammals is for males to cover the home ranges of as many females as possible (Cameron & Spencer 1985), raising the question, can boars detect the presence of sows at a substantial distance and can they also detect the sow's sexual status or do they rely on random encounter?

There are obvious selective advantages to a male in being able to detect a female's sexual status at a distance. The evidence from domestic pigs is equivocal. In domestic pigs Signoret (1970) concluded boars were unable to detect a sow's sexual status without mounting but McGlone and Morrow (1987) showed some boars consistently preferred sows in oestrous in T-maze trials.

It is possible given the variation in the responses of domestic boars to domestic sows in oestrus that during domestication boars have lost their acuity in detecting a sow's sexual status. Barrett (1978) observed up to 10 feral boars gathered around oestrous sows in the wild. As one boar dominated mating before less dominant boars participated, most of the boars would not have had the opportunity to mount the female and elicit the "standing response", diagnostic of oestrus. This implies they must be responding to some other cue such as, the scent of feral sows, a pheromone released by the oestrous sows, a pheromone released by the boars during their

frequent urination during sexual excitement or simply the commotion raised by the other boars.

Choquenot *et al.* (1993) could not improve trapping success for feral boars by placing oestrous sows in traps. However the population they studied had been extensively trapped and 80% of pigs removed and so only extremely trap shy individuals remained.

If boars can detect the presence of sows and their sexual status it has important implications for the spread of exotic livestock diseases. This is because movement rates of individuals and contact rates between individuals are important parameters governing the likelihood of persistence and rate of spread of an exotic livestock disease (Pech & Hone 1988, Pech & McIlroy 1990). The aim of this study was to determine whether free ranging feral boars were attracted to caged sows in oestrous, non-oestrous caged sows or empty cages. If there was a strong attraction between boars and caged sows it offers a useful technique for manipulating the movements of feral boars and hence constraining the spread of an exotic disease and enhancing the efficacy of control measures.

3.2 Methods

In the 9 months prior to this experiment 12 adult boars (> 1 year old) were trapped and fitted with radio collars using the method described in chapter 2. Data from these boars was also used in the analysis of habitat selection described in Chapter 2.

The eight sows used in this experiment were wild caught in the Macquarie Marshes 500 k east of the study site and housed in individual pens at the Agricultural Research Centre, Trangie, New South Wales. All sows were morphologically indistinguishable from Nocolleche sows. Sows were allocated at random to one of two groups non-oestrous or oestrous. Oestrus was induced in the oestrous group by

including 20 mg day⁻¹ of the progesten altrenogest (Regumate®) in their ration for a period of 14 days. altrenogest was withdrawn from the ration nine days prior to the desired date of oestrus, as Kilgour and Choquenot (1994) have shown that oestrus appears in feral sows commences eight to 11 days after the cessation of altrenogest feeding. Ovarian activity was also suppressed in the non-oestrous group by 20 mg day⁻¹ of altrenogest in their ration which was maintained throughout the duration of the study. Oestrus was determined by inspecting the vulva and assigning it a rank. The ranks were 1; dry with no swelling, 2; thick creamy mucus and some swelling, 3; thin copious mucus with pronounced swelling. Sows are considered to be in oestrus only if their vulvae are ranked at 3. Of the four sows in which an attempt was made to induce oestrous only two had vulvae ranked 3. Only two sows are therefore deemed to have come into oestrus.

In July 1992 sixteen 3m x 3m weldmesh steel cages were built within the home ranges of most of the 12 boars. The position of each boar was recorded at hourly intervals for five days according to the protocol described in chapter 2. The hourly position of each boar was calculated using the program LOCATE II and from this his distance to each cage was measured. From these, data was calculated a mean distance for each boar for the entire five days. Mean distances rather than individual distances were used in subsequent analyses because as the hypothesis being tested is about the population of boars rather than individual boars, using individual distances pooled for all boars will inflate the number of degrees of freedom and therefore increase the probability of making a Type-I Error (Aebischer *et al.* 1992).

One day after cessation of this tracking session a single sow was installed in each of eight cages. Two of the sows were oestrous and six were non-oestrous. Each sow was provided with food (wheat) and water *ad libitum*. Branches were placed over and around one corner of the cage to provide shelter. The vulvae of sows were examined daily by an experienced observer. Four of the 12 cages remained empty

as controls but were provisioned identically to the cages containing sows. The cages were widely dispersed and spaced at least 500m apart. Treatments were allocated so as to be interspersed (Hurlbert 1984), this was qualified by the failure of all treated sows to come into oestrus.

Radio tracking recommenced 48 hours after the end of the first tracking session and 24 hours after the sows were installed. This tracking session followed an identical procedure to the first tracking session and continued for four days until all sows showed no signs of oestrus. Again the mean distance between each boar and each cage was calculated.

This procedure produced two data sets, the first being the mean distance between each boar and each cage before exposure to the sows, the second being the mean distance between each boar and each cage after exposure to the sows. From the after exposure mean distances the shortest mean distance between a boar and a cage for each treatment was selected. This gives three shortest mean distances for each boar, one to each treatment. The shortest mean distance was chosen because it was assumed that if boars are attracted to a particular treatment they will move close to one particular cage in that treatment. From these three shortest mean distances were subtracted the mean distance to the same cage for the tracking session prior to the installation of the sows. The difference if positive indicated that the boar had moved on average closer to a cage between tracking sessions. If negative the boar had on average moved further away. The differences in mean distance for all 12 boars were then compared for significant difference from zero in three *t*-tests, for oestrous, non-oestrous, and control treatments. If the *t*-ratio is significant and positive it indicates attraction by the boars to a treatment, if negative and significant a repulsion by the boars to a treatment.

3.3 Results

The mean minimum distance between boars and treatments is shown in Figure 3.2. None of the three *t*-tests had significant outcomes (Table 3.1). This indicates there was neither attraction or repulsion to any of the three treatments. When three of the mean change in distances for boars were eliminated whose home ranges were on the periphery of the study area the *t*-ratio remained non-significant (Table 3.2). However, the tracks of a juvenile pig were detected in the sand next to an oestrous sow cage and the tracks of a juvenile and adult pig were detected in the sand next to the cage of a non-oestrous sow.

3.4 Discussion

This experiment was designed to test whether oestrous sows could be used to alter the dispersion of boars. It was not designed to test the interaction between sexes of free ranging feral pigs. These results show it is not possible to influence the dispersion of feral boars by the placement of oestrous or anoestrous sows. If it is assumed an oestrous sow is innately attractive to a boar then several factors could have militated against a significant result:

1) The metal cages may have repelled boars. This is possible but most of the boars had been caught several times in metal traps similar to the cages and continued to be caught after this experiment. Radio collared sows could have been released and their positions monitored and compared to the position of boars. However given the uncertainty in inducing oestrus and the impossibility of determining the status of free ranging radio-collared sows this technique may not have yielded reliable results.

2) The sows were not local and the boars may have been wary of unknown pigs. An alternative approach to this would be to use sows caught at Nocolche for the

experiment but the lack of facilities for holding pigs at Nocoleche (2-3 weeks to acclimatise, and then induce oestrus) precluded this.

3) There were abundant free ranging feral sows, and boars may have been responding to the movements of these rather than the caged oestrous sows. Sows were seen in the company of boars at Nocoleche.

4) Encounter between sows and boars is entirely opportunistic and the length of time the oestrous sows were exposed was insufficient for boars to encounter the caged sow, remain by the cage and be detected by radio telemetry. By analogy Choquenot and Kilgour (1993) demonstrated that percentage of bait taken by feral pigs in the New South Wales highlands did not peak until the fourth day of baiting.

Reasons 1 to 3 presuppose that boars can detect the presence of sows or metal cages at a distance. This remains unknown but pheromones do play a role in the reproductive behaviour of both male and female pigs (Booth 1980, Dorries *et al.* 1991). Pigs have a keen sense of smell although the effective range of the pheromones is unknown and likely to be strongly influenced by intensity of odour, wind direction and ambient temperature.

While the attraction of boars to oestrous sows is problematic, the attraction of oestrous sows to boars is established (Signoret 1970). A more appropriate experiment may have been to place boars in traps and monitor the locations of sows.

Table 3.1 *t*-test of change in mean distance between cages and boars following addition of treatments. M.C.D.: Mean change in distance in metres. S.E. of M.C.D.: Standard error of mean change in distance in metres. N = 12.

	Oestrous sows	Non-oestrous sows	Empty cages
M.C.D.	-95.87	-8.83	69.98
S.E. of M.C.D.	139.79	118.1	127.99
t-ratio	-0.686	-0.075	0.547
Significance	<0.5	<0.9	<0.5

Table 3.2 *t*-test of change in mean distance between cages and boars following addition of treatments. Three boars on periphery of study area excluded. M.C.D.: Mean change in distance in metres. S.E. of M.C.D.: Standard error of mean change in distance in metres. N = 9.

	Oestrous sows	Non-oestrous sows	Empty cages
M.C.D.	-62.52	53.21	164.32
S.E. of M.C.D.	162.10	143.59	135.43
t-ratio	-0.386	0.371	1.213
Significance	<0.5	<0.5	<0.2

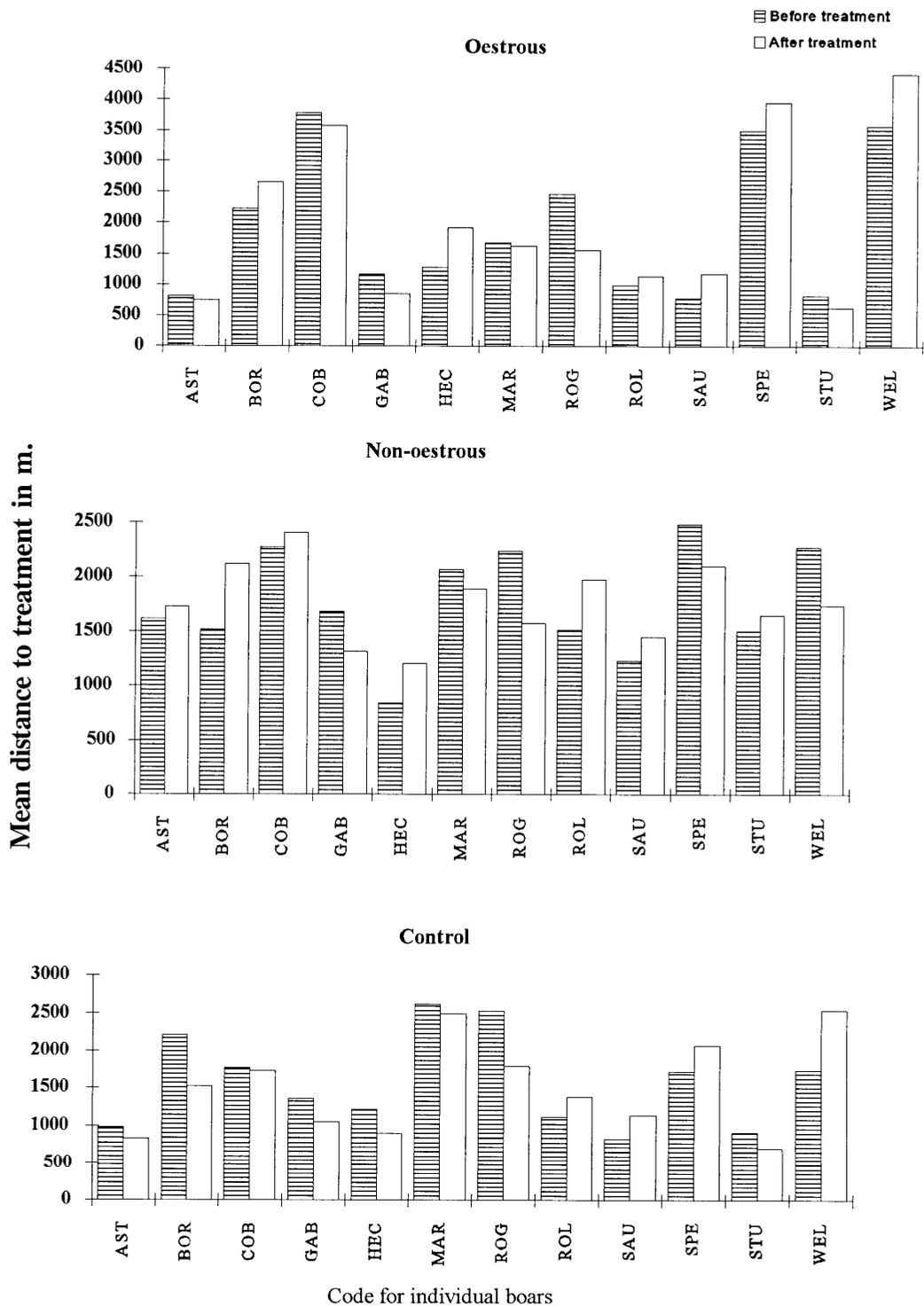


Figure 3.1 Mean before treatment and after treatment distances in metres, between boars and oestrous sows, non-oestrous sows and control.

Chapter 4

Models of Foot and Mouth Disease in Feral Pigs in the Semi-arid Rangelands.

4.1 Introduction

The danger to Australia's livestock industry posed by feral pigs as potential vectors of exotic diseases is well recognised (O'Brien, 1989, Wilson and O'Brien 1989). FMD, because of its potential to severely damage Australia's livestock export industry, has received particular attention. Feral pigs share the semi-arid rangelands with large numbers of domestic cattle and sheep with which they are often in close contact (O'Brien 1989).

In the event of an outbreak of FMD, current policy is to slaughter all host animals within a core area and test all animals within a surrounding buffer zone (Hone & Pech 1990). However, because feral pigs occupy large areas of Australia remote from human settlement receiving only sporadic veterinary surveillance, Hone and Pech (1990) estimated that the probability of detecting FMD in feral pigs is very low and that up to 3000 cases may occur before detection. Further problems occur because feral pigs are shy, nocturnal, and cryptic so that even in the best case scenarios only 80% could be killed by helicopter shooting (Saunders & Bryant 1987). This means that the goal of slaughtering all animals within a core will be difficult to achieve. An alternative may be to force the abundance of feral pigs below the threshold abundance N_T , below which the disease can not persist.

A complimentary approach has been to develop models which predict the level of feral pig control required to eliminate FMD in feral pig populations (Pech and Hone 1988) and the rate at which an FMD outbreak would spread through such populations (Pech and McIlroy 1990). Demographic and behavioural parameters for these models were derived from studies of feral pigs, while disease parameters were inferred from veterinary literature on epizootics of FMD in domestic pigs. Both models were

derived from deterministic fox rabies models (Anderson *et al.* 1981) which assume that populations of hosts grow logistically, demographic rates being a direct function of prevailing population density.

As host population density is a critical parameter in any non-sexually transmitted disease (Anderson & May 1991), the unpredictable nature of semi-arid grazing systems implies that disease models with deterministic population parameters for the herbivore (host) component of the system are unlikely to be realistic. Despite eating some carrion and live animals, pigs are overwhelmingly herbivores in the semi-arid rangelands (Giles 1980). Semi-arid grazing systems are characterised by low and erratic rainfall, high summer temperatures and an evaporation rate that exceeds rainfall (Robertson *et al.* 1987). In these environments rate of change in herbivore abundance is heavily dependent upon prevailing vegetation biomass (Bayliss 1985), which in turn is largely dependent on rainfall which fluctuates unpredictably (Noy-Meir 1973). Resultant stochastic variation in herbivore density must be taken into account if disease models are to be accurate. Feral pig populations in semi-arid environments do not grow logistically (Giles 1980, Choquenot 1994). Variation in demographic rates and consequent direction and rate of change in population abundance are more related to prevailing environmental conditions (primarily food supply), than to population density.

Another critical parameter in disease models is β . This parameter describes the rate at which disease is transmitted between individuals which is partially determined by the contact rate between individuals and the infectiousness of the disease. Pech and Hone's (1988) model used data from Giles (1980) to infer contact rate between pigs. Pech and McIlroy (1990) measured contact rate from radio collared pigs in Namadgi National Park, Australian Capital Territory. As contact rate is in part a behavioural parameter it is likely to be influenced by a complex of environmental and social forces and vary according to prevailing conditions. Although Pech and Hone (1988)

suggest a range of contact rates and hence β neither they nor Pech and McIlroy (1990) allow for stochastic or systematic variation in β . In this chapter contact rate in each of the 7 tracking sessions discussed earlier is measured and the variance in contact rate correlated with some environmental parameters.

In the spatial model of Pech and McIlroy (1990) the velocity of advance of an FMD epidemic is partially influenced by the diffusivity parameter D . The parameter D is equivalent to a diffusion constant (Okubo 1980) and assumes the movement of pigs approximates a random walk. While this is an unrealistic assumption about the movements of most animals it has successfully described the movement of bubonic plague through human populations in Europe in the 14th Century (Noble 1974) and the spread of rabies in foxes (Murray *et al.* 1986). In this study D is estimated from hourly distances moved in each of the 7 tracking sessions.

The models described in this chapter differ from the models of Pech and Hone (1988) and Pech and McIlroy (1990) in that first the assumption of logistic population growth in feral pigs is removed and replaced with a series of functions which link variable rainfall to demographic rates through food supply. This stochastic model of feral pig population dynamics is linked to the compartmental disease model of Pech and McIlroy (1990). The next assumption removed is that of constant β and D within the disease model. This model is then run to examine (1) the behaviour of an FMD epizootic in a feral pig population inhabiting an unpredictable environment, (2) the probability of disease persistence in such an environment, (3) the influence of variable demographic and disease parameters on N_T , (4) the influence of variable demographic and disease parameters on the velocity of advance, and (5) the likely control effort required to contain an epizootic in such an environment.

4.2 Methods

FERAL PIG DENSITY AT NOCOLECHE

Feral pig density is a parameter necessary for calculating both the population and epidemiological components of this model. Density in the trapping session prior to each tracking session was estimated using the Jolly-Seber mark recapture technique for open populations (Caughley 1977). This technique was used for the first five trapping sessions but recaptures were too few for the tracking sessions April 93 and July 93, therefore the sum of all pigs caught, seen, and known to be in the study area by radio telemetry are used as a minimum estimate of density. As the Jolly-Seber method makes daily estimates of abundance the average daily estimate of abundance for the whole trapping session was calculated. To estimate density the area of the minimum convex polygon described by all radio telemetry locations for each tracking session was divided by the mean abundance estimated for the preceding trapping session. Results are contained in Table 4.1. The estimates of density are lower than those estimated by Choquenot (1994) for the whole of Nocolleche (3.36 pigs km⁻² with a standard deviation of 1.5 pigs km⁻²), although Choquenot's figures also covered very good environmental conditions when pig abundance was high preceding the drought. The decline in density with improving conditions in 1993 may be related to pigs spreading out to occupy the shrubland habitat rather than an actual decrease in density.

Table 4.1 Density of Feral pigs at Nocoleche Nature Reserve by Jolly-Seber technique. *Minimum number of pigs known to be in the area.

Trapping session	Jolly-Seber estimate \pm 1SE	Area of minimum convex polygon in km ²	Density km ⁻²
November 91	39.9 \pm 7.9	46	0.85
February 92	39.4 \pm 16.0	39	1.18
April 92	25.0 \pm 10.3	58	0.41
July 92	26.7 \pm 5.2	103	0.26
November 92	29.8 \pm 5.3	73	0.41
April 93	16*	57	0.28
July 93	17*	78	0.21

STOCHASTIC POPULATION MODEL

The model of pig population dynamics used in this study was an extension of a stochastic herbivore model derived empirically by Caughley (1987) to describe the interactive grazing system comprising red kangaroos *M. rufus* and the chenopod shrubland pastures of Kinchega National Park in south-western New South Wales. To this is added the population dynamics of feral pigs through their numerical response to pasture biomass.

The three components of this system are change in vegetation biomass, change in kangaroo abundance, and change in pig abundance. These changes can be described by

$$dV/dt = F(V,R) - C(K,P,V) \quad (4.1)$$

$$dK/dt = r_k(V)K \quad (4.2)$$

$$dP/dt = r_p(V)P \quad (4.3)$$

In these equations R is rainfall that fluctuates stochastically, V is vegetation biomass, F is a function describing vegetation biomass in the absence of grazing, and C is a function describing the removal of vegetation by kangaroos K and pigs P . In equations 4.2 and 4.3 r_k and r_p are the rates of increase for kangaroos and pigs respectively. The function F takes the form

$$F = -55.12 - 0.01535V - 0.00056V^2 + 4.9R \quad (4.4)$$

This function was derived empirically by Caughley (1987) for pastures similar to those at Nocolche and describes the influence of rainfall and existing vegetation biomass on change in vegetation biomass. Biomass increases with increasing rainfall but the rate of increase decreases with increasing biomass as there is density dependent limitation on plant growth. The function C takes the form

$$C = K[86(1 - e^{-V/34})] + P[58(1 - e^{-(V-92)/302})] \quad (4.5)$$

This function describes the amount of vegetation biomass eaten as the sum of the functional responses of pigs and kangaroos. The kangaroos functional response was estimated by Short (1987) for kangaroos of a uniform 35 kg in graze down trials at Kincheha National Park, while the functional response of pigs was estimated by Choquenot (1994) for pigs of a uniform 40 kg in graze down trials at Trangie Agricultural Research Station. The numerical response equations describing the change in herbivore abundance were

$$r_k = -1.6 + 2(1 - e^{-0.007V}) \quad (4.6)$$

$$r_p = -2.045 + 2.78(1 - e^{-0.0055V}) \quad (4.7)$$

In both equations r increases asymptotically with increasing vegetation abundance. Equation 4.6 was estimated by Bayliss (1987) for kangaroos at Kinchega National Park while 4.7 was estimated by Choquenot (1994) for pigs over the entire Paroo-Cuttaburra System.

The model devised by Caughley (1987) was interactive (Caughley & Lawton 1981) with vegetation biomass strongly affecting kangaroo abundance and also kangaroo abundance lowering the long term vegetation biomass by deepening the troughs in vegetation biomass during drought, and cropping off the peaks in vegetation biomass during flushes in vegetation growth following abundant rains. The chief characteristic of this system was that it was centripetal. That is there is a negative feedback loop such that the system tends to return towards some equilibrium which is never achieved because of the perturbing effects of erratic rainfall. While this two species model may seem to violate the competitive exclusion principle (Barlow 1987) kangaroos and feral pigs do coexist in the rangelands. It is likely that this model mirrors reality because although red kangaroos are more efficient grazers than pigs, and in a completely stable environment kangaroos would eliminate pigs, the pigs much higher rate of increase would allow pigs to out compete kangaroos when pasture biomass is extremely high. The validity of adding feral pigs to the model was tested by converting each of 4.1, 4.2 and 4.3 into difference equations at a quarterly time step. The driving variable for this model R was drawn from the relevant quarterly rainfall distribution with mean and variance equal to the 100 year seasonal average for Wanaaring. For each quarter for a 100 year simulation R was a random draw from this distribution. Initial vegetation biomass estimates were 295 kg ha^{-1} , initial kangaroo abundance was 45 km^{-2} , both from Caughley (1987) while pig abundance was 0.47 km^{-2} from the average density of pigs from the seven estimates of density in Table 4.1. The criteria for validity were whether the biomass of vegetation, and abundance of both herbivores remained within levels reported in the

literature and did not decline or decrease exponentially. This can be seen in a sample run of 100 years in Fig. 4.1.

CALCULATING β

Before developing the disease model and adding it to the model of pig population dynamics the transmission coefficient β must be calculated from the radio telemetry data gathered by the radio-telemetry methods described in Chapter 2. β is critical in the probability of establishment and velocity of spread of epidemic diseases such as rabies (Anderson & May 1979), classical swine fever (Hone *et al.* 1992), and FMD (Pech & Hone 1988).

Ideally β should be gathered from data from a real epidemic of FMD in feral pigs however this is not practical. β in this study was estimated using the method described by Pech & McIlroy (1990) and modified by Cayley (1993). Parameters used in these calculations are contained in Table 4.2.

For each tracking session the hourly locations of all k radio collared pigs were recorded using the methods described in Chapter 2. Many locations were not recorded because signals were not received. From this the total number of possible distances s between pairs of pigs were calculated by $k!/(k - 2)!2!$. Using the same criterion as Pech and McIlroy (1990) a contact was recorded when the distance between a pair of pigs was ≤ 200 m. Thus c/s contacts as a proportion of pair wise distances occurred. To estimate contact rate C and from this β the following equations are taken from Cayley (1993). If all pigs in the study area had been fitted with radio collars then the total number of pairwise distances would be

$$S = tN!(N - 2)!2! \quad (4.12)$$

Assuming k pigs are randomly mixing and representative of the total population then

$$C = cd(N - 1)/2sA \quad (4.13)$$

Hence contact rate pig^{-1} for a given area is proportional to N (Cayley 1993). From this β can be calculated as

$$\beta = cdA/sN \quad (4.14)$$

Cayley (1993) noted an error in Pech & McIlroy's (1990) calculation of β in that they calculated β in units of $\text{km}^2 \text{ day}^{-1}$ while β must be in units of $\text{km}^2 \text{ day}^{-1} \text{ pig}^{-1}$ for the βXY term to have the correct units of $\text{pigs km}^{-2} \text{ day}^{-1}$. This error increases β by a factor equal to the population size. Estimates of β calculated for each tracking session are contained in Table 4.3.

Table 4.2 Parameters used in the estimation of the transmission coefficient β .

k	=	number of collared pigs
c	=	number of individual contacts (pairwise distances $\leq 200\text{m}$)
s	=	number of pairwise distances
t	=	number of recording intervals day^{-1}
N	=	number of pigs
d	=	number of days in tracking session
A	=	study area in km^2 (minimum convex polygon of all locations for that tracking session)
C	=	contact rate

Table 4.3 Estimates of the transmission coefficient β for each tracking session.

Tracking session	β
November 91	0.27 km ² day ⁻¹ pig ⁻¹
February 92	0.36 km ² day ⁻¹ pig ⁻¹
April/May 92	0.32 km ² day ⁻¹ pig ⁻¹
July 92	1.26 km ² day ⁻¹ pig ⁻¹
November 92	0.54 km ² day ⁻¹ pig ⁻¹
April 93	1.64 km ² day ⁻¹ pig ⁻¹
July 93	0.25 km ² day ⁻¹ pig ⁻¹

DETERMINISTIC DISEASE MODEL

To describe the progress of an outbreak of foot and mouth disease in a feral pig population, Pech and Hone (1988) adapted a fox-rabies model of Anderson *et al.* (1981). This model assumed logistic population growth with an equilibrium pig density, K . Per capita birth rate, a , was fixed and death rate in the absence of FMD, b , assumed to be density-dependent and linearly related to population density, N . Hence, death rate when density-dependent resources are not limiting, b , is modified by $(b + gN)$, where g summarises the constraints on survival with increasing density. The logistic model of animal population growth assumes that food supply is constant, and not modified by the animals utilising it (Caughley 1976).

Pech and Hone (1988) constructed a compartmental model in which individual pigs move through four categories according to their disease status; susceptibles (X), latents (I), infectives (Y) and immunes (Z). Susceptibles have never been exposed to

FMD or have lost their immunity, latents have acquired the disease but are not excreting the virus, infectives are excreting the virus and immunes have recovered from the disease and have temporary immunity. Pech and Hone (1988) estimated the rate animals move between these categories by:

$$dX/dt = (a - b - gN)X - \beta XY + \omega Z \quad (4.6)$$

$$dI/dt = \beta XY - (b + gN + \sigma)I \quad (4.7)$$

$$dY/dt = \sigma I - (b + \alpha + gN + \upsilon)Y \quad (4.8)$$

$$dZ/dt = \upsilon Y + (a - b - gN - \omega)Z \quad (4.9)$$

$$dN/dt = a(X + Z) - (b + gN)N - \alpha Y \quad (4.10)$$

The parameter estimates used to derive rates of movement between compartments for the deterministic model (taken from Pech and Hone (1988)) are described in Table 4.4. Pech and Hone (1988) showed that at a density of 15 pigs km⁻² and a β of 0.026 model the disease became endemic after initial oscillations in abundance of pigs within disease classes. This model of Pech and Hone (1988) was tested with data obtained in this study. K was set at the mean density of pigs recorded at Nocoleche 0.47 pigs km⁻², and β was set at 0.73 km² day pig⁻¹.

Table 4.4 Parameters used in FMD-feral pig model

X = density of susceptibles

I = density of latents

Y = density of infectives

Z = density of immunes

N = density of pig population

a = birth rate in absence of FMD = 0.0025 day⁻¹

b = death rate in absence of FMD = 0.00089 day⁻¹

r = rate of increase in absence of FMD (= $a-b$) = 0.0016
day⁻¹

K = carrying capacity 0.47 pigs km⁻²

g = density dependent death rate in the absence of FMD =
0.00011 day⁻¹

α = death rate due to FMD alone = 0.0064 day⁻¹

β = FMD transmission coefficient = 0.73 pigs⁻¹ km⁻² day⁻¹

σ = rate of change from latent to infective = 0.5 day⁻¹

υ = rate of recovery = 0.17 day⁻¹

ω = rate of loss of immunity = 0.011 day⁻¹

STOCHASTIC DISEASE MODEL I

To remove the assumption of logistic growth in the host population and the requirement for an equilibrium pig density from the model of Pech and Hone (1988), day-to-day variation in demographic rates are estimated from the numerical response of pigs in the grazing system described earlier in this chapter rather than from the ratio of N to K . This involved first converting equations (4.1) to (4.3) to discrete

equations at a daily time step more appropriate to the rapid dynamics of a disease like FMD than the quarterly time step appropriate for pig population dynamics. The second step required eliminating the density-related component of death rate, gN , in equations (4.6) to (4.10) and replacing constant death rate, b , with variable death rate, b' , which fluctuates according to available pasture biomass. Values of b' are estimated daily as the difference between the prevailing rate of population increase, r , estimated by the numerical response of pigs and the instantaneous daily birth rate, a . In this way, while instantaneous birth rate remains constant, mortality rate varies stochastically with prevailing pasture biomass; increasing when food availability is low and decreasing asymptotically when it is high. Thus the equations describing the progression of the FMD epizootic become:

$$dX/dt = (a - b')X - \beta XY + \omega Z \quad (4.15)$$

$$dI/dt = \beta XY - (b' + \sigma)I \quad (4.16)$$

$$dY/dt = \sigma I - (b' + \alpha + \upsilon)Y \quad (4.17)$$

$$dZ/dt = \upsilon Y + (a - b' - \omega)Z \quad (4.18)$$

$$dN/dt = a(X + Z) - b'N - \alpha Y \quad (4.19)$$

where b' , like the density of pigs in various compartments, is recalculated daily. In this stochastic model I (SMI), β is deliberately kept constant at $0.73 \text{ km}^{-2} \text{ pig}^{-1} \text{ day}^{-1}$, the mean value of the seven estimates of β from Table 4.3. This is to determine the effect of stochastic variation in pasture biomass and hence death rate b' on the likelihood of establishment and persistence of an FMD epizootic.

To assess the influence of b' on the behaviour of FMD in pig populations the stochastic FMD model was run 300 times with initial density of pigs N_0 a random draw from a normal distribution of densities taken from Tab. 4.1 (truncated at 0.1 so as to avoid random draws of 0 density), initial density of infectives Y_0 set at 0.1 pigs km^{-2} (the same value as the Pech and Hone (1988) model), and initial density of

susceptibles X_0 set at $X_0 = N_0 - Y_0$. The model was run until the epizootic was deemed extinct when the density of latents fell below 0.0005 km^{-2} . (the same criterion used as Pech and Hone (1988)). For each iteration the duration of the epizootic in days and X_0 were recorded. X_0 was recorded because if X_0 is below N_T then the epizootic will not become established.

CALCULATING THRESHOLD DENSITY

As has been mentioned in the discussion of epidemiology in Chapter 1, R_0 and hence N_T is a parameter critical to the establishment of an epizootic. N_T is an abundance of susceptibles below which an epizootic will not persist if an infected individual is introduced to a susceptible population. To derive N_T for this model consider that the epizootic will not persist when the rate of change in latents and infectives = 0. So that $dI/dt = 0$, and $dY/dt = 0$, (Hone pers. comm.) therefore:

$$\beta XY - (b' + \sigma)I = 0 \quad (4.20)$$

$$\sigma I - (b' + \alpha + \upsilon)Y = 0 \quad (4.21)$$

When 4.21 is rearranged it gives:

$$Y = \sigma I / (b' + \alpha + \upsilon) \quad (4.22)$$

and when 4.22 is substituted into 4.20 and 4.20 rearranged:

$$X = [(b' + \sigma)(b' + \alpha + \upsilon)] / \sigma \beta \quad (4.23)$$

So that $X = N_T$. Therefore N_T will be sensitive to variation in death rate b' as well as β . This means N_T will be variable over the course of the epizootic unlike other disease models.

STOCHASTIC FMD MODEL II

The disease component of the model described in 4.15 to 4.19 is unrealistic in that β remained a constant despite the measurement of considerable variation in β over the seven tracking sessions. The purpose of the constant β was to describe the behaviour of an FMD epizootic where the demographic component alone varied. The next step is to include a variable β in the disease component of SMI to create a second disease model SMII. Before constructing this model it must be determined whether β varies according to some environmental parameter or whether it varies at random. To test this β was entered as the dependent variable into a stepwise multiple regression with pig density, temperature, and \ln total available pasture biomass in each tracking session as the dependent variables. Total available pasture biomass is the kg ha^{-1} of pasture available in each of the four habitat types multiplied by the area of that habitat in the minimum convex polygon enclosed by all pig locations. These four quantities are then summed and converted to natural logarithms to give an index of the total amount of pasture available. Total pasture availability is used because an explicit model for overall pasture growth is available (equation 4.5) but not one for each habitat. There was no significant effect of either density (despite density being incorporated in the calculation of β), temperature, or total pasture biomass on β ($F_{3,3}=0.27$, $R^2=0.2$, $P<0.84$). Therefore β in this model becomes a random variable β' . To incorporate β' into the stochastic disease model all other parameters remain the same but β' is a weekly draw from a normal distribution of β described by the seven values of β estimated from the seven tracking sessions. As it is assumed $\beta' > 0$, because there will always be some contact between pigs, to prevent β' equalling zero the distribution of β was truncated at 0.25 the lowest value of β which occurred in July 93. β' was redrawn at weekly intervals because that approximates the length of a tracking session, the interval β' was measured over in this study. I have no knowledge of how β' changes between tracking sessions.

As with SMI, this model was run for 300 simulations with the persistence time (measured as the time in days till density of latents fell below 0.0005 km^{-2}) recorded for each iteration as well as the initial density of susceptibles X_0 .

SPATIAL STOCHASTIC MODEL

The purpose of the spatial stochastic model SSM is to predict how fast the disease will travel. The SSM of FMD described here is an adaptation of the model of Pech and McIlroy (1990) who modified the compartmental model of Pech and Hone (1988) to accommodate movement in one dimension by incorporating a diffusivity constant D .

Diffusivity is calculated using the same formula used by Pech and McIlroy (1990) derived originally by Wilkinson (1952).

$$D = 1/4m(\Omega^2) \quad (4.24)$$

In this equation m is the number of daily straight line distances moved which as locations were estimated hourly gives $m = 24$. Ω^2 is the mean square length of straight line movements. The straight line movements were estimated in Chapter 2 under the heading movements. The values of D for each tracking session are contained in Table 4.5. As with β it is important to establish whether D should vary in accordance with some environmental parameter or whether it should fluctuate at random. To do this D for each tracking session was entered as the dependent variable in a stepwise regression with pig density, total pasture biomass available, and temperature as independent variables. None of the independent variables were significant ($F_{3,3}=0.45$, $R^2=0.31$, $P<0.73$), therefore D' is a random draw from the normal distribution of possible D described by the estimates of D for each tracking session. As pigs are assumed to always be doing some moving the distribution of D was truncated at 0.22 the lowest value of D to prevent D' equalling 0.

Table 4.5 Estimates of diffusivity D for each tracking session.

Tracking session	D
November 91	2.01 km ²
February 92	2.76 km ²
April/May 92	4.28 km ²
July 92	1.57 km ²
November 92	1.40 km ²
April 93	1.89 km ²
July 93	1.34 km ²

The model of Pech and McIlroy (1990) was used to calculate the minimum velocity V_{\min} in km day⁻¹ of an FMD epizootic in feral pigs for data collected from Namadgi National Park. The model I use takes the form

$$\partial X/\partial t = (a - b')Y - \beta'XY + \omega Z + D' \partial^2 X/\partial x^2 \quad (4.25)$$

$$\partial Y/\partial t = \beta'XY - (b' + \alpha + \upsilon)Y + D' \partial^2 Y/\partial x^2 \quad (4.26)$$

$$\partial Z/\partial t = \upsilon Y + (a - b' - \omega) + D' \partial^2 Z/\partial x^2 \quad (4.27)$$

In this model 4.25 corresponds to 4.15, 4.26 to 4.17, 4.27 to 4.18, and 4.28 to 4.19, while x is distance moved in one dimension. The equation describing the latent period has been combined with the equation describing the infective period in 4.26. This is because for a full model with a separate latent category V_{\min} can only be calculated numerically rather than analytically (Pech pers. comm.). To calculate numerically with simultaneously varying β' and D' would be mathematically

intractable. Pech and McIlroy (1990) presented some biological justification for this amalgamation citing Sellers *et al.* (1977) who showed that domestic pigs can redistribute FMD virus as soon as 30 minutes after exposure. The only difference this alteration makes to parameter values is to combine the latent and infectious period to give a value of $\nu = 0.125 \text{ day}^{-1}$.

The equation describing the minimum velocity of advance of an FMD epizootic in Pech and McIlroy's (1990) model is

$$V_{\min} = \sqrt{(\beta'ND')v_{\min}} \quad (4.30)$$

where v_{\min} is the scaled velocity. In the equation used by Pech and McIlroy (1990) K carrying capacity is used instead of N but K has been discarded for pigs in the semi-arid rangelands so that K is replaced by N for this equation. To derive v_{\min} using a derivation of the formula contained in the appendix of Pech and McIlroy (1990) gives,

$$v_{\min} = 2\sqrt{[1-a-b']/\beta'N-b'/\beta'N-\omega/\beta'N-\alpha/\beta'N-\nu/\beta'N]} \quad (4.31)$$

To estimate how V_{\min} changes during the course of an epizootic 100 simulations of the spatial model were run and the mean V_{\min} , maximum V_{\min} , and minimum V_{\min} for each iteration were recorded.

CONTROL EFFORT

To estimate the effort required to eliminate an FMD epizootic 100 simulations of the spatial model were run with the addition of a term calculating N_T according to equation 4.23 and subtracting this from N to give a density of pigs km^{-2} to be removed to place N below N_T and thus eliminate the epizootic. To give an estimate of the total effort required to eliminate the epizootic the effort km^{-2} was multiplied by

the total area covered by the epizootic. The total area covered by the epizootic was calculated by assuming the sum of the daily distances covered estimated from the V_{min} was the radius (r) of a circle describing the area covered by the epizootic. This meant that the total area covered by the epizootic equalled πr^2 with r equal to the sum of the daily advances made by the epizootic. The area covered and the total number of pigs required to be removed was calculated at weekly intervals for a simulation of an epizootic lasting six weeks.

4.3 Results

DETERMINISTIC DISEASE MODEL

Despite a much higher β (0.73 km^{-2} compared to 0.026 km^{-2}) and a much lower overall density of feral pigs (0.47 km^2 compared to 15 km^2) the dynamics of the FMD epizootic were similar to Pech and Hone's (1988) model with the disease parameters rapidly approaching stable equilibrium values after initial fluctuations in the abundance of the four disease classes (Figure 4.2).

STOCHASTIC DISEASE MODEL I

In contrast to the deterministic disease model the stochastic disease model described here predicted that FMD would never approach a stable equilibrium. The epizootic failed to persist longer than 4860 days in 300 simulations. The results of a typical simulation are presented in Figure 4.3 and Figure 4.4. These figures demonstrate that although FMD mortality in this model is low (5%) it can still lower density of feral pigs especially during periods when conditions are good and population growth high.

In this model N_T varies over the course of the epizootic as asserted in the methods. This can be seen in Figure 4.5 which is the variation in N_T over the course of an epizootic for the simulation shown in Figure 4.3. The influence that the stochastically varying parameter b' has over N_T can be seen in Figure 4.6 showing

that increasing b' increases N_T linearly and hence increases the probability of disease extinction.

The mean persistence time for the epizootic was 1045 days with a standard deviation of 1131 days. However in 38% of simulations the disease did not persist longer than 100 days. This is evident in the distribution of persistence times (Figure 4.7). For these brief outbreaks of the disease with a persistence times arbitrarily selected at less than 100 days, the mean was 50 days with a standard deviation of 20 days. The distribution of persistence times less than 100 days can be seen in Figure 4.8.

Persistence time for epizootics that lasted less than 100 days was highly dependent on the initial density of susceptibles with a regression of persistence time on X_0 being highly significant ($F_{1,112}=1495$, $R^2=0.93$, $P<0.0001$) (Figure 4.9). This is because the initial density of susceptibles will frequently be below N_T and so the higher the density of susceptibles the longer it takes the density of latents to fall below 0.0005 pigs km². This relationship between initial density of susceptibles and mean persistence time is not apparent when persistence times longer than 100 days are considered with a regression of persistence times greater than 100 days on X_0 being non-significant ($F_{1,181}=2.51$, $R^2=0.01$, $P<0.1152$) (Figure 4.10). This is because X_0 will be above N_T and so persistence time will be dependent on the supply of susceptibles which will increase or decrease according to prevailing pasture biomass.

STOCHASTIC DISEASE MODEL II

An example of how the addition of β' influenced the behaviour of the epizootic can be seen in Figure 4.11 and 4.12. The density of pigs in all disease classes fluctuates enormously. This high amplitude oscillation is also apparent in N_T with the amplitude of oscillation in N_T being very much greater (Figure 4.13) than for SMI. This indicates β' has a much greater influence over N_T than b' which is confirmed by examining Figure (4.14).

The major difference the addition of β' had to the results of this model compared to SMI was that mean persistence time was reduced. The mean persistence time for SMII is 679 days with a standard deviation of 875 days. The longest persistence time was also shorter at 3960 days. The differences can be seen by comparing the frequency distribution of persistence times for SMII (Figure 4.15) with SMI (Figure 4.7). All this indicates that the addition of a stochastically varying β' lowered the probability of an FMD epizootic persisting.

The proportion of persistence times less than 100 days was also greater for SMII at 45% of all simulations, than for SMI with 38% of all simulations (Figure 4.16). When the dependence of persistence time on initial density of susceptibles is examined the trend of tight dependence of persistence time on initial density for persistence times less than 100 days seen in SMI is weakened in SMII with a regression of persistence time on X_0 , still highly significant at ($F_{1,134}=66.99$, $R^2=0.33$, $P<0.0001$) Figure (4.17). However when persistence times greater than 100 days are considered the trend is paradoxically stronger for SMII than SMI, with the regression of persistence time on X_0 being significant ($F_{1,161}=50$, $R^2=0.24$, $P<0.0001$) (Figure 4.18).

SPATIAL STOCHASTIC MODEL

The change in V_{\min} over the course of a simulation is shown in Figure 4.19. The mean V_{\min} for the 100 simulations of the spatial model was 2.51 km day⁻¹ with a standard deviation of 0.53 km day⁻¹ but the maximum V_{\min} recorded was 8.75 km day⁻¹ while the minimum V_{\min} recorded was 0.17 km day⁻¹. The distributions of mean V_{\min} , maximum V_{\min} , minimum V_{\min} are shown in Figure 4.20.

CONTROL EFFORT

With increasing time since the inception of the epizootic control effort and total area of the epizootic rose exponentially (Figure 4.21 and Figure 4.22). This is principally due to the area of the epizootic being a power function of distance covered since the inception of the epizootic.

4.4 Discussion

Heterogeneity in behaviour, distribution and abundance of hosts is cited as strongly influencing the likely prevalence and persistence of diseases (Anderson 1991, Anderson & May 1991). This study extends the concept of heterogeneity to include temporal heterogeneity in the population dynamics and behaviour of pigs. Several important results flow from the small alterations made to the compartmental models of Pech and Hone (1988) and Pech and McIlroy (1990) to accommodate temporal heterogeneity.

An important observation made clear in Figure 4.3 is that FMD can lower the density of an infected population of feral pigs substantially more than the 5% mortality entered into the model. Anderson *et al.* (1981) noted that for high density fox populations (10 km^{-2}) despite rabies only infecting 5% of the fox population it could reduce long term abundance of foxes below 50% of K .

The estimates of β are higher than those of Cayley (1993) at 0.091 to 0.307 for tropical woodland, and 0.119 for Pech and McIlroy (1990) (see Cayley's 1993 corrected estimate) in temperate montane forest. This is quite surprising since both areas had higher densities of pigs 2.5 to 3.5 km^{-2} for Cayley's site and 1.4 km^{-2} for Pech and McIlroy's site which should lead to higher contact rates. There is no reason why there should be an upper limit to contact rate and hence β , set by spacing behaviour. Pigs are non-territorial and frequently exhibit close physical contact with one another (Frädrieh 1974). The high β observed in this study may be due to the

concentration of pigs for much of the time in the relatively small area of riverine woodland. This would elevate contact rate because while overall density was low density in riverine woodland would have been quite high. It is also possible that the different vegetation types in the different habitats may have influenced the likelihood of pigs coming in contact with each other, with the less dense vegetation at Nocoleche making contact easier between individuals. Alternatively food, water and shelter may have been more uniformly distributed in the more mesic habitats and thus pigs were less likely to congregate in a small area and come into contact.

The lack of a significant effect of either total pasture biomass, temperature, or density on β suggests that β is very much dependent on the idiosyncrasies of individual pig behaviour and their influence on contact rate. It may be that the lack of these parameter's influence is due to the relatively small number of pigs collared and tracked (7-22), and that on the scale of the whole feral pig population of western New South Wales these parameters do have an influence. Even if this is the case it emphasises the importance of small scale spatial heterogeneity in contact rate in potentially maintaining the epizootic.

The eventual extinction of the FMD epizootic due to environmental variability is a novel finding. Anderson & May (1991) discussed the possibility of such a phenomenon and called it "endemic fadeout", suggesting the possibility of diseases going extinct due to fluctuations in host density without elucidating a mechanism. Unlike the dynamics of the kangaroo and pig populations the disease dynamics was less stable with weaker centripetality than the herbivore populations. There are probably three main reasons for this. The first is that when density of herbivores decreases during drought the death of each herbivore relieves a little of the pressure on the surviving herbivores because the food it has forgone by dying is now available to the survivors. This is implicit in the population growth equation 4.1. No such compensatory negative feed-back is available for the virus in this model. The FMD

virus is entirely dependent on its host, once the host dies the virus dies and the host is obviously not free for reinfection. The second reason is that at low pasture densities herbivores have a behavioural flexibility captured in the functional response equation, that viruses do not. As pasture declines pigs can search harder for food, or switch to less preferred more abundant foods, viruses cannot increase their infectiousness or increase their persistence time in the environment (other than through selection) to increase its probability of encountering one of the sparsely distributed pigs. A third reason that the virus is at a disadvantage at low host density compared to herbivores at low pasture density, is that the resource pigs depend on (pasture) responds much more rapidly to improvements in conditions than the resource the virus is dependent on; pigs. Thus, there will be a time lag in an increase in new susceptibles after a drought breaks during which an FMD epizootic may run out of susceptibles. The purported advantages for herbivores could be argued to be advantages for the virus given it is an obligate parasite of one of the herbivores and these are mechanisms for maintaining host abundance. If the dynamics of directly transmitted microparasites were completely linearly dependent on host density this argument would be valid. However, because N_T so clearly represents a threshold below which extinction is inevitable the low densities the pigs maintain themselves during drought are below N_T and the epizootic cannot be maintained.

The reason the distribution of persistence is so skewed to short persistence times in simulations of both SMI and SMII is twofold. First for SMI and SMII, in many instances the X_0 drawn in the simulation will be below N_T and hence the disease will rapidly decline to extinction. Second for SMII, due the phenomenon of "epidemic fadeout" (Anderson & May 1991) the disease will disappear because when the disease is initiated the entire population is susceptible and hence almost the entire population rapidly enters the latent, infectious and immune classes leaving very few susceptibles. This phenomenon can be seen in Figure 4.2. When this happens density

of susceptibles will be very low and the possibility of some random factor such as a decrease in β forcing N_T above X will be much higher.

The strong relationship between X_0 and persistence times less than 100 days is a reflection of the phenomenon discussed above. What seems anomalous is that the relationship between persistence time and X_0 is strongest for SMI but the relationship persists for longer in SMII (Figures 4.9, 4.10, 4.17 & 4.18). This can be resolved when the relative effects of low X_0 and endemic fadeout are considered in isolation. The tight relationship between persistence time and X_0 in SMI is due to X_0 being below N_T by chance and the entirely deterministic process of the disease dying out due to an insufficient supply of susceptibles at the inception of the epizootic, which will take longer the higher X_0 . If X_0 is above N_T then the epizootic can persist for longer and it is only going to be extirpated by "endemic fadeout" because it is only the environmental parameters influencing b' that change relatively slowly, that will force X below N_T . In comparison the relationship between X_0 and persistence times less than 100 days, is less tight for SMII because even if X_0 is below N_T , within a week N_T could be below X because β' will be a new draw from the distribution of β . Equally if X_0 is above N_T then within a week a new β' could place N_T above X and the epizootic may fade out. This is also the reason the relationship between persistence time and X_0 continued for longer in SMII than SMI. In SMI persistence time is only dependent on the probability of X_0 being below N_T and the associated rapid deterministic decline to extinction if X_0 is below N_T , as well as endemic fadeout. In SMII the probability of epidemic fadeout will be in part dependent on the size of X_0 the higher X_0 the more likely it is to be above N_T , so the epizootic will be more buffered against sudden extinction. This effect will last longer than the simple deterministic relationship of persistence time to X_0 when N_T is higher than X_0 in SMI.

The imposition of β' in SMII imparts several differences on the course of the FMD epizootic. β' varies randomly, and with much higher frequency and amplitude than b' . This means that the course of the epizootic for SMII will approximate a random walk by comparison with SMI. The high amplitude and frequency of fluctuation in β' in SMII means that N_T will fluctuate much more in relation to X than for SMI so that N_T will be above X further and more often in SMII and hence more prone to extinction than SMI.

The contrast between β' and b' has some similarity to the concepts of demographic stochasticity and environmental stochasticity used in models of population extinction (Lande 1993). Demographic stochasticity is "...caused by the chance realisations of individual probabilities of death and reproduction in a finite population." (Lande 1993). Environmental stochasticity "...arises from a nearly continuous series of small or moderate perturbations that similarly affect the birth and death rates of all individuals (within each age or stage class) in a population." (Lande 1993). Demographic stochasticity has parallels with β' in that in this model β' is a function of chance and probably deliberate encounters amongst a relatively small group of pigs and can be strongly influenced by the behaviour of an individual pig. β does have an explicit density component to its calculation but as was seen by the failure to find a significant relationship between density and β there was an overriding effect of contact rate between individual pigs. Environmental stochasticity is encapsulated in b' a parameter describing the ups and downs inflicted on the pig population as a whole by the unpredictable environment. Lande (1993) argued that with increasing population size demographic stochasticity will decrease in importance and environmental stochasticity will increase in importance in defining the probability of population extinction because individual events tend to average out in large populations. This is not entirely true for the models of FMD in pigs, because the influence of β' remains strong at all densities of pigs. This highlights a potential problem with SMII discussed earlier, in that the high degree of variability in β'

may be an artefact of sample size and that as sample size increased the temporal variability in β' may decline. However, looked at another way it highlights potential problems for models such as Lande (1993) in that small aggregations where the demography (analogous to β') is particularly different may confound predictions based on overall population parameters. For this reason Barlow (1991) proposed the existence of small foci for bovine tuberculosis transmission within the brush-tailed possum population in New Zealand to maintain the overall epizootic. He did not however, identify whether this was due to the dynamics of the disease or the ecology of the host.

This study showed V_{\min} will slow and speed up in a non-systematic way according to variation in β' and D . The velocity of advance of the FMD epizootic in this study is of a similar order to that calculated by Cayley (1993) at 2.8 km day⁻¹ to 3.5 km day⁻¹ and 2.8 km day⁻¹ to 5.9 km day⁻¹ for Pech and McIlroy (1990) depending on which method was used to calculate v_{\min} .

There are a number of caveats associated with interpreting the results of the spatial stochastic model. The first is that feral pig movements can be approximated by diffusion equations. In the literal sense this is obviously not true as movements may be more limited because pigs occupy defined home-ranges and prefer some habitats above others although the random walk assumption of the diffusion equation may be accurate in describing the diseases dynamics. The strong dependence of V_{\min} on β' rather than D' (Pech and McIlroy 1990) may mean that this is not such a concern. A greater problem may be the occurrence of rare long distance movements by pigs in the latent stage, that may speed the velocity of advance of the disease an order of magnitude faster than estimated here (Mollison 1987). Having D' drawn at random from a distribution of D goes some way to addressing this concern but important very rare events will not be captured by considering the standard deviations of a normal distribution. This is a more general problem in ecology and behaviour than is

recognised (Gaines & Denny 1993) and a more realistic approach may be to model the movements of individual animals as is being attempted in the AUSPLAGUE model developed at CSIRO Division of Wildlife and Ecology (Pech pers. comm.). Another consideration that could severely qualify the outcome of this model is that FMD induces lameness in feral pigs during the infectious phase of the disease (Callis 1984). This could reduce both β and D though it would only affect the infectious pigs. As there were no obviously lame pigs collared at Nocoleche how this might affect disease transmission remains unknown. A final qualification of this model is that in this analysis the latents were combined with infectives to make calculation of v_{\min} in this stochastic model mathematically tractable. This has the effect of elevating V_{\min} in relation to V_{\min} calculated with latents and infectives kept as separate categories. Three of the four caveats mentioned; non-random movement, lameness of infectives, and combining latents and infectives suggest that estimates of V_{\min} may be an overestimate while rare long distance movements suggest the estimates of V_{\min} will be an underestimate. It is not known whether these factors are additive or compensatory.

There are several important practical consequences of this study for controlling FMD. Hone and Pech (1990) suggest ranking areas of Australia at risk from FMD in feral pigs, according to criteria such as proximity to ports, feral pig density, and the likelihood of detection. To this could be added seasonal conditions with good conditions increasing an areas risk ranking and poor seasonal conditions lowering an areas risk ranking. These results qualify Hone and Pech's (1990) suggestion that areas with a feral pig population density below N_T should attract a low risk ranking. As demonstrated, N_T can fluctuate depending on b' or on β' .

While it is desirable to eradicate FMD as swiftly as possible and it is also likely that enormous financial resources will be available for the control of an FMD epizootic (Wilson & O'Brien 1989) total eradication of the feral pig population may not be

practical on the local or even regional scale. This study reinforces the advice of Pech and Hone (1990) and Hone and Pech (1990) in targeting N_T as the goal for disease eradication rather than total feral pig eradication. However N_T has become a moving target and because N_T is so dependent on β which is very difficult to assess in the field. The safest course would be to assume β is at its highest and aim to reduce pig density to below N_T for the combination of the highest possible β and a b' that can be deduced from the pigs numerical response to prevailing pasture biomass.

The total effort and hence cost required to eliminate FMD by lowering density of pigs below N_T in the area covered by the epidemic increases geometrically with time since the inception of the epizootic. This is partially offset by the increased likelihood of the disease dying out with time since inception of the epizootic. The area covered by the epizootic was assumed to be circular. This is unlikely to be realistic as local variation in β and other parameters as well as the tendency of pigs to live along rivers in the rangelands will deform the shape of the circle. Therefore, the robustness of estimates of the area of the epizootic and level of control required will tend to decline with increasing time since the inception of the epizootic.

As the cost of controlling pigs to a particular density increases exponentially with decreasing density targeted (Hone 1987) the costs of controlling feral pigs to a level substantially below N_T will be disproportionately larger than controlling pigs to a level just below N_T . This means that it may be most appropriate to target a density of pigs km^{-2} below N_T then reduce the pig population to that level and intensively monitor of the disease status of the pig population. If the epizootic is persisting then control effort should be intensified but if it has disappeared then effort should be switched to areas beyond the periphery of the epizootic front so that there is a buffer of pig populations below N_T that will halt the epizootic if undetected diseased pigs remain in the core area.

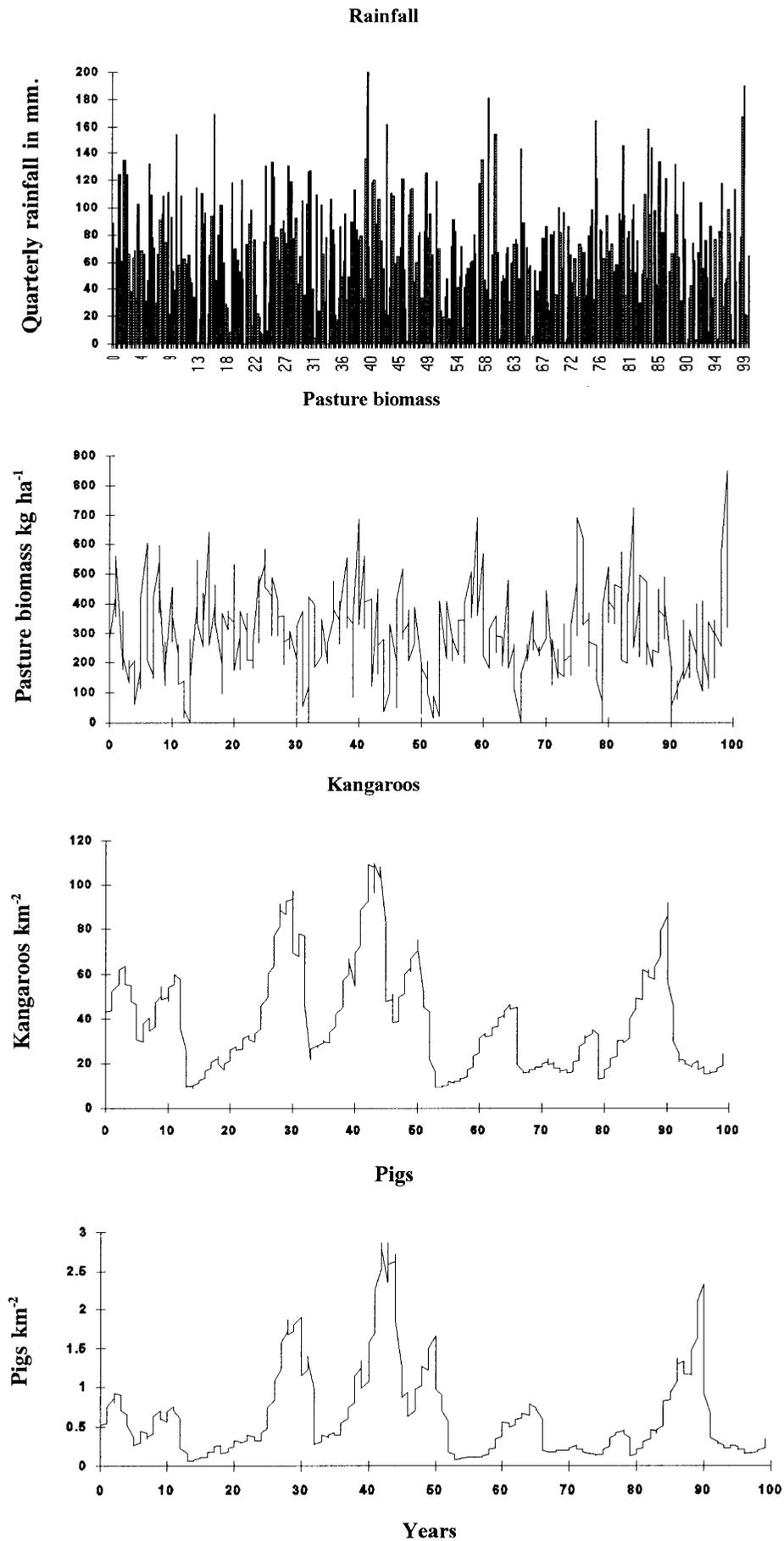


Figure 4.1 An example of modelled 100 year rainfall for Wanaaring with the associated changes in abundance of vegetation, kangaroos and feral pigs.

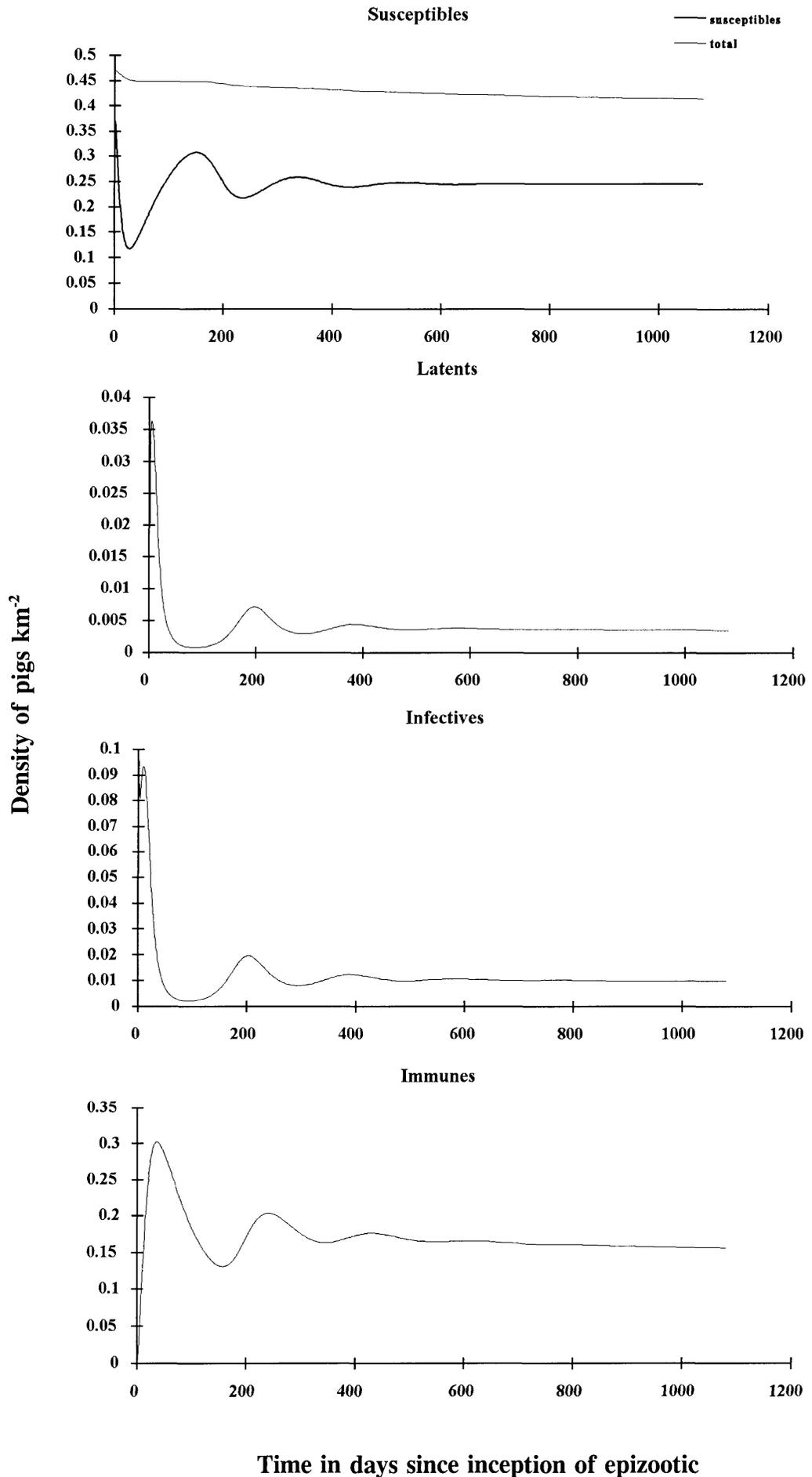
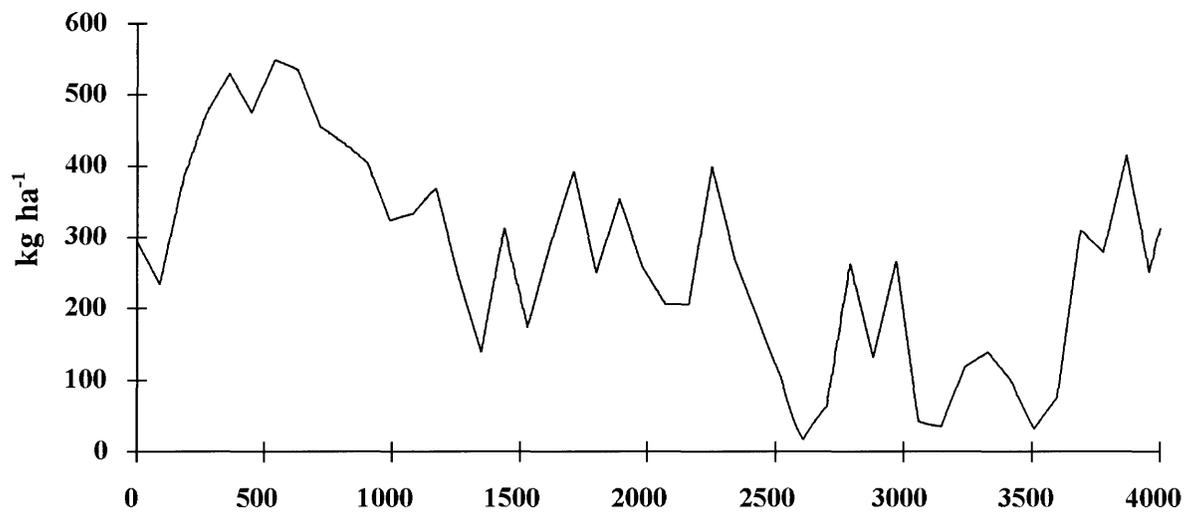


Figure 4.2 Change in densities of total pig population, susceptibles, latents, infectives, and immunes following the introduction of FMD for the deterministic disease model.

Pasture Biomass



Pig Density

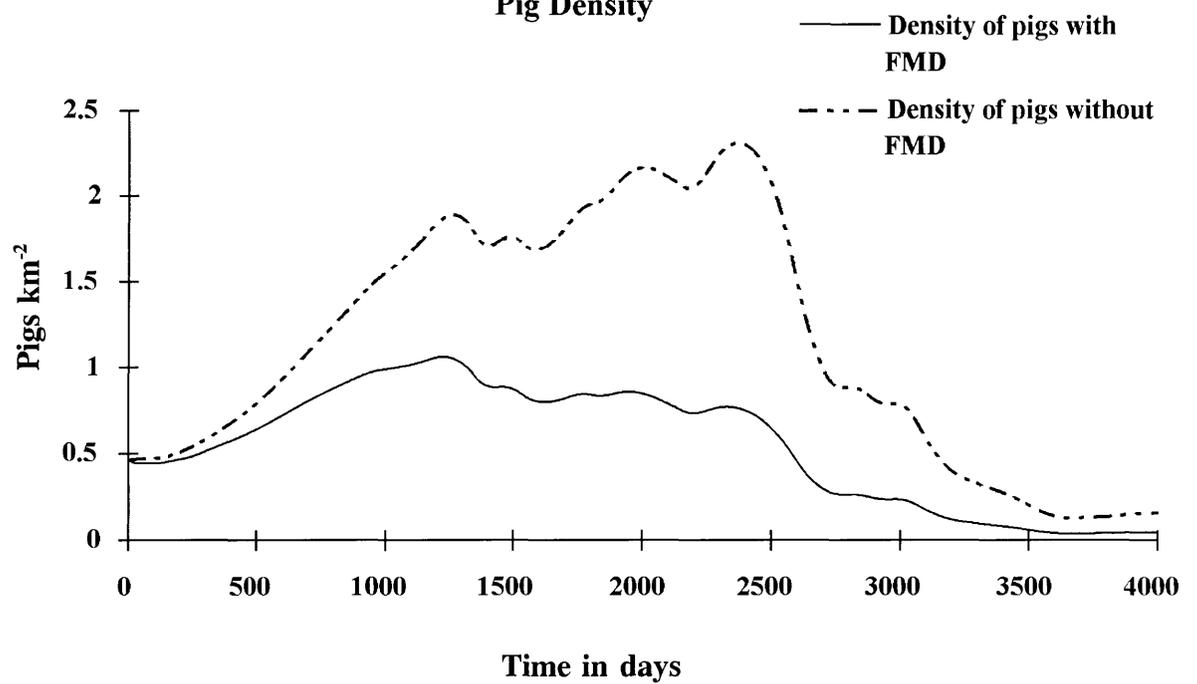


Figure 4.3 Example of simulated change in vegetation abundance and associated change in density of pig population infected with FMD (stochastic model I) and density of an uninfected pig population.

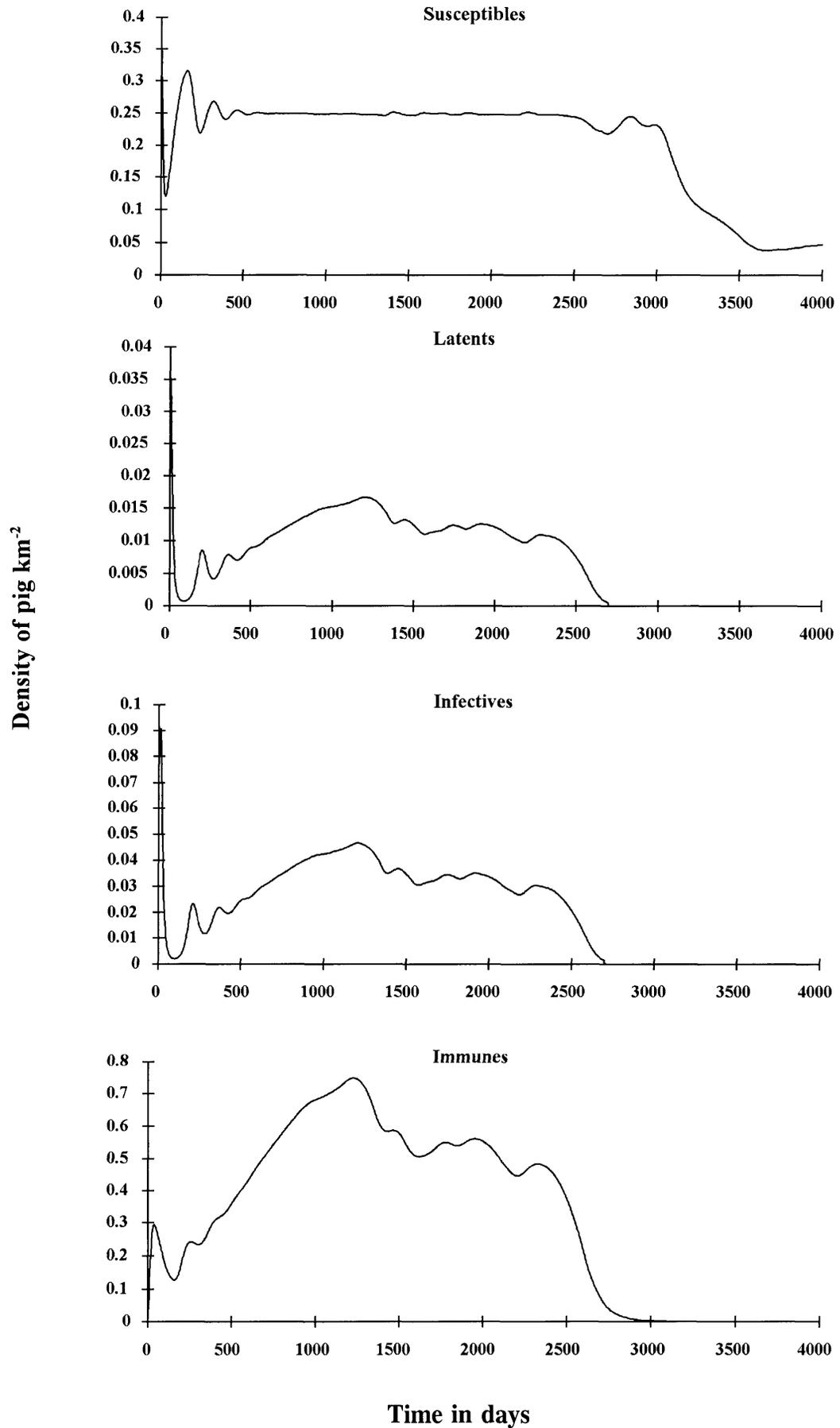


Figure 4.4 An example of change in abundance of susceptibles, latents, infectives and immunes, for a simulation of stochastic model I shown in Figure 4.3.

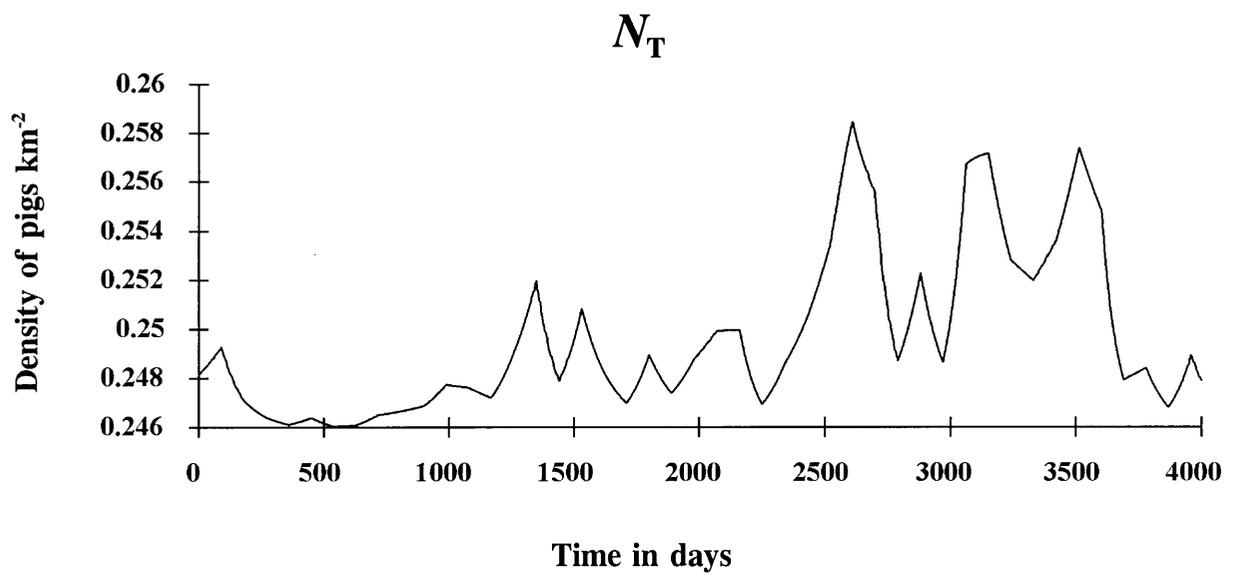


Figure 4.5 Change in threshold density N_T for the simulation of stochastic model I shown in Figure 4.4.

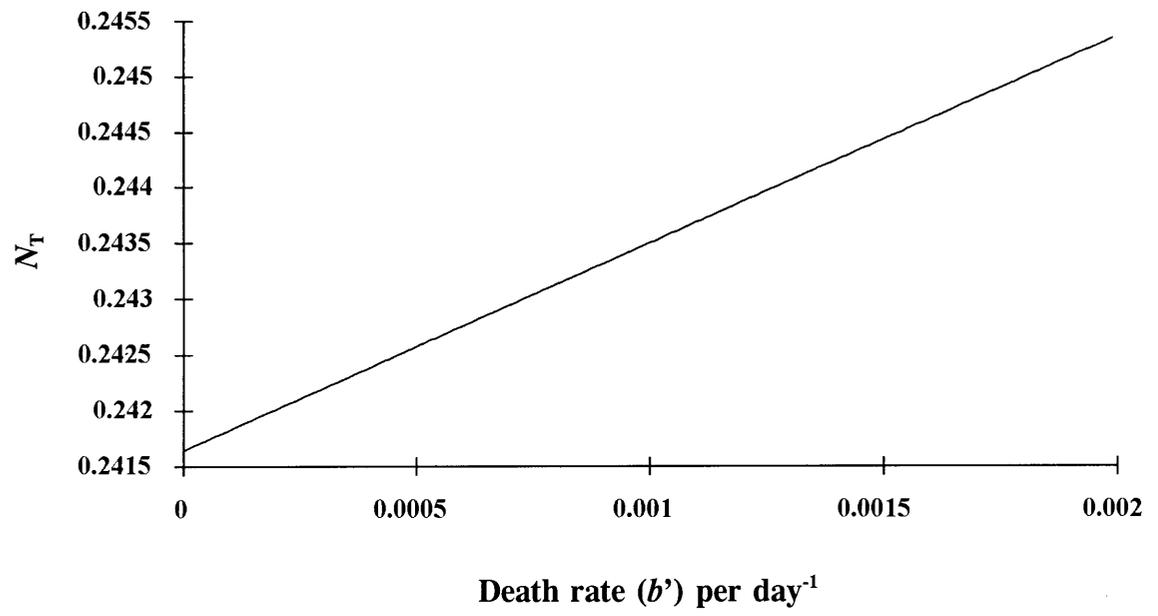


Figure 4.6 Relationship of threshold density N_T , to death rate b' .

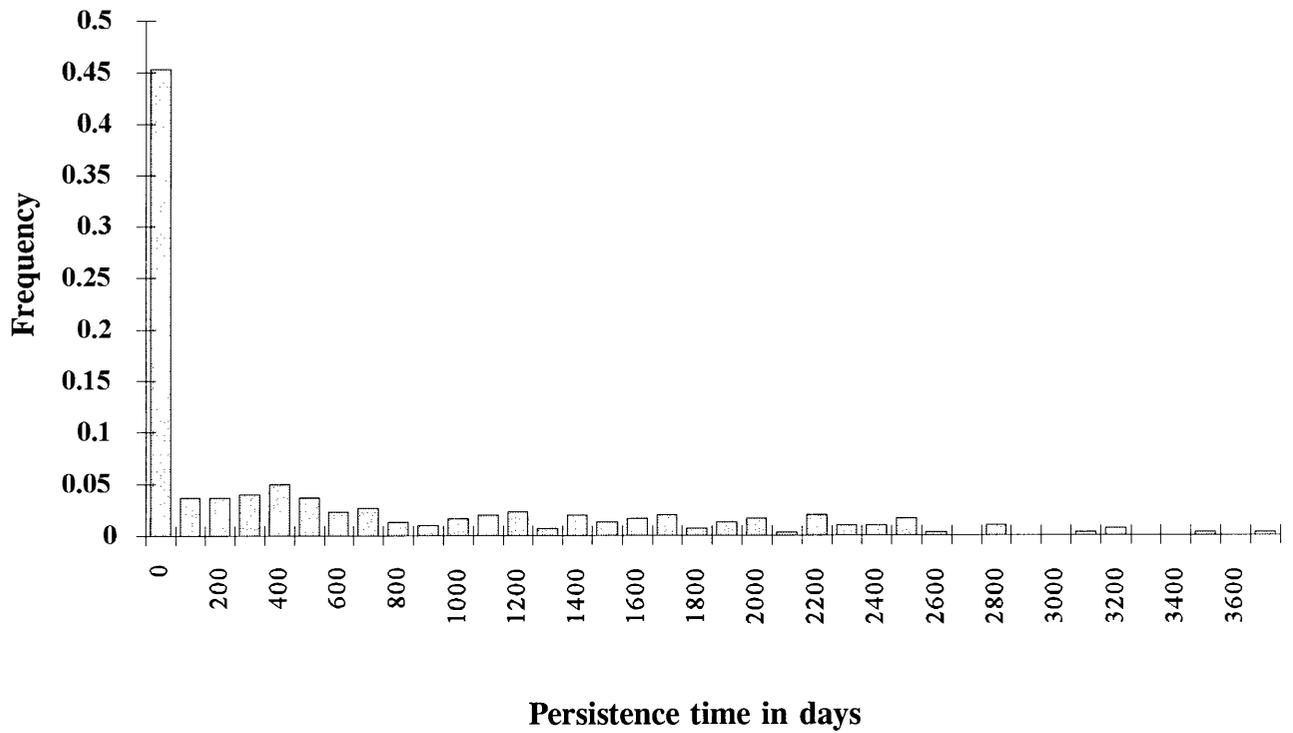


Figure 4.7 Frequency distribution of persistence times for 300 simulations of stochastic model I.

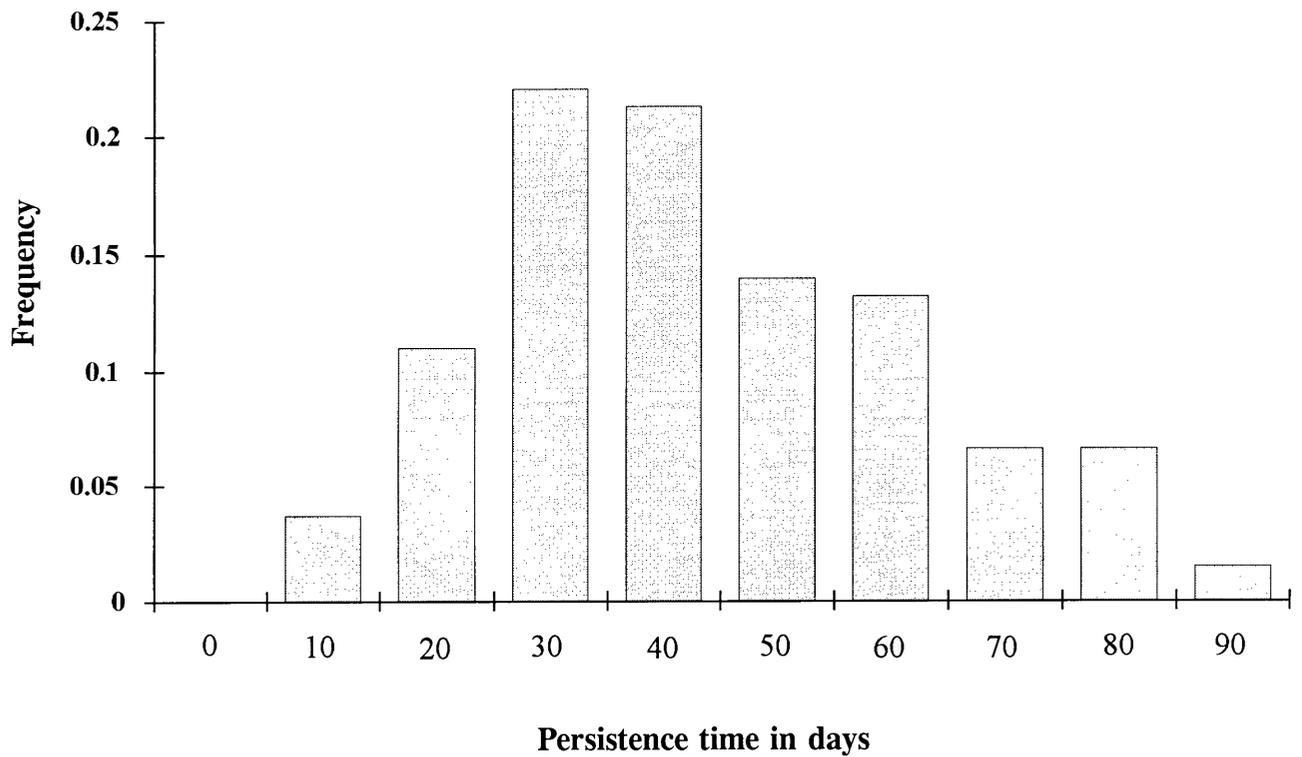


Figure 4.8 Frequency distribution of stochastic model I persistence times for simulations lasting less than 100 days.

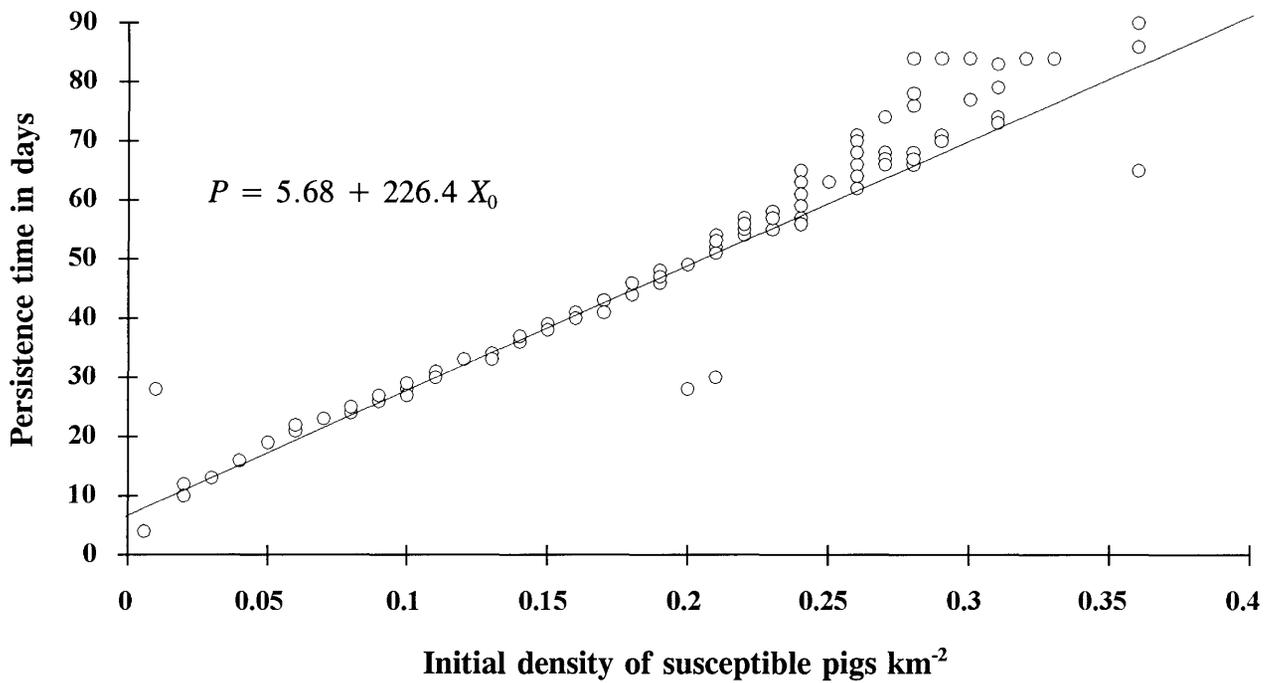


Figure 4.9 Relationship between persistence time (P) and initial density of susceptibles (X_0) for stochastic model I persistence times less than 100 days.

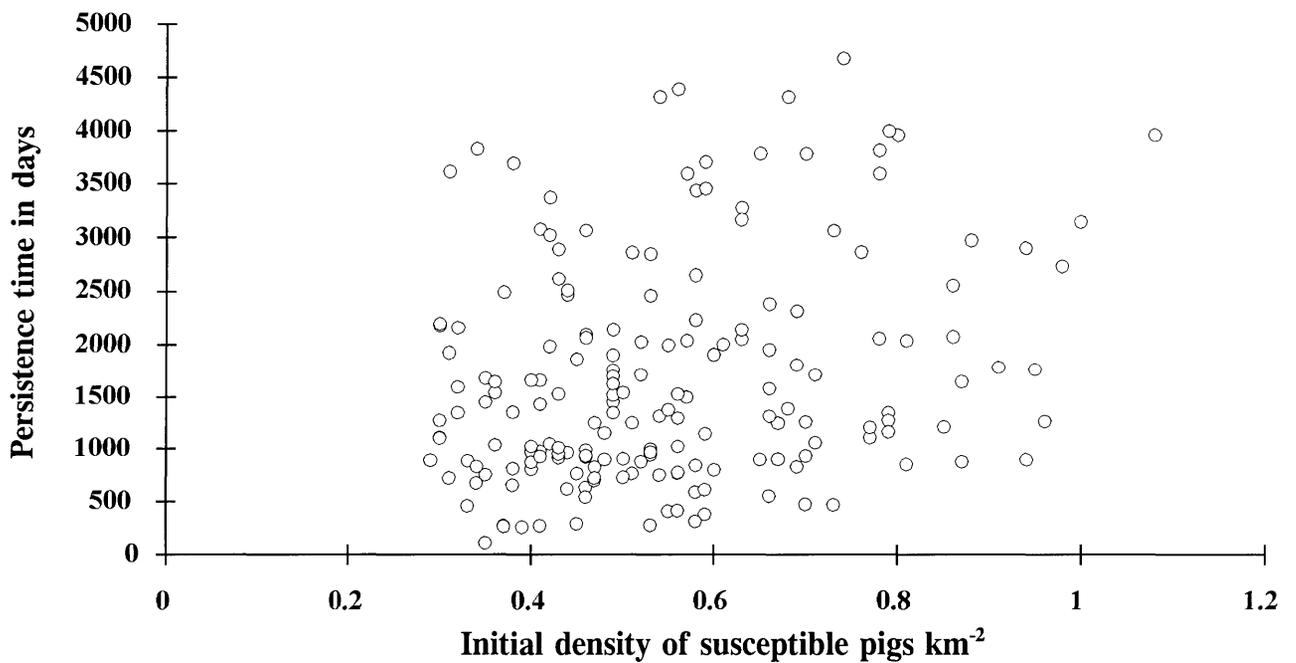
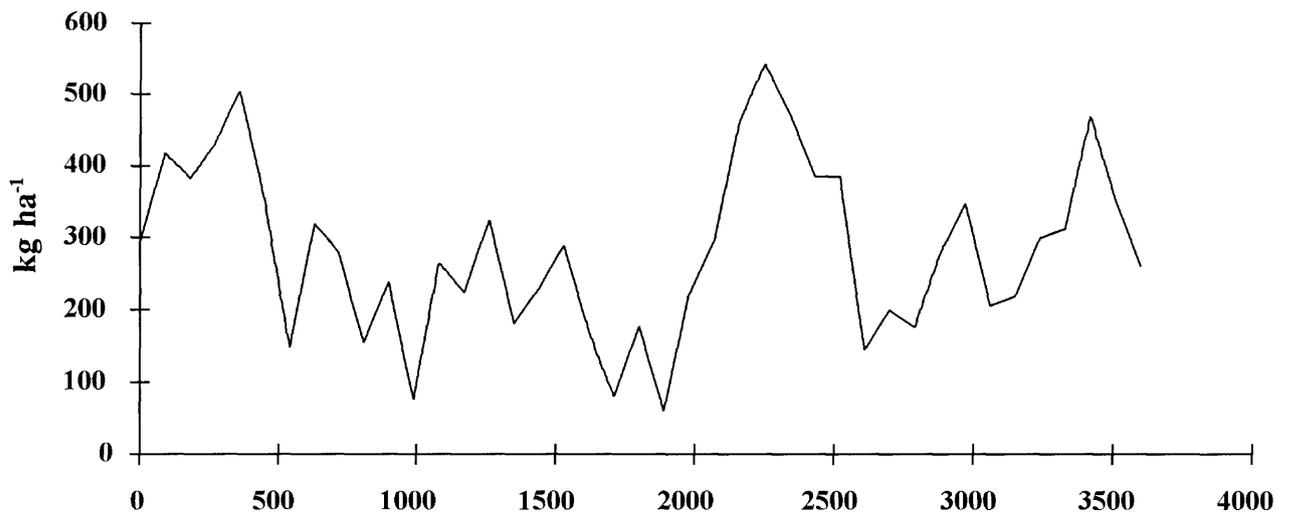


Figure 4.10 Relationship between persistence time (P) and initial density of susceptibles (X_0) for stochastic model I persistence times greater than 100 days.

Vegetation Biomass



Pig Density

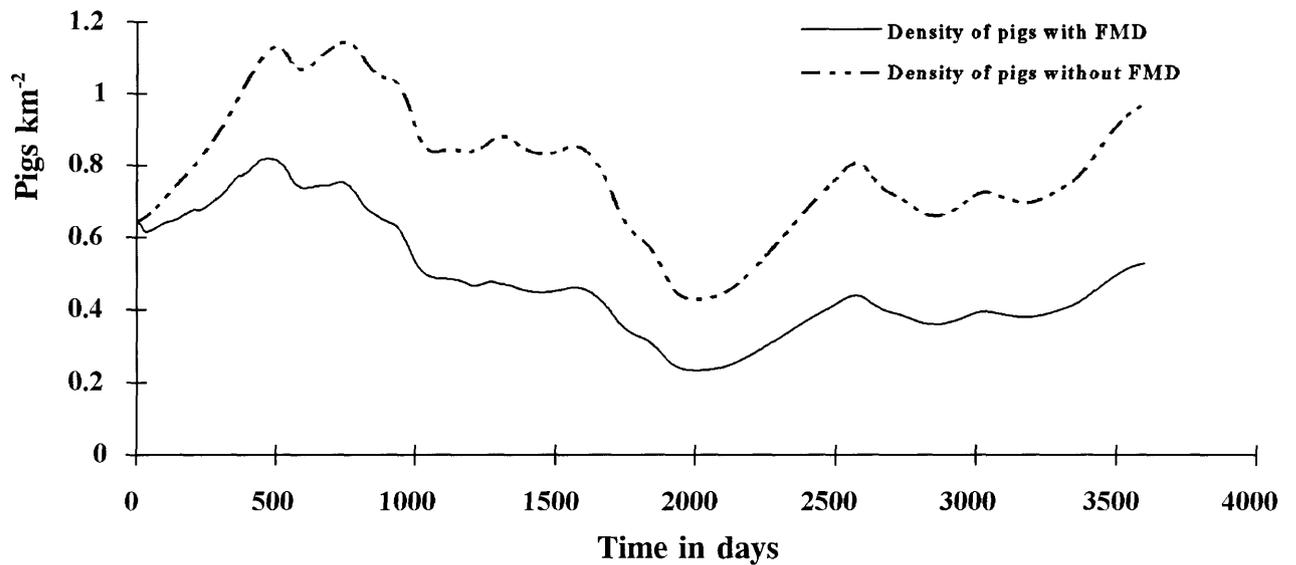


Figure 4.11 Example of simulated change in vegetation abundance and associated change in density of pig population infected with FMD (stochastic model II) and an uninfected pig population.

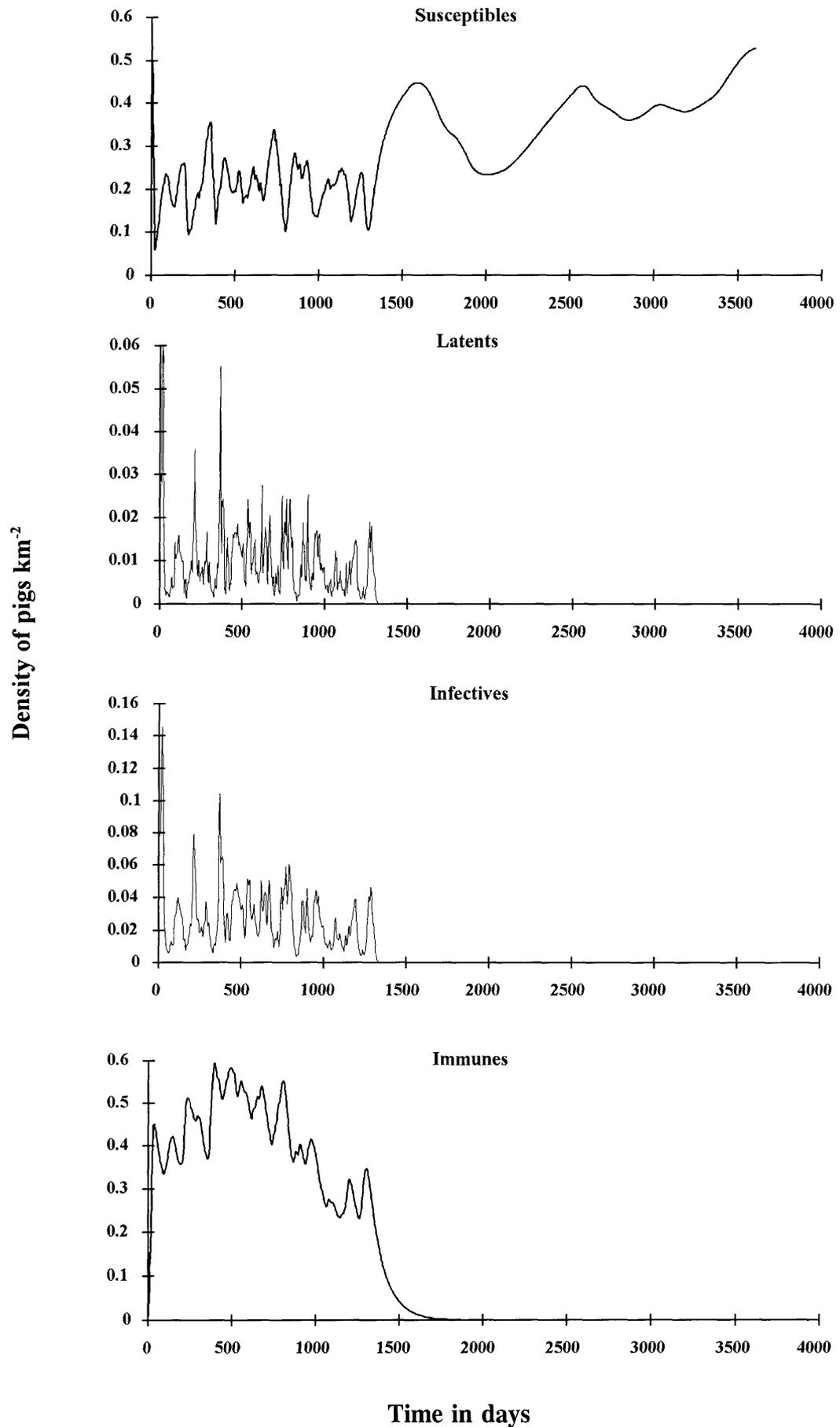


Figure 4.12 An example of change in abundance of susceptibles, latents, infectives and immunes for a simulation of stochastic model II shown in Figure 4.11.

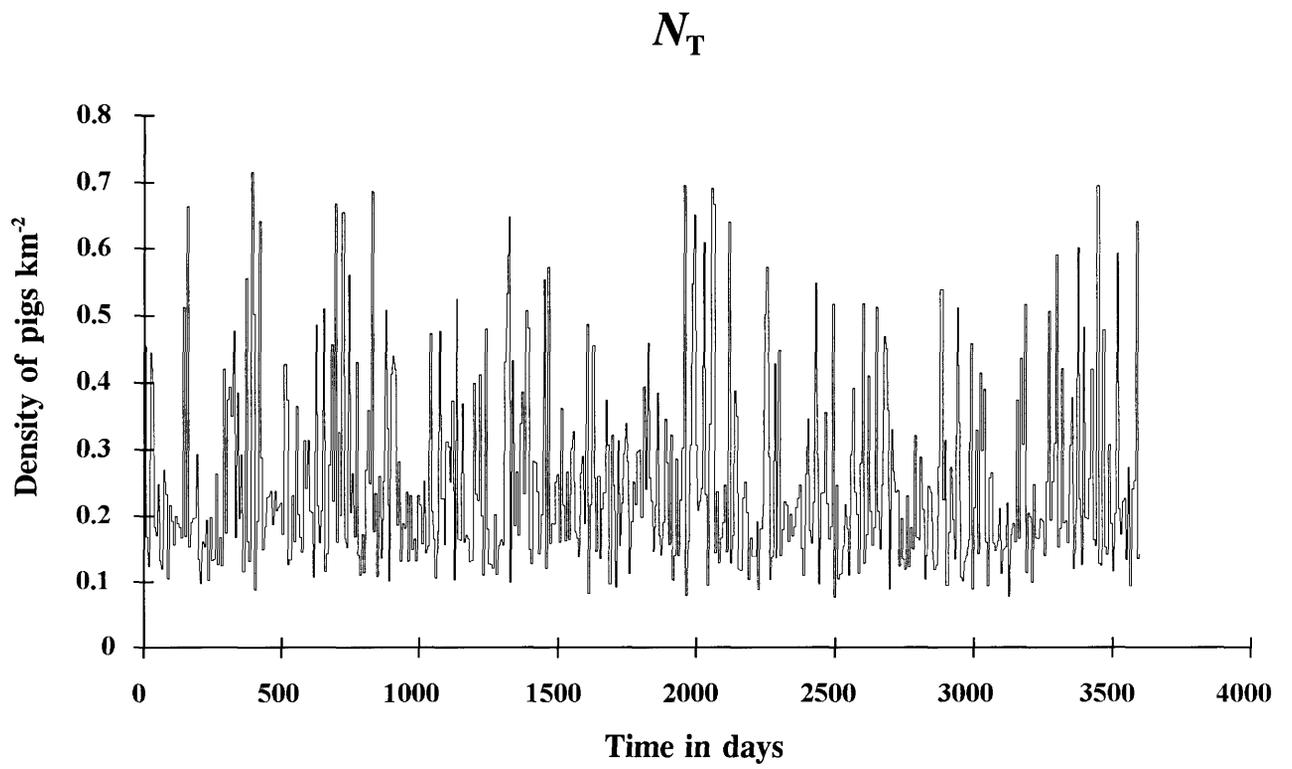


Figure 4.13 Change in threshold density N_T for the simulation of stochastic model II shown in Figure 4.11.

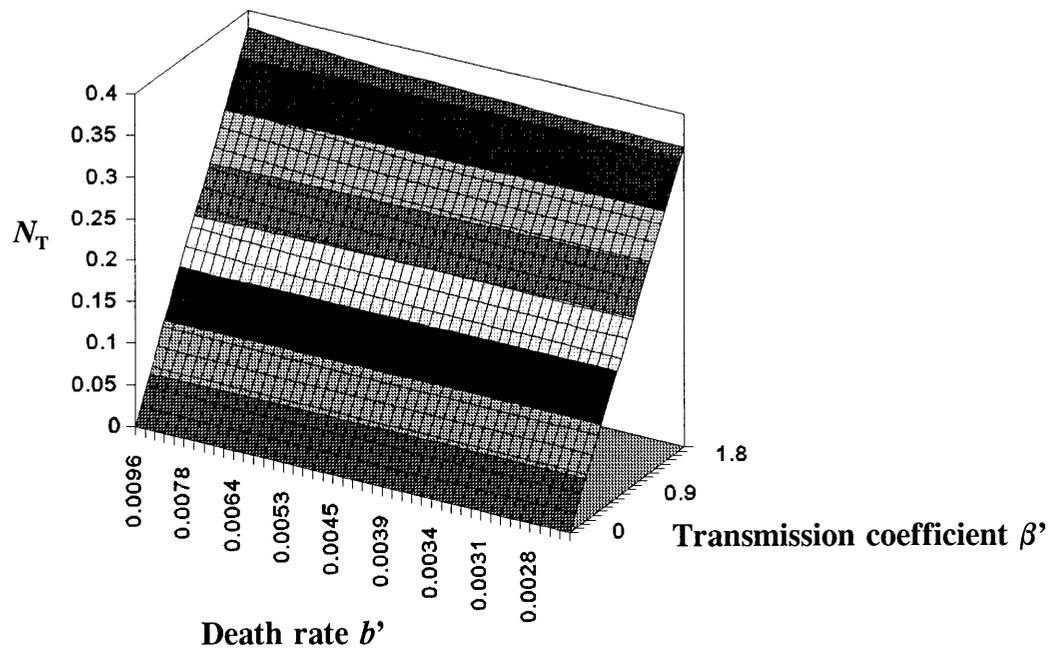


Figure 4.14 Relationship of threshold density N_T , to death rate b , and transmission coefficient β' .

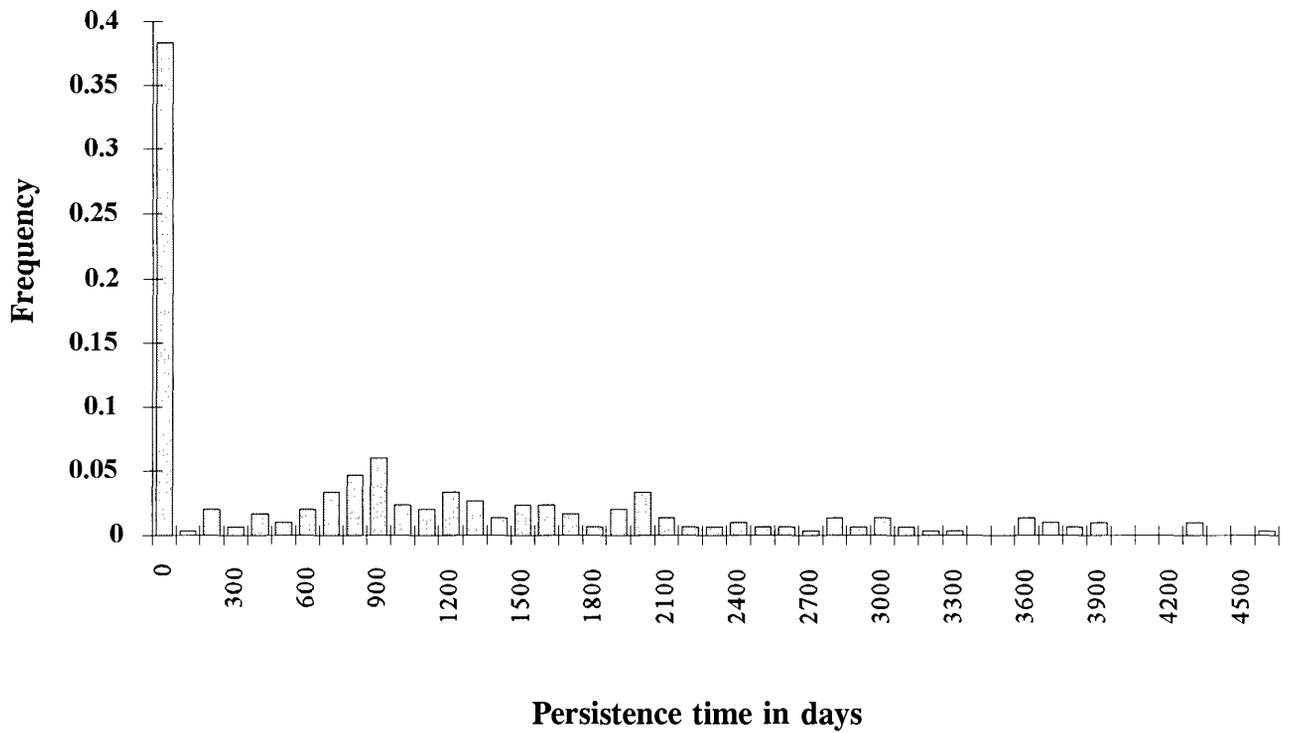


Figure 4.15 Frequency distribution of persistence times for 300 simulations of stochastic model II.

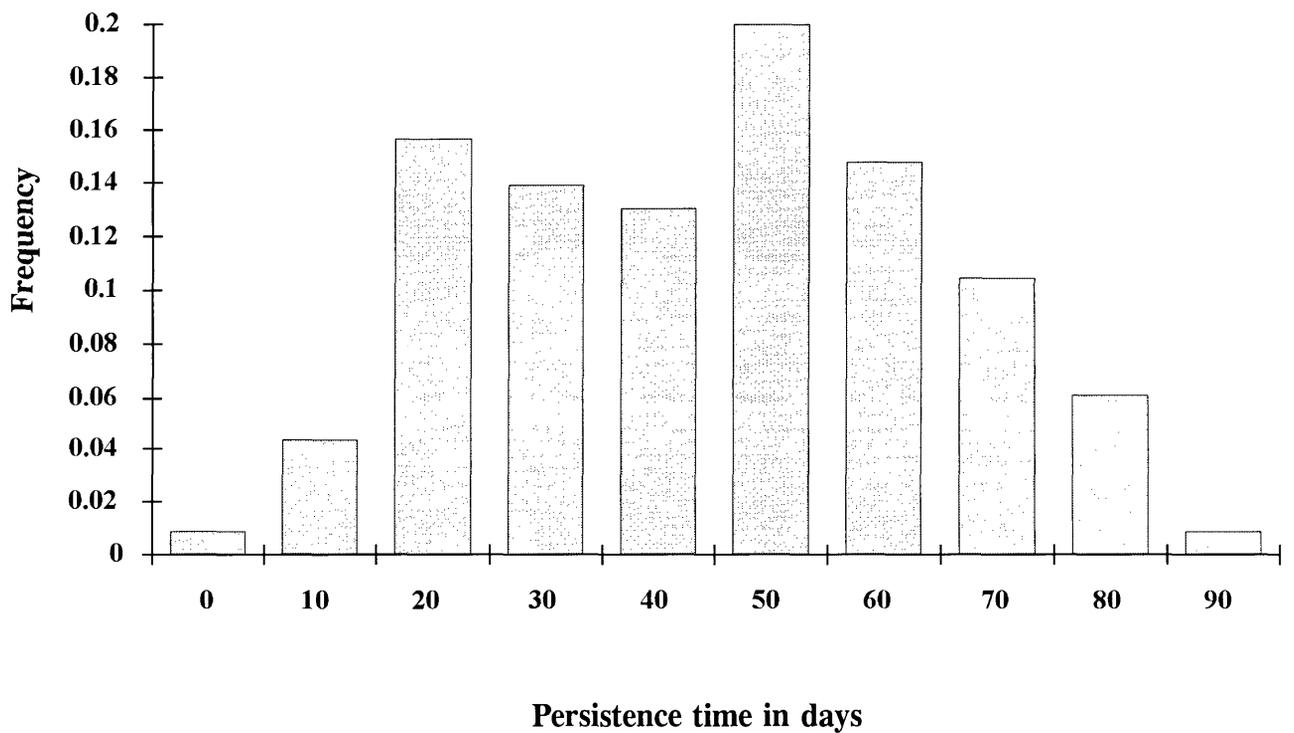


Figure 4.16 Frequency distribution of stochastic model II persistence times for simulations lasting less than 100 days.

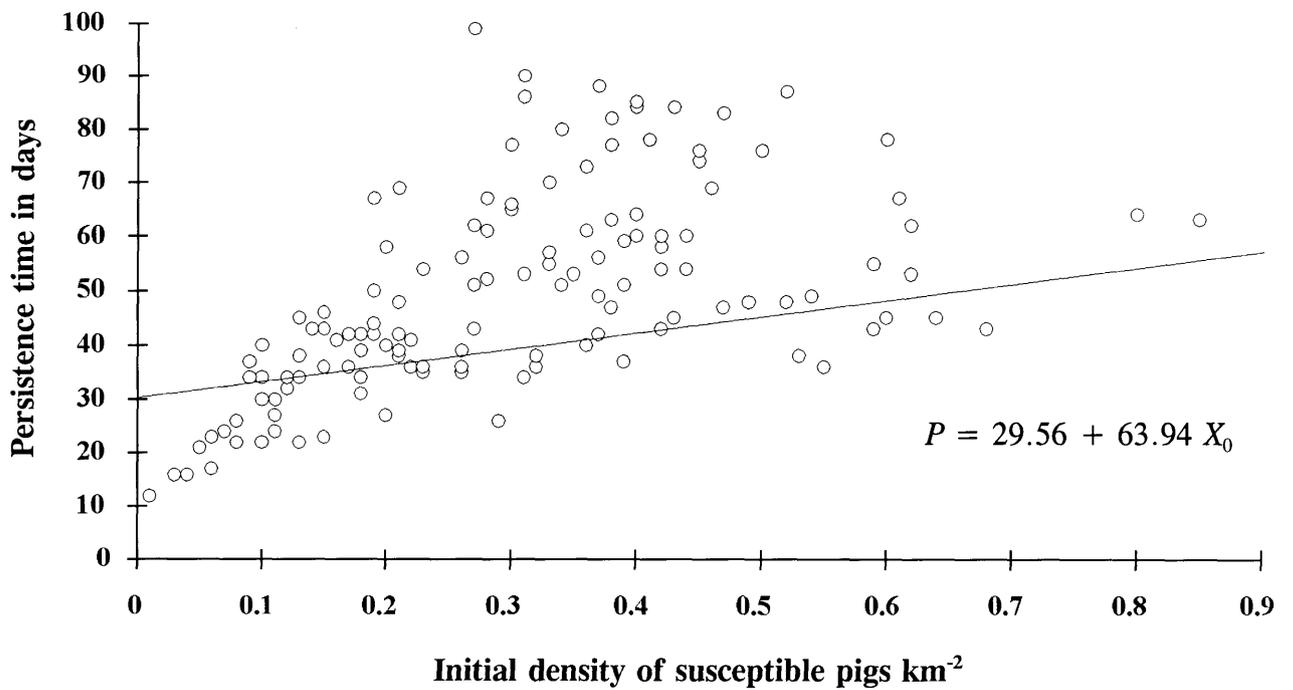


Figure 4.17 Relationship between persistence time (P) and initial density of susceptibles (X_0) for stochastic model II persistence times less than 100 times.

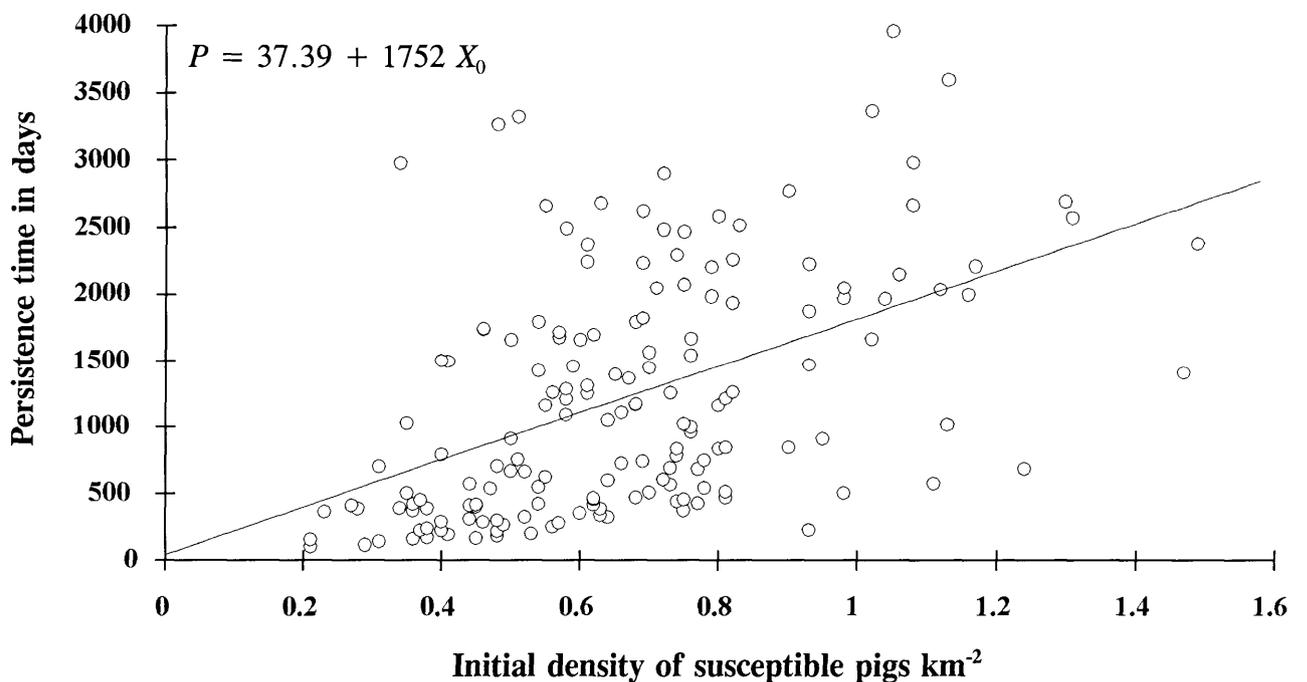


Figure 4.18 Relationship between persistence time (P) and initial density of susceptibles (X_0) for stochastic model II persistence times greater than 100 times.

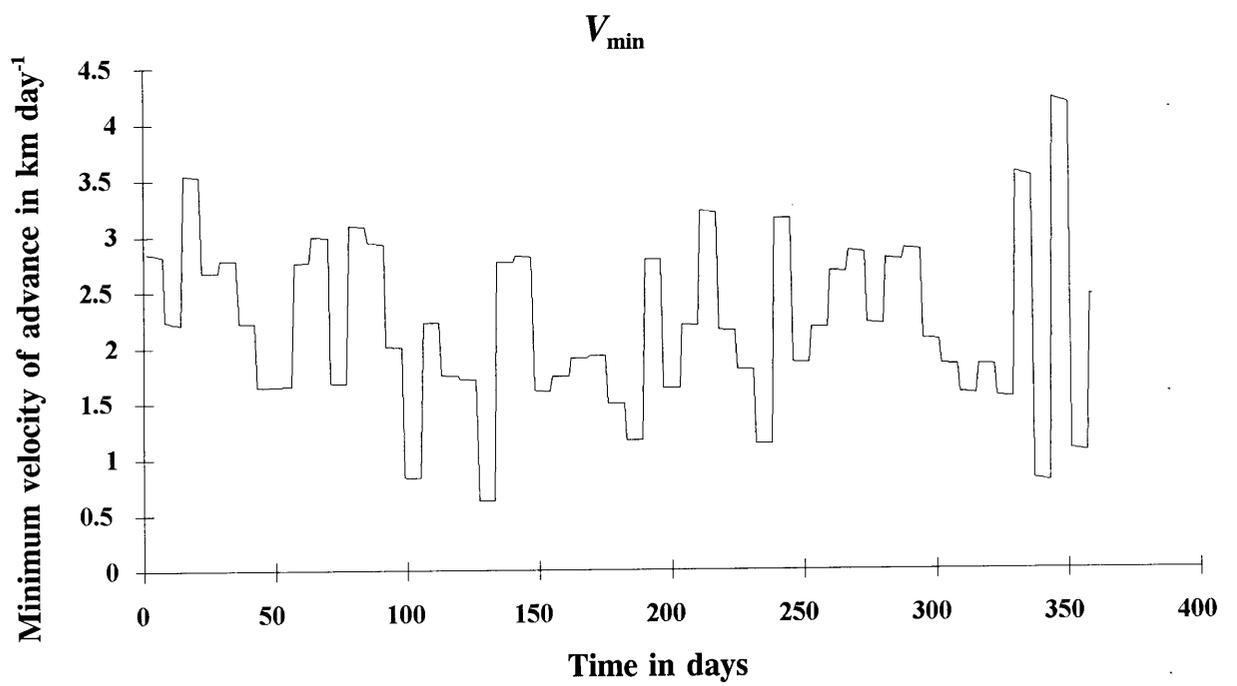


Figure 4.19 Change in V_{\min} for a simulation of the spatial stochastic model.

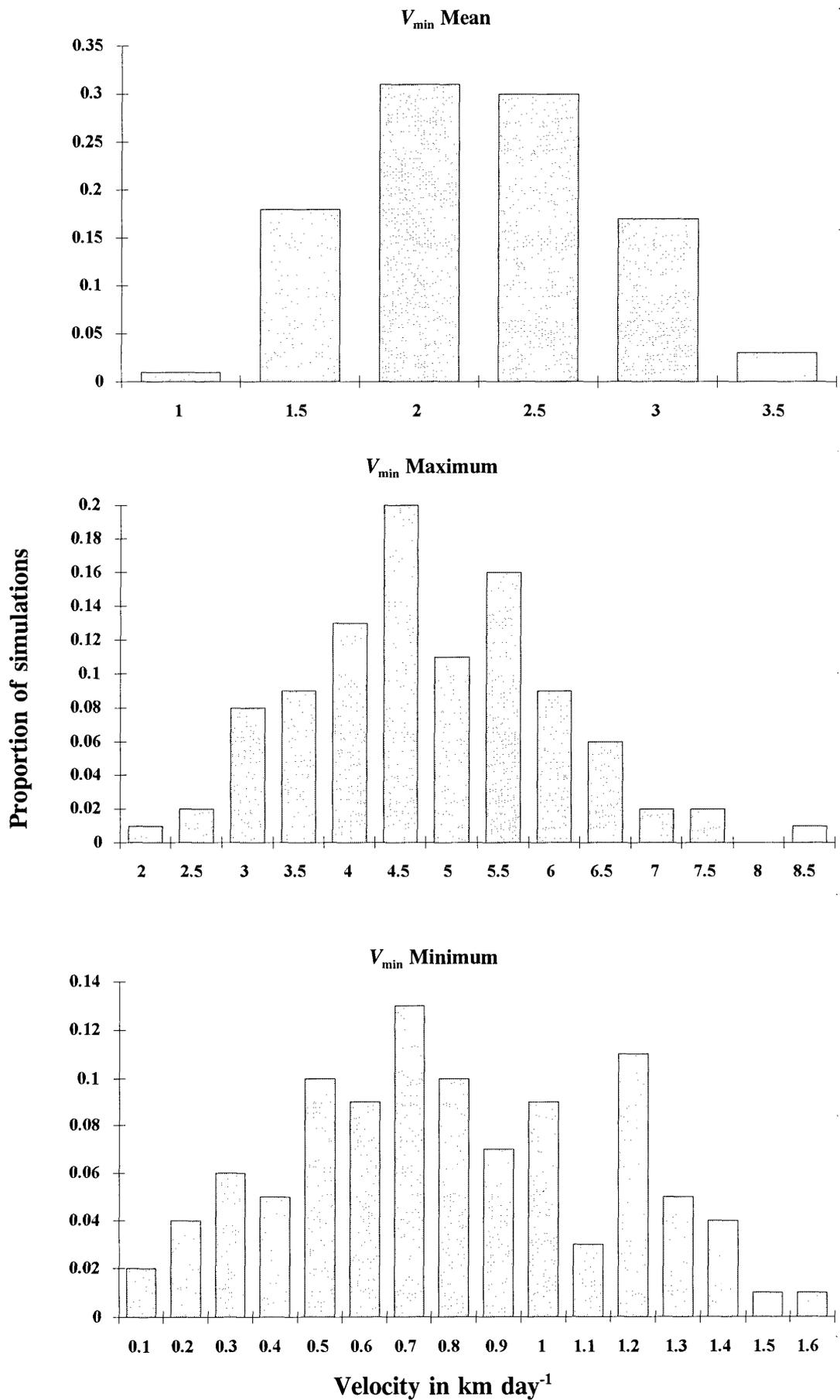


Figure 4.20 Distribution of mean V_{\min} , maximum V_{\min} , and minimum V_{\min} for 100 simulations of the spatial stochastic model.

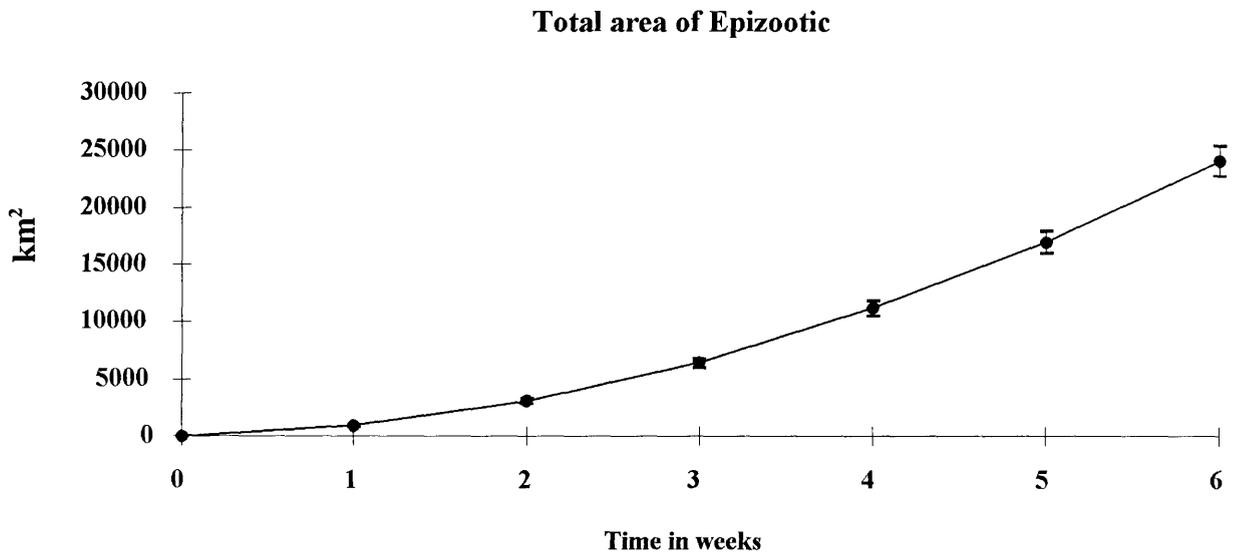


Figure 4.21 Change in mean total area of FMD epizootic in km² over time \pm 1SE.

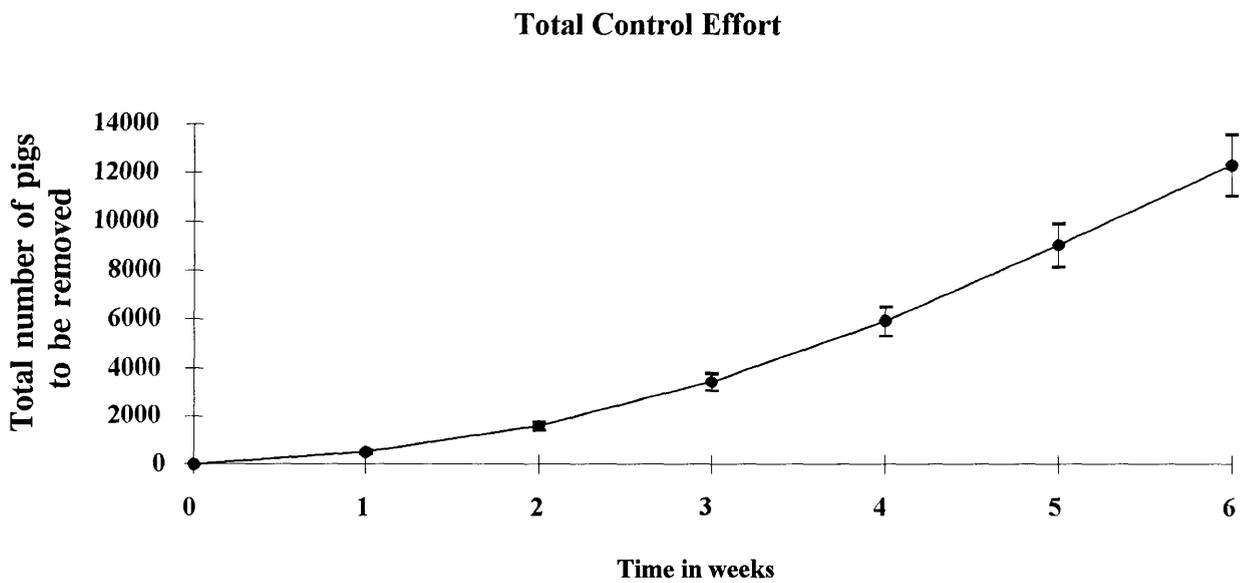


Figure 4.22 Change in mean control effort km² to eliminate FMD epizootic over time \pm 1SE.

Chapter 5

Conclusion

This thesis has achieved two major contributions. The first is to describe how a range of ecological variables are sensitive to variation in the spatial and temporal distribution of food (pasture biomass) and also to a climatic parameter (high temperature). The second contribution was to adapt an existing model of FMD in feral pigs to accommodate the demographic variability inherent in herbivore populations living in such an environment and then to incorporate the pig's natural behavioural variability manifested through the parameter β .

The patchiness of food resources at Nocolche is apparent to the casual observer and this patchiness is important to the pigs as was shown by the results of this study. However, patchiness of food was only measured in one dimension; food abundance in different habitats. Other studies of herbivores have shown habitat preference to be strongly related to some nutritional quality such as potassium content (Braithwaite *et al.* 1983) or protein content (Taylor 1984). However, pasture biomass in semi-arid environments varies far more spatially and temporally than in more mesic environments due to sharp gradients in soil moisture (Stafford-Smith & Morton 1990). Further the importance of variation in pasture biomass to the ecology of the feral pig was demonstrated by its significant effect on a number of ecological variables. To a herbivore in more mesic environments environmental heterogeneity is more likely to be manifest as patches of different quality, because food is generally more abundant and the gradient in food abundance less steep between habitats. Of course in some more mesic environments there are substantial seasonal changes in pasture biomass often associated with wet and dry seasons and in these cases there may be major movements of herbivores between habitats (Sinclair 1975). Pasture biomass is unlikely to be the full story, as suggestive evidence that pigs may have been partially responding to two

aspects food quality was speculated upon in the discussion of Chapter 2. The first is the lack of preference for riverine woodland during winter 1992, despite its high pasture biomass. That pasture biomass however, was dominated by the coarse tussock grass *P. jubiflorum*, which may have been unpalatable to pigs. Similarly the aromatic chemicals in the *Centipedia cunninghamia* that tended to dominate the ephemeral swamps may have repelled the pigs. As covered in the introduction to this thesis pigs are relatively inefficient herbivores so it is likely that small differences in quality may have been more important to them than herbivores with more efficient digestive system. Some high protein animal food resources may have been important in maintaining pigs during drought even though the overall population dynamics of the pigs may have been driven by vegetation.

This study confirmed the speculations of earlier studies that high temperature limited how far and where pigs would forage. That pigs were heat sensitive was well established by earlier studies, but this study showed how a heat sensitive animal like the pig could survive by shifting between habitats and switching between nocturnal and diurnal foraging. In this study the influence of temperature was inferred from increased use of habitats with greater cover during hot seasons. The influence of temperature on fine scale habitat selection in pigs could be further examined by monitoring the microclimate characteristics of the shelters pigs use in different habitats and at different times of year. The interaction between temperature and water supply could also be profitably pursued by intensive observations of individual pigs. As feral pigs are rather shy, solitary and nocturnal at Nocolche and at many locations in inland Australia, the most robust data may be provided by an experiment with captive feral pigs allowed differing access to water and shelter over seasonally varying temperature.

In the first paragraph of Chapter 1 I stressed that the unifying theme to this thesis was the influence of a variable environment. Spatio-temporal variation in food supply for a large herbivorous mammal in semi-arid regions may be particularly acute but it is

probably a more general phenomenon than realised for many taxa, even occurring in such predictable environments as lowland tropical rainforest (Karr & Freemark 1983). High variability would favour animals that are physiologically and behaviourally flexible both of which are attributes of feral pigs. This flexibility would go part of the way to explaining how an animal that is a newcomer to the semi-arid environment and that so patently lacks the adaptations of so many arid zone large herbivores can persist. Overlaying this flexibility is the constraint of high temperatures which will severely compromise where and when a pig can forage. High temperature doesn't act like risk of predation identified as a constraint on foraging in other studies, pigs probably rarely die from heat stress, they just try to avoid the discomfort caused by high temperatures and so compromise the amount of time they can spend on other self maintaining activities. The characterisation of large herbivores as energy maximisers (Belovsky 1984) may be inaccurate for feral pigs as they become time minimisers during times of severe heat stress.

The influence of the sexual status of sows on the movements of feral boars was not fully determined. The oestrous sow experiment could be extended by monitoring the movements of free ranging radio collared oestrous sows and boars. However, the results would be problematic as only 50% of the treated sows showed positive signs of oestrus and determining the success rate of the treatment in free ranging sows would be impossible.

The disease models presented in this thesis are developments of relatively simple deterministic compartmental models expanded to include the natural demographic and behavioural variability of pigs. These additions changed the interpretation of the models from the calculation of single values of N_T and V_{min} in the deterministic models of Pech and Hone (1988) and Pech and McIlroy (1990) to the interpretation of persistence time probabilities, and variable N_T and V_{min} . This makes the models more sophisticated and

hopefully more realistic but without knowledge of the real dynamics of FMD in wild pigs the interpretations of these results remain qualified.

There are two important omissions in the FMD models presented in this thesis. The first is the lack of consideration of how the dynamics of the disease would be altered if the large population of feral goats on Nocoche were also included. Feral goats occur in higher density and occupy different habitats to feral pigs being widely distributed through the shrubland. It is quite possible that left uncontrolled the disease could become endemic in feral goats while dying out in pigs. In Africa where there is a diverse community of ungulates of varying susceptibility to FMD there are four possible inter-species transmission scenarios (Halpin 1975). The first is two self contained epizootics with little transmission between the two species such as cattle and buffalo. The second scenario is for maintenance of the epizootic in one species to be dependent continual infection from the other such as the maintenance of FMD in wildebeest *Connochaetes taurinus* by infection from cattle. The third scenario is transmission from one species to another but no transmission within the species. This occurs with elephants *Loxodonta africana* which can be infected by cattle and can transmit the disease to cattle but cannot infect other elephants. The final scenario is transmission to a dead end host in which cattle may transmit the disease to a diverse range of non-ungulate hosts but the disease cannot be transmitted any further by these hosts. In much of Australia there are usually several sympatric feral hosts of FMD besides feral pigs such as goats, water buffalo, camels *Camelus dromedarius*, and deer *Cervus* spp. as well as many free ranging cattle and sheep (Wilson *et al.* 1991). A fuller understanding of the potential dynamics of the disease should include multi-species models with contact rates estimated for a community of feral ungulates. These models should also include identification from the veterinary literature of which of the four possible disease transmission scenarios each pair of host combinations would be.

The second major omission is consideration of the wind borne route for dissemination of FMD. This has been extensively studied in Britain with good concordance between patterns of disease outbreak and wind direction (Smith & Hugh-Jones 1969). This may not be as important an omission as neglecting the potential role of goats in maintaining the epizootic as the FMD virus for long distance dispersal requires low temperatures and high humidity which are rare at Nocolche.

An approach for improving the estimation of β would be more accurate systems of radio telemetry and possibly the use of collars that sensed the presence of other radio tagged animals closer than a certain distance. These collars would be complex and likely to be extremely costly requiring an integrated radio-transmitter, radio-receiver and data-logger all in the one unit. However, several of these units could be used as controls to test the accuracy of data collected by conventional radio-telemetry.

The major contribution of the disease models has been to identify how behavioural and demographic stochasticity will inevitably drive the disease to extinction as it lacks any centripetality at low host densities to buffer it against variation in β' and b' . Many diseases are characterised by outbreak and disappearance only persisting in areas of high host density (Yorke *et al.* 1979). This suggests the disease dynamics described by the models in this thesis approximate the real world.

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