



## An individual based model of bearded pig abundance

P.A. Hancock<sup>a,\*</sup>, E.J. Milner-Gulland<sup>a</sup>, M.J. Keeling<sup>b</sup>

<sup>a</sup> Renewable Resources Assessment Group, Department of Environmental Science and Technology, Royal School of Mines, South Kensington Campus, Imperial College, London SW7 2AZ, UK

<sup>b</sup> Department of Biological Sciences, Institute of Mathematics, University of Warwick, Gibbet Hill Rd, Coventry CV4 7AL, UK

Received 30 September 2003; received in revised form 13 May 2004; accepted 6 June 2004

### Abstract

We develop an individual based model of bearded pig abundance which predicts population dynamics based on the processes of energy accumulation and expenditure, reproduction and mortality of individual pigs. Because fatness is a key indicator of condition and reproductive potential in bearded pigs, processes are represented in terms of a fatness index variable. Only a small number of parameters are used in this simple model; these were chosen on the basis of fatness index data and qualitative observations of bearded pig population dynamics. The model was found to be accurate in predicting the timing of observed pig eruptions, and robust in that model results were unaffected by moderate variation in parameter values. There was insufficient quantitative data to obtain precise predictions of fatness and abundance, but qualitative insights about the effects of the size and timing of fruiting events on pig abundance were obtained. The results showed that a single fruiting peak will not produce a bearded pig eruption, no matter how large the fruiting event is, because the duration of the fruiting is too short to allow exponential growth of the population. Consecutive masting events are necessary for an eruption, because if events are separated by more than 1 year, the population will decline to its minimum fatness and abundance levels. It is also necessary for at least one of the fruiting events in a consecutive sequence to be a large event, as consecutive small fruiting events do not increase the fatness enough to cause an eruption. These insights help to explain and predict the effects of changes in mast fruiting patterns on bearded pig populations, such as the predicted increase in frequency and reduction in size of masting fruiting events as a result of climate change.

© 2004 Elsevier B.V. All rights reserved.

**Keywords:** *Sus barbatus*; Population dynamics; Borneo; Masting; Fatness

### 1. Introduction

The bearded pig (*Sus barbatus*) has a long established ecological and socio-economic significance for Borneo and its people. It is by far the most preferred and most consumed species of wild meat throughout

\* Corresponding author. Tel.: +44 207 594 9346; fax: +44 207 589 5319.

E-mail address: [p.hancock@imperial.ac.uk](mailto:p.hancock@imperial.ac.uk) (P.A. Hancock).

Sarawak and Sabah (Caldecott, 1988; Bennett et al., 1999). Bearded pigs, as major seed predators, also play a key role in the forest ecosystem. Pig populations are adapted to exploit the regional scale fruiting regimes of Borneo's forests. During mast fruiting events population numbers increase explosively and the pigs migrate across large areas to feed on Dipterocarp seeds. Curran and Webb (2000) presents evidence suggesting that a single pig travelled a distance of over 50 km in a few days. After the end of the masting season the population declines dramatically (Caldecott, 1988).

The mast fruiting phenomenon in Borneo's dipterocarp forests is thought to be a reproductive strategy to allow seeds in some areas to escape predation, by satiating nomadic predators at a landscape scale (Curran and Webb, 2000). Curran and Webb (2000) found that a key factor predicting the potential for seed escape was the distribution and density of the bearded pig. They further note that the duration between dipterocarp masting events seems sufficient to depress populations of the bearded pig, one of the longest living dipterocarp seed predators. Thus, Curran and Leighton (2000) state that, in order to predict the population dynamics of dipterocarp seedling recruitment across large spatial scales, it is necessary to understand the density dependent and independent processes influencing bearded pig populations.

Despite its significance, very few studies focus on bearded pig population ecology, and no estimates of abundance have been published. Fundamental aspects of bearded pig ecology remain poorly understood, including their spatial distribution, aspects of their habitat and food sources that are important for survival, mechanisms by which bearded pigs aggregate and migrate between different feeding areas, and the driving influences on bearded pig migration. This is largely because bearded pig population dynamics are complex, regional in scale, and highly variable in space and time.

The most detailed study was conducted in Sarawak by Caldecott (1988 and 1991), in 1984–1986. Interviews with local people, records of meal contents at boarding schools, trade records, and observations of pigs and pig carcasses were analysed, providing a largely qualitative understanding of bearded pig ecology in terms of their preferred habitat, reproductive characteristics, diet, social grouping and migration. Other studies include Curran and Webb (2000) and Curran and Leighton (2000), who investigated bearded

pig predation of dipterocarp seeds, and seed escape during masting events due to regional satiation of bearded pig populations. Pfeffer (1959) also observed bearded pigs, and noted some aspects of their migratory behaviour.

These studies give information about how pig populations respond to various fruiting scenarios in Bornean forests. Caldecott (1991) outlines a number of different fruiting patterns exploited by pigs in the interval between masting seasons, at a variety of spatial scales. During times when fruit availability is very low, the pig population is small, static and dispersed, relying on low-level food sources that are discontinuous and unpredictable. Pigs are also thought to regularly aggregate and move in large groups along set paths to exploit predictable, regular fruiting events. Migrations of masses of pigs, highly directional in nature, have been observed but the drivers of this behaviour are unknown. Fruiting during non-masting periods can also be unpredictable and highly dispersed over a wide area, as tends to be the case for dipterocarp species. Pig populations are thought to aggregate to increase chances of locating food in this situation.

Studies of bearded pigs often emphasise the close relationship between food supply and reproduction. Curran and Webb (2000) note that rutting behaviour occurs at the onset of dipterocarp flowering, allowing pigs to optimise their use of food resources to successfully produce offspring as fruiting occurs. Caldecott (1988) presents graphs showing fluctuations in fatness over a 1-year period (Fig. 1). Fat can be attained at a rapid rate and lost quickly, and the size and condition of piglets depends on the fatness of the mother. These observations imply that fluctuations in fatness are largely related to changes in the food supply, and are key to bearded pig population dynamics.

We extend these ideas to develop a population model for bearded pigs relating fatness index, fruit supply and reproduction. Fatness, or condition, is often an important component of energy/resource flow modelling of ungulate populations, as it is closely related to fecundity and mortality (Illius and Gordon, 1997; Saether, 1997). Illius and Gordon (1997) describe a model of a herbivore grazing system which predicts state dependent fecundity and mortality with a simple dependence on fatness. Generally, the aim of these energy/resource flow models is to describe animal processes in terms of the metabolism and expenditure of energy and protein

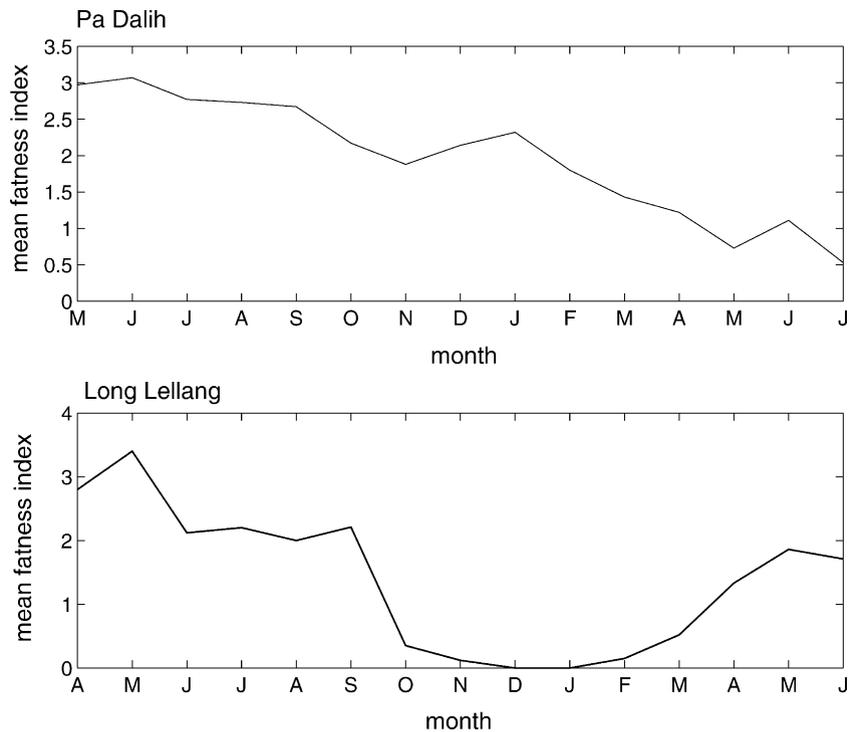


Fig. 1. Mean monthly fatness index of bearded pigs killed at Pa Dalih and Long Lellang over 15 months, from April 1984 to July 1985. Adapted from Caldecott (1988).

in maintenance, activity, reproduction, growth of fat-free mass, depletion and repletion of fat reserves, and heat loss to the environment. Observational data are used to develop and parameterise these processes, and to model the daily flux of material and energy through compartments representing the vegetation and the ungulate population (Illius and Gordon, 1997).

Bearded pig ecology has not been observed sufficiently to allow modelling of the flow of materials and energy through the system. Instead we use the data presented in Caldecott (1988), as well as qualitative observations gathered from past studies, to make simple biologically intuitive assumptions, incorporate them into a model and observe their effect on simulated behaviour. This concept is similar to that used in individual based models of wildlife populations by Turner (1993) and Sutherland (1996), and more recently by Fielding (2004) and Lewison (2004). The model presented here is a non-spatial, individual based stochastic model considering only the relationship between food supply, fatness and reproduction. This modelling aims

to explore general relationships between the size and timing of mast fruiting events and bearded pig population abundance. By identifying aspects of the model and the data that are responsible for the large population eruptions simulated by the model, we gain insight into this largely unstudied phenomenon.

## 2. Vegetation dynamics in Bornean forests

The size, timing and spatial extent of fruiting events in Borneo's forests is highly variable and unpredictable (Leighton and Leighton, 1983). Bearded pigs cope with this complexity through long-range migrations, and by exploiting a diverse range of food sources.

The forests of Borneo are well-known for their irregular, regional scale general flowering events. During general flowering, which occurs at intervals of 3–10 years, nearly all dipterocarp species, together with species of other families, come heavily into flower (Sakai et al., 1999). Abundant fruiting follows

several months later. In Borneo, interest is often focussed on Dipterocarpaceae, which represent the major component among the canopy and emergent trees (Sakai et al., 1999). In this case, the term ‘mast fruiting’ is used, which refers to episodic, synchronous fruiting by populations of a single species, or closely related species (Caldecott and Caldecott, 1985; Sakai et al., 1999). Wich and van Schaik (2000) present evidence that the synchrony between nearby areas in masting increases towards the eastern edge of Malesia. Curran et al. (1999) reported masting synchrony over Gunung Palung National Park in West Kalimantan. However, according to Caldecott and Caldecott (1985), Dove (1993) and Wich and van Schaik (2000), there is some spatial variation in the occurrence of dipterocarp masting in Borneo, which suggests that masting is influenced by local factors. It is suggested that minor imperfections in synchrony may make it profitable for animals to move around and track masting events (Dove, 1993; Wich and van Schaik, 2000).

Mast fruiting is not an all or nothing event (Wich and van Schaik, 2000), and some events have greater regional synchrony, spatial extent and fruit density than others. Even a major mast does not involve fruiting of all individual trees within a species. The data presented in Sakai et al. (1999) show that, within a Sarawak study site, approximately 60% of the individuals of the Dipterocarpaceae species *Dryobalanops aromatica* flowered during a general fruiting event in 1996. In contrast, less than 3% of the total number of individuals, composed of 257 species, flowered during the non-general flowering period.

Mast fruiting in dipterocarps is thought to be triggered by sharp drops in night time temperature (Ashton et al., 1988). In the case of eastern Malesia, this is widely thought to result from El Niño-induced droughts (Ashton et al., 1988; Curran et al., 1999; Wich and van Schaik, 2000), although the interaction between drought severity and frequency and the forest ecology of Borneo remains poorly understood (Walsh, 1996). Curran et al. (1999) found that all four mast fruiting episodes between 1986 and 1999 in Gunung Palung National Park occurred during years with a positive multivariate ENSO index, although Numata et al. (2003) point out the importance of considering the triggering time of mass flowering. Dipterocarp forests are currently under considerable threat

from global climate change, and logging and plantation clearing. Increased severity of ENSO-induced droughts, coupled with smoke and forest fires from land clearing activities, is thought to be a major factor contributing to the increased failure rate of dipterocarp fruiting events in recent years (Curran et al., 1999).

During intervals between mass fruiting events, bearded pig populations are supported by supra-annual, annual and sub-annual fruiting species, although most plant species flower only during general flowering periods (Sakai et al., 1999). Sakai et al. (1999) observed that only a few trees of each species participate in flowering events during a non-general flowering period. The spatial distribution of fruit fall can therefore be sparse and unpredictable.

Most studies of bearded pigs note their exploitation of the oak family (Fagaceae). The Fagaceae are widespread throughout most parts of Borneo, with the largest number of species in the lower montane forest at elevations of 1200–1800 m (Kaul et al., 1986). Most fagaceous trees in Borneo have regular, annual fruiting episodes, and there is general reproductive synchrony amongst the species and individuals (Kaul et al., 1986). Caldecott (1988) states that between roughly October and April, large elements of the local bearded pig population reside in submontane forests along the Sarawak–East Kalimantan border, an area found to be extremely rich in the trees of Fagaceae.

Bearded pigs have also been noted feeding on a number of other plant taxa, including *Tetamerista glabra* and *Palaquium leiocarpum* in peat swamps (Curran and Leighton, 2000) and seasonally fruiting *Dinochloa* bamboo groves in Sabah (Davis and Payne, 1982 in Caldecott, 1988). Fig plants produce fruit asynchronously, and provide a continual, but stochastically fluctuating, local food source (Leighton and Leighton, 1983). Sakai et al. (1999) noted that *Ficus* species exhibited the highest percentage of fruiting individuals out of all annual and sub-annual flowering species studied.

In addition, pigs consume a diverse range of other food items, including roots, worms, grubs and agricultural crops. Dove (1993) reports a resident population of pigs that is principally supported by cassava in the Kantu swiddens. However, the most important food sources for bearded pigs are the fat rich

fruits of the Fagaceae and the Dipterocarpaceae, as fat accumulation is important for successful reproduction.

### 3. Data sources

Data from Caldecott (1988) on exports of seeds from the *Shorea* species of dipterocarp, as well as data on mean fatness index of bearded pigs culled at various locations throughout Sarawak, were used in the development of a model relating bearded pig abundance to changes in fruit supply. These data sources are described in the following.

#### 3.1. Enkabang export data and bearded pig eruptions

Fruit supply data was obtained from records of the annual export of enkabang (*Shorea* seeds) from Sarawak from 1948 to 1987 as shown in Table 1 (Caldecott, 1988). Bearded pig eruptions were reported in the years 1953–1954, 1958–1959, 1982–1983 and 1986–1987, according to Caldecott (1988). Caldecott (1988) observed that these time periods have consecutive enkabang exports of over 1000 tonnes, implying that major eruptions require consecutive years of heavy fruiting. We have assumed that the eruptions began in the later part of the time periods reported, to account for lags in pig response to mast fruiting. We have therefore interpreted the observations to mean that bearded pig eruptions started in the years 1954, 1959, 1983 and 1987 (Table 1).

#### 3.2. Fatness index

Caldecott (1988) describes a fatness index, given by the number of finger widths of the hand that can be inserted in a slash at the shoulder before hitting muscle. Results presented by Caldecott (1988) show large changes in the fatness index over a period of 18 months. The fatness trend differs between different locations in the upper Baram region of Sarawak. Fig. 1 shows fatness trends for the longhouses Pa Dalih and Long Lelang. These data were used to guide the calibration of bearded pig fatness in the individual based model.

### 4. The simulated food supply

The records of enkabang exports allow comparison of the relative amount of dipterocarp fruiting in different years. These data were used as the basis for estimating variation in fruit supply over the 40-year period. The main aim of the simulated fruit supply was to show the timing of masting events, and compare the relative size of masting events. Given that masting is a seasonal event, it was necessary to represent the fruit supply in terms of the fruit amount in each 3-month season. These seasons are actually longer than the masting season, which usually lasts for around 6 weeks (Curran and Leighton, 2000; Curran and Webb, 2000). It was assumed that all the fruit export for that year fell in the fruiting season, set arbitrarily to the first season of the year. In all other seasons, a low constant food level was assumed. The value chosen was low enough to allow the mast to have a major effect, but not so low

Table 1  
Export of enkabang (*Shorea* seeds) from Sarawak

Year	Export (tonnes)	Year	Export (tonnes)	Year	Export (tonnes)	Year	Export (tonnes)
1948	23	1959	22358 <sup>a</sup>	1970	16554	1981	1619
1949	765	1960	0	1971	0	1982	22950
1950	0	1961	0	1972	0	1983	1476 <sup>a</sup>
1951	22	1962	19883	1973	28061	1984	0
1952	31	1963	0	1974	0	1985	144
1953	2852	1964	0	1975	8	1986	8443
1954	16305 <sup>a</sup>	1965	205	1976	50	1987	23444 <sup>a</sup>
1955	1481	1966	6761	1977	4820		
1956	161	1967	0	1978	94		
1957	0	1968	16032	1979	429		
1958	6305	1969	0	1980	11106		

<sup>a</sup> The time of bearded pig eruption. Data obtained from Caldecott (1988).

Table 2  
Parameters of the individual based model

Symbol	Explanation	Value
$R_{\min}$	Low constant fruit supply level (tonnes)	300
$R_i$	Fruit supply (tonnes)	Calculated
$\alpha$	Rate of fatness accumulation	600
$\beta$	Rate of fatness expenditure	1.7
$P_i$	Population size (individuals)	Calculated
$F_i^j$	Fatness index for pig $j$ in season $i$	Calculated
$X_i^j$	Fatness increase of pig $i$ in season $j$	Calculated
$c_i$	Mean fatness increase	Calculated
$\sigma_F$	Standard deviation of fatness increase	1
$F_R$	Fatness level required for reproduction	3
$\Delta F_{\max}$	Maximum rate of increase in fatness	4
$F_M$	Fatness level at which mortality occurs	0.7
$\Delta F_R$	Fatness lost due to reproduction	1.5
$K$	Positive difference between modelled fatness index and true fatness index	2
$\sigma_P$	Standard deviation of piglet fatness index	1
$P_{\min}$	Threshold population size for density dependence (individuals)	1000
	Number of piglets per litter (individuals)	2
	Time between litters (months)	6
	Age at first reproduction (months)	12
	Season length (months)	3

Parameter values are estimated based on information in Caldecott (1988), as described in the text, or calculated in the model. Values are in arbitrary units of fatness unless otherwise stated.

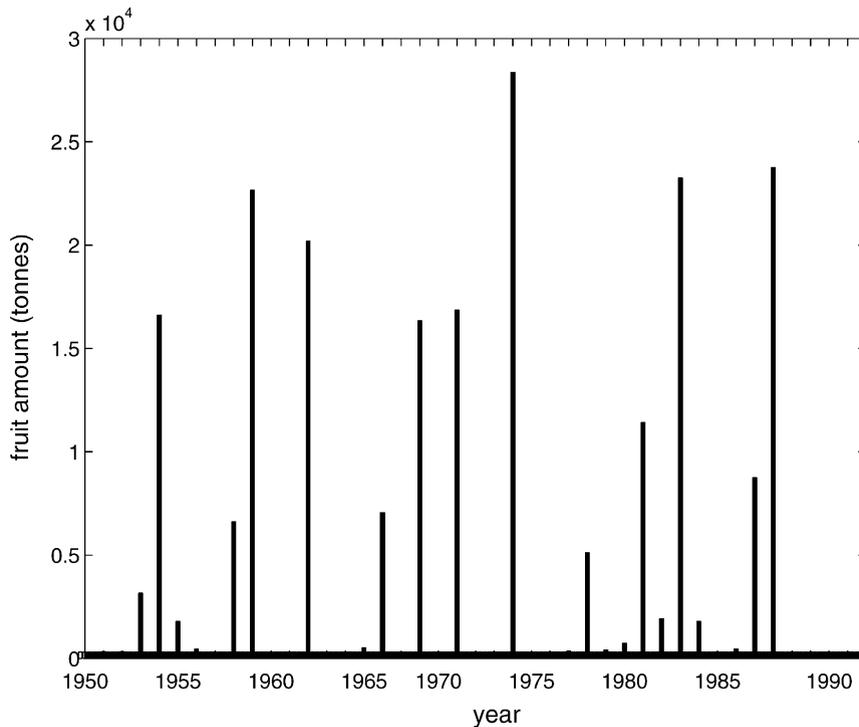


Fig. 2. The simulated fruit supply used for the individual based model.

that the population became extinct during the interval between mast periods (Table 2). The simulated fruit supply based on the enkabang export records is shown in Fig. 2.

## 5. The individual based model

An individual based model (IBM) was developed, whereby changes in abundance were related to food supply through the state variable fatness. Individual based models have some key advantages over population based models, which have been widely discussed (Huise et al., 1999; Berec, 2002; Fielding, 2004). In the case of this study, using an IBM avoids calibration of a population growth rate, which is advantageous when little quantitative data is available. Instead, births and deaths are directly linked to the fatness of each individual. Thus, the underlying mechanisms controlling the system dynamics are more transparent. Secondly, the IBM allows for greater within population variability, because the impacts of reproduction and stochastic variation in food supply affect the fatness of the individual rather than the mean population fatness as a whole. This greater flexibility means that such impacts can have a smaller effect on the population as a whole, which gives greater stability to the individual based model in comparison to a population based model.

The fatness of each individual pig was assumed to depend stochastically on fruit supply and population density, as follows:

$$F_{i+1}^j = F_i^j + X_i^j - \beta \quad (1)$$

where  $F_i^j$  is the fatness index of the  $j$ th pig in season  $i$ . Fatness increases according to the stochastic consumption of food, modelled by realisations of a normal random variable  $X_i^j \sim N(c_i, \sigma_F)$ , with mean  $c_i$  and standard deviation  $\sigma_F$ , where  $c_i$  is the per capita resource:

$$c_i = \frac{\alpha R_i}{P_i} \quad (2)$$

$R_i$  is the fruit supply,  $P_i$  is the population abundance in season  $i$ , and  $\alpha$  is a constant. Negative realisations of the random variable  $X_i^j$  were set to zero. Thus, the pigs have a greater chance of increasing their fatness if the food supply is higher, but less chance if the population is larger. In the absence of food the fatness declines at

a constant rate  $\beta$ . A similar model of weight accumulation and metabolic expenditure is used for grasshoppers in Fielding (2004)

Once the population size goes below a certain threshold,  $P_{\min}$ , it is assumed that the food supply obtained per pig no longer increases as the population size decreases. This gives

$$c_i = \frac{\alpha R_i}{P_{\min}} \quad \text{if } P_i \leq P_{\min} \quad (3)$$

which mimics satiation. When population numbers are low, the effect of population density is not a dominant factor determining the amount of food found by each individual pig. At low population sizes, each pig cannot make use of all, or even a large proportion of, the fruit available across the entire spatial region, so the density dependence relationship is not appropriate.

Fecundity and mortality depend directly on the fatness of the pig. A pig was assumed to die if its fatness index was below a threshold  $F_M$ . The model considers only female pigs, as ecological characteristics particular to male pigs would not significantly affect system dynamics. Pigs reproduce if their fatness index gets to a value  $F_R$  or above. Documentation by Pfeffer (1959), Caldecott (1988) and Curran and Webb (2000) was used to define the reproductive characteristics of the population. Bearded pigs reach reproductive maturity when they are between 8 and 18 months, so a condition was emplaced allowing only pigs older than 12 months to reproduce. An individual pig produces a litter containing two female piglets every time it reproduces. Given that the median litter size of bearded pigs is seven (male and female) piglets, though it is highly variable, the model assumes that approximately half the piglets in the litter survive. To our knowledge there are no published estimates of piglet mortality in bearded pigs, though Pfeffer (1959) reported that the number of piglets accompanying a female was two. This implies that a significant proportion of piglets in the litter do not survive beyond infancy. Bearded pigs are able to produce up to two litters per year. Accordingly the model specifies a minimum separation time of 6 months between litters.

Using the state variable fatness as a system driver allows the incorporation of energy expenditure and storage into the model. One primary mechanism is reproductive investment (Fielding, 2004). The process of reproduction is assumed to cause fatness of the mother

to decline by an amount  $\Delta F_R$ . Fatness of the piglets depends on the fatness of the mother, as has been observed by Caldecott (1988). This dependence is assumed to be stochastic, given that condition varies within a litter. Piglet fatness is therefore given by realisations of a normal random variable with the fatness index of the mother as the mean and a constant standard deviation  $\sigma_P$ . Finally, a limit was placed on the rate of increase in fatness,  $\Delta F_{\max}$ . This reflects our assumption that there is a limit to how quickly pigs can accumulate fat, and hence how fat they can get (Illius and Gordon, 1997). Incorporation of the above conditions into the model allow it to better explain the ecology of the system.

The parameters of the model are summarised in Table 2. To select values for these parameters, the two data sources discussed in the previous section were used. Firstly, the accuracy of predicted eruption times was assessed using the records of observed pig eruption years. Secondly, the data on the fatness index of bearded pigs presented in Caldecott (1988) were used to calibrate the scale of variation for the modelled fatness index. Caldecott (1988) observed that the fatness index can vary widely, and is likely to be an important determinant of reproductive capacity. The minimum mean fatness index in Fig. 1 is zero. The model used in this study does not allow negative fatness index, so a mean of zero is not possible without total extinction. We therefore shifted the modelled fatness so that it was equal to the true fatness plus a positive constant  $K = 2$ . The maximum mean fatness recorded in Fig. 1 is 3.4. For both locations the maximum occurs in April 1984. This is likely to be due to the heavy fruiting in the previous 2 years. It is probable that the fatness index during the fruiting peak was higher than the maximum observed fatness. We have therefore determined that an appropriate range for the fatness index is approximately 0–5, giving the range of the modelled fatness index as 2–7. Caldecott (1988) further notes that the median fatness index of pregnant females was 1.5. This guided choice of the value of the minimum fatness required for reproduction,  $F_R$ . Clearly the data do not allow accurate quantitative prediction of fatness as a function of time, however, the modelling in this study aims to identify qualitative patterns and relationships.

Qualitative observations of bearded pigs were also used. According to Caldecott and Caldecott (1985) and Caldecott (1991), bearded pig populations erupt from a small, sparsely distributed population to reach numbers

of the order of one million, within the Baram district of Sarawak alone. Following the masting season, the population quickly dies back to its original level. Parameters were adjusted to give patterns that best agreed with these observations.

## 6. Results

Fig. 3 shows a sample run of the model using the chosen parameter values (Table 2). The model predicts marked population increases (eruptions) in response to certain fruiting patterns. The times at which eruptions are predicted are the same as the times of observed eruptions. The relative size of the eruption predicted by the model depends on both the size of the fruiting peak and the population size prior to the fruiting season. The model supports the observation of Caldecott (1988) that two consecutive masting years are needed for a major eruption, as Fig. 3 shows that the largest eruptions correspond to times when fruiting peaks are close together. Generally speaking, a larger eruption will be simulated if the population before the fruiting peak is relatively high, having been boosted by a mast in recent years. If population numbers are very depressed, a single mast event can have little effect. This is why the largest fruiting peak in the simulation, peak 12, produces only a minimal population response.

It is clear that the linear relationship between fatness and food supply is being modified by limiting the rate of fatness increase according to  $\Delta F_{\max}$ . This is why, in many cases, large fruiting peaks have a similar effect on the population size as relatively small peaks. Without restricting the fatness increase, fatness values become huge following the larger peaks, because the variation in fruit supply is so extreme. The smallest peaks in the simulation, numbers 4, 8, 14 and 20, result in much smaller fatness peaks than the other fruiting peaks. However, when the small peaks follow a large fruiting peak, as is the case for peaks 3, 16 and 19, the population abundance is greatly amplified, and an eruption usually occurs. This is because fatness is maintained above the reproduction threshold long enough to allow a large number of pigs to reproduce.

The shape of the fatness index graph at the time of a population eruption often features two sharp peaks, corresponding to consecutive fruiting events. The width of these peaks indicates that the mean fatness takes about

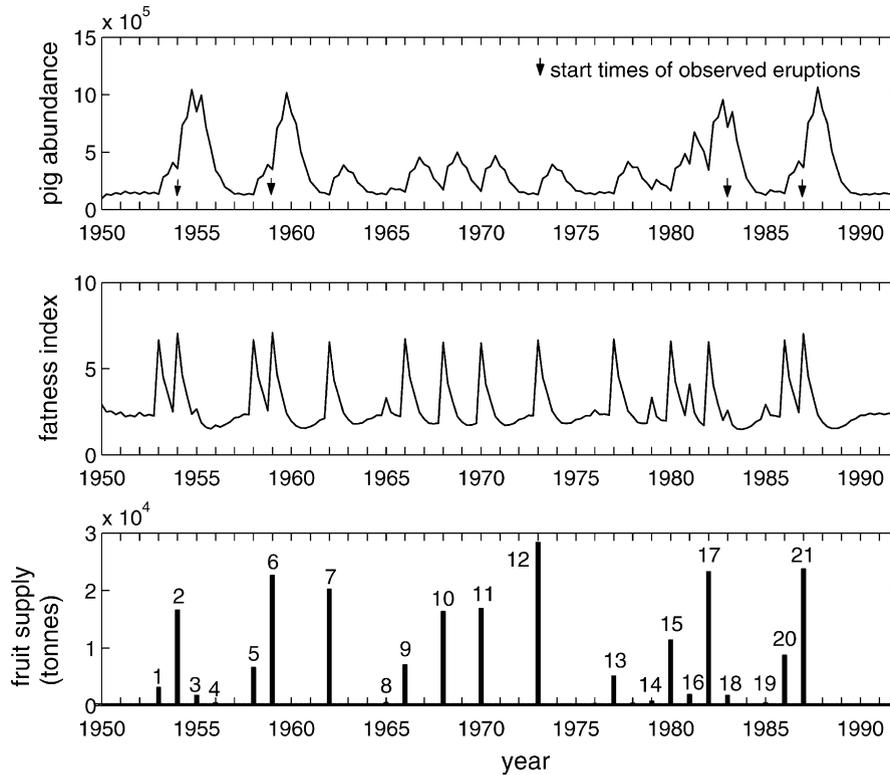


Fig. 3. Simulated abundance and fatness index for the fruiting scenario in Fig. 2. Predicted eruptions correspond to the approximate times of observed eruptions. The fruiting peaks have been numbered for convenient reference.

1 year to complete the peak and return to its minimum level. Following the first fatness peak, the population declines only slightly before the next fatness peak prevents further population decline. The abundance graph indicates that the population takes around 1 year to decline from a peak, regardless of the height, because the decline is steeper if the peaks are higher due to density dependence. This implies that a pig eruption would not occur for most events separated by more than 1 year, because the population would have returned to its original state between most events.

To investigate the underlying relationships represented by the model, the seasonal values of abundance and fatness was plotted, as shown in Fig. 4a. This demonstrates that high abundance and high fatness cannot occur simultaneously, a result of density dependence. Fig. 3 also reflects this, showing a lag between peaks of fatness and abundance. Fatness reaches its peak, and then takes time to decline to a level below the reproduction threshold, although it declines at

the maximum possible rate because the population is very large so per capita food supply is low. During this time reproduction occurs and the abundance reaches its peak, causing fatness to continue to decline at the maximum rate. This time-dependent process of fatness decline is facilitated by the use of the discretised time derivative of fatness in the model. The effect of fatness on abundance can be seen by lagging the fatness index by three seasons, as shown in Fig. 4b. The general linear trend is clear, although the relationship is noisy due to the importance of the timing of fruiting events.

### 6.1. The effect of varying model parameters

Given that there are limited quantitative data with which to calibrate the parameters of this model, it is important to determine the model's robustness, in terms of how the above results are affected by variation in the parameters. This was tested by running the model many times, with different parameter values. In each

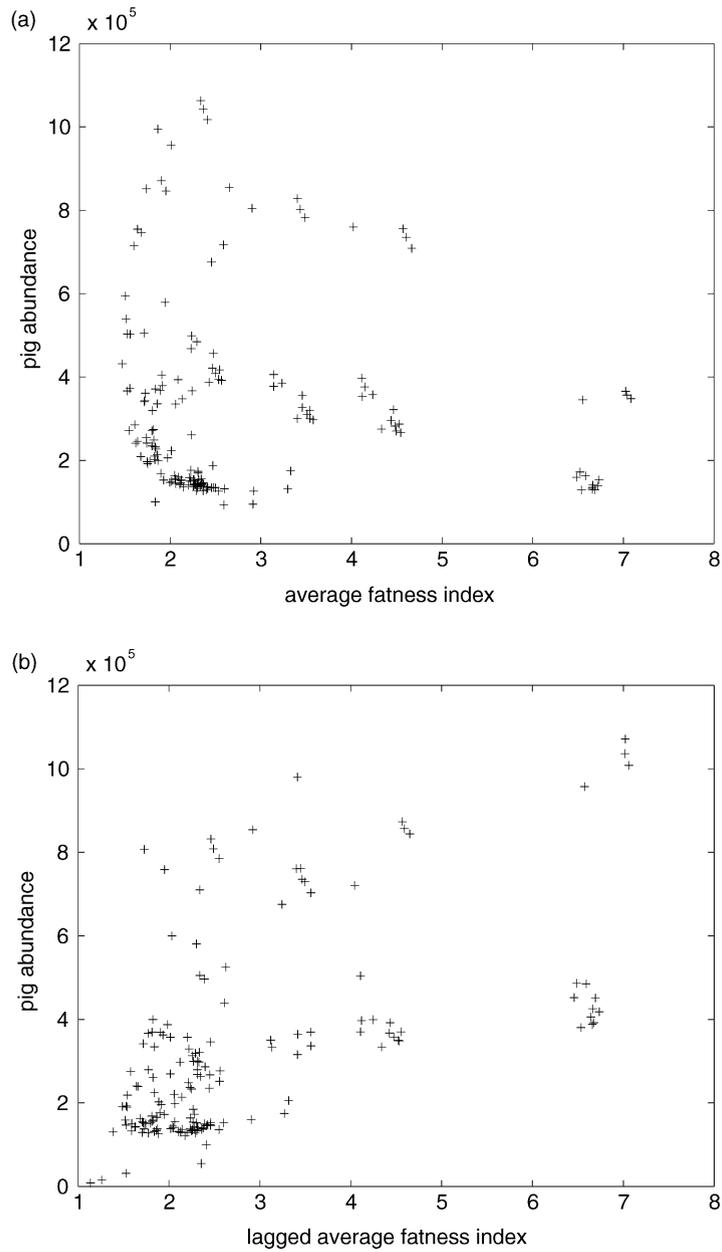


Fig. 4. (a) Relationship between fatness and pig abundance, (b) relationship between pig abundance and fatness index, where fatness index is lagged by 3 seasons (9 months).

simulation, parameters were allowed to vary according to a uniform distribution within a range of 20% lower to 20% greater than their chosen values. The influence of variation in parameters on model results was assessed by analysing the effect on the agreement of model predictions with observed data. This involved comparing the years in which the model-predicted bearded pig eruptions to the years in which eruptions were actually observed.

In 100 simulations, the four highest eruptions predicted by the model always occurred in the same years as the observed eruptions. This implies that the pattern in Fig. 3 is robust. The main validation of the modelling exercise is that it accurately predicts the timing of bearded pig eruptions, according to past observations. This test demonstrates that moderate changes to parameter values do not affect this conclusion.

An example of the effect of variation in parameters on the abundance trajectory is shown in Fig. 5. While

these trajectories do not necessarily represent the extremes of model behaviour, they show that the imposed parameter changes can alter the abundance magnitude considerably, but the position of the peaks is not greatly affected.

### 6.2. Abundance patterns for low fruiting, and regular annual and biennial fruiting scenarios

The food sources used by bearded pigs during the intermast interval is clearly an important aspect of their ecology, however, very little is known about their behaviour during this period as the pigs are not often seen. The model was run to investigate the predicted dynamics when the food supply level was low, with no significant fruiting events, and also when regular fruiting events occur, both annually and biennially. These simulations build up a picture of population dynamics during the intermast interval, and explain the importance of consecutive fruiting events.

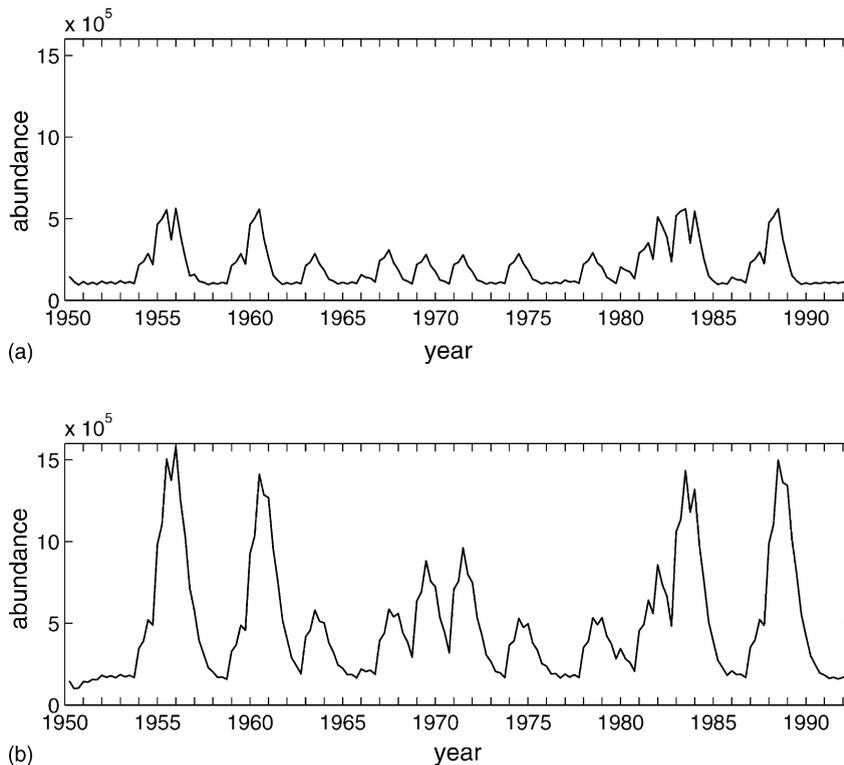


Fig. 5. Simulated abundance trajectory for (a) all parameter values 20% lower and (b) all parameter values 20% greater than the values specified in Table 2.

### 6.2.1. Constant low-level fruiting

In the absence of significant fruiting events, Caldecott (1991) describes the pig population as dispersed, static populations exploiting small, dispersed, unpredictable and discontinuous ‘background’ food sources, with low breeding and growth rates. In our model, the population abundance is essentially static when food supply is constant at a low-level ( $R_{\min}$ , Table 2), which is consistent with the description given by Caldecott (1991). If the fruit level is low enough, the model predicts extinction of the population. The level below which extinction occurred was found to be  $R_{\min} = 20$  tonnes.

Comparing the causes of mortality for this fruiting pattern and the mast fruiting scenario shows that the processes affecting population size are different for each case. The mean age reached by pigs throughout the simulation was approximately 2 years for both fruiting scenarios. The mast fruiting scenario involves much higher levels of reproduction, and it was found that individuals who reproduced often died in the following sea-

sons, due to the associated fitness loss. Approximately 57% of deaths followed a recent reproduction for the mast fruiting scenario. In the case of the low-level constant food supply, the majority of deaths resulted from not finding enough food in a particular season. Only around 5% of the deaths followed a reproduction.

### 6.2.2. Regular annual fruiting

Annual fruiting, in the first season of each year, was incorporated by adding an annual amount  $R = 700$  tonnes to the fruit supply, whilst maintaining the low-level constant supply  $R_{\min}$ . The results are shown in Fig. 6a. Pig abundance responds to each fruiting peak, but the effect is not cumulative, as the population dies back to its lowest level before the next peak arises. The model predicts that regular annual fruiting increases the average abundance of the population in comparison to just a low-level constant food supply, and provides a temporary boost to the population during the fruiting season. Population eruptions, such as those observed for the mast fruiting pattern, do not occur. This is

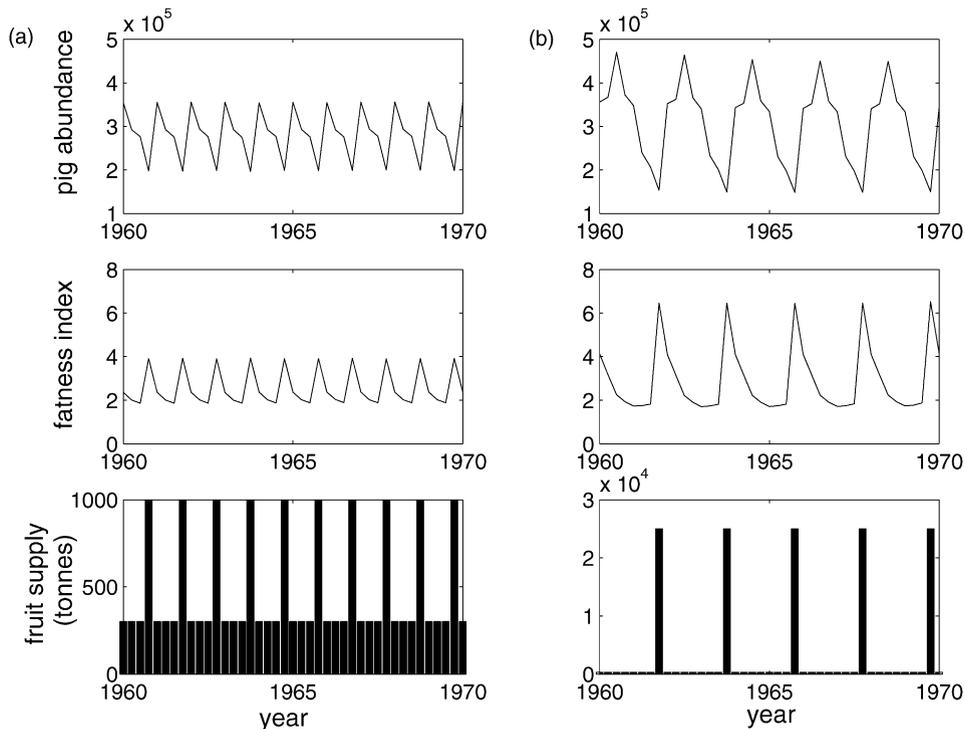


Fig. 6. Predicted fatness index and pig abundance for (a) annual fruiting of 1000 tonnes and (b) biennial fruiting of 25,000 tonnes. The 10-year slice shown is representative of the pattern for the 40-year period.

because the fruiting level is lower, not because of the time between fruiting events, since the events are separated by a year, which is the minimum separation time for most fruiting events. The fruiting peaks for this scenario were of magnitude 1000 tonnes, which is the minimum amount required in consecutive years to cause a bearded pig eruption, according to the ‘rule of thumb’ suggested by Caldecott (1988). These results suggest that the size of the at least one of the fruiting peaks in a consecutive pair needs to be considerably larger than 1000 tonnes to generate a bearded pig eruption. In the case of the observed eruptions, they all corresponded to consecutive years of fruiting amount greater than 1000 tonnes, but the fruit amount in at least one of the years was always at least 15,000 tonnes. Thus, it appears that neither a large peak on its own can generate an eruption, nor can two small consecutive peaks. Both the size of the mast event and the temporal separation are necessary factors in predicting pig eruptions.

### 6.2.3. Regular biennial fruiting

To further investigate the influence of the timing of fruiting events on the predictions of this model, a fruiting scenario was created whereby large fruiting events were simulated every 2 years. The size of the fruiting event was set to 25,000 tonnes, which is close to the largest enkabang export value in the time period considered. If two such events occurred in consecutive years, an eruption would definitely result. However, 2 years may be long enough for the population to return to the state corresponding to a low-level food supply after a fruiting peak. The results in Fig. 6b show that this is the case, as the abundance peak heights for these large fruiting events are not greatly different from the peaks heights in Fig. 6a, when the fruiting amount was only 1000. This shows that consecutive fruiting events are necessary for a population eruption to occur.

Varying the timing of fruiting events for a given average annual fruit supply further demonstrates the

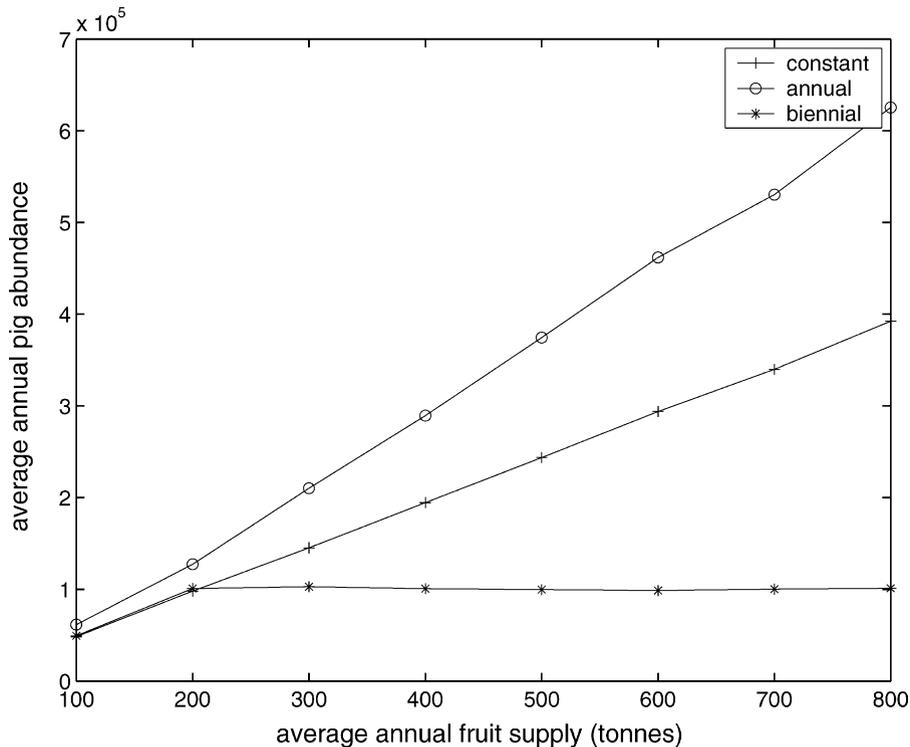


Fig. 7. The average annual pig abundance for a range of mean annual fruit supply levels, and three fruiting patterns. The constant fruiting scenario has the same fruit amount for all seasons. For the annual and biennial scenarios, the fruiting level in seasons not containing annual or biennial fruiting events was set to 100 tonnes.

importance of consecutive fruiting events (Fig. 7). The biennial fruiting scenario produces abundances that are not much higher than that for a constant fruit supply of 100 tonnes, regardless of the fruiting amount, whereas the abundances for annual fruiting reflect the height of the fruiting peaks. The response of the population to annual fruiting events further illustrates the importance of reproductive activity in controlling population size. High reproduction levels can only occur if the mean fatness and population size are elevated for a sustained period of time. For the biennial fruiting pattern the fruiting peaks do not maintain high fatness for long enough to significantly boost the population, even though the peaks are almost twice as high as the annual fruiting peaks.

## 7. Discussion

An individual based model of bearded pig abundance was developed in order to obtain qualitative insights into population dynamics. Quantitative predictions were not possible, as there was insufficient quantitative data to accurately calibrate model parameters. Construction of the model was guided by the limited quantitative data on the mean fatness index of bearded pig populations, which revealed the importance of fatness in controlling population dynamics, and allowed estimation of the range of variation of the fatness index. However, these data could not be relied upon for precise quantitative estimation of fatness. The data on fruiting exports were used to parameterise fruiting, while times of observed eruptions provided a means of assessing the accuracy and robustness of the model. The qualitative knowledge of bearded pig population dynamics obtained through observations of other researchers was equally important in guiding model construction. This gave an understanding of the magnitude and duration of population eruptions, bearded pig reproductive ecology, and fluctuations in fruit supply resulting from vegetation dynamics in Bornean forests.

The results of this study demonstrate that our model accurately predicts the timing of bearded pig eruptions in comparison to existing observations. The model gives insights into the effect of the timing of mast fruiting events, and the relative size of the mast, on bearded pig populations. It shows that consecutive years of heavy fruiting are required to generate an eruption, be-

cause if the gap between fruiting events is longer, population abundance and average fatness return to minimum levels between events. A single fruiting event does not generate an eruption, because the period of increased fatness and reproductive activity is too short, and fatness levels decline before the population can increase exponentially. For a model-predicted eruption, it is also necessary that at least one of the consecutive masting years features a major fruiting event, as consecutive minor fruiting peaks do not generate an eruption. A major fruiting peak on its own will not have a strong effect on population numbers, but a major event occurring in succession with another large or relatively small fruiting peak will result in a population eruption.

These findings show that the model is primarily driven by the timing of the fruiting events, rather than by precise parameter values. This explains the robustness of the model, as measured by its ability to accurately predict eruption times when parameters are varied by a moderate amount. Changes in parameter values, provided they are not too large, will affect population abundance but will not alter the times at which eruptions are predicted. The ability of the model to differentiate between various fruiting scenarios without precise calibration of parameters is an asset in data-poor situations such as that considered here.

The results show the link between fatness and abundance, and how the process of accumulating fat allows the prediction of population eruptions. For a certain time, fatness is retained, allowing consecutive peaks to have a cumulative impact on population size. This relationship specified by the difference equation was moderated by the external constraint  $\Delta F_{\max}$ , which prevented the fatness from becoming larger than reasonable in comparison to the data records. The rate of change in fatness was also influenced by the energy expended due to reproduction,  $\Delta F_R$ , which increased the mortality of reproducing pigs. These processes were imposed on the model because they were considered to be biologically realistic, and thus allowed the model to better explain the true system dynamics.

We can apply the results of this modelling exercise to help understand and predict the effect of future changes in masting patterns on bearded pig populations. Curran et al. (1999) suggests that dipterocarps may respond to the increasing intensity of ENSO events with more frequent, low fruit production. The consecutive masting events in the years 2001 and 2002 were both weak

events (Colin Maycock, personal communication), but there were also no strong ENSO events in these years. If dipterocarps do respond as Curran et al. (1999) suggests, the results presented here indicate that, as the masting events get weaker, pig eruptions would be less likely to occur for consecutive masting years, and the average abundance would decrease. This will have consequences for the entire forest dynamics in the region.

The fact that the model is non-spatial limits its ability to represent reality. Clearly the spatial distribution of pigs and the spatial variation in food supply will have an important effect on abundance, particularly during the intermast interval. The way in which pigs respond to spatial variation in their food supply will be the subject of future modelling research.

### Acknowledgements

We are very grateful to Julian Caldecott, Lisa Curran, Jaboury Ghazoul, Colin Maycock, Mark Newman, David Burslem and Liz Bennett for their help and advice. This work was funded by the Leverhulme Trust.

### References

- Ashton, P.S., Givnish, T.J., Appanah, S., 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* 123 (1), 44–66.
- Bennett, E.L., Nyaoi, A.J., Sompud, J., 1999. Saving Borneo's bacon: the sustainability of hunting in Sarawak and Sabah. In: Robinson, J.G., Bennett, E.L. (Eds.), *Hunting for Sustainability in Tropical Forests*. Columbia University Press, New York, pp. 305–324.
- Berec, L., 2002. Techniques of spatially explicit individual-based models: construction, simulation and mean field analysis. *Ecol. Model.* 150, 55–81.
- Caldecott, J., 1988. *Hunting and Wildlife Management in Sarawak*. IUCN, Cambridge.
- Caldecott, J., 1991. Eruptions and migrations of bearded pig populations. *Bongo* 18, 233–243.
- Caldecott, J., Caldecott, S., 1985. A horde of pork. *New Sci.* 13, 32–35.
- Curran, L.M., Leighton, M., 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* 70 (1), 101–128.
- Curran, L.M., Webb, C.O., 2000. Experimental tests of the spatiotemporal scale of seed predation in mast-fruiting Dipterocarpaceae. *Ecol. Monogr.* 70 (1), 128–148.
- Curran, L.M., Caniago, I., Paoli, G.D., Astianti, D., Kusneti, M., Leighton, M., Nirarita, C.E., Haeruman, H., 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. *Science* 10, 2184–2188.
- Davis, A.G., Payne, J.B., 1982. *A Faunal Survey of Sabah*. WWF, Malaysia, Kuala Lumpur.
- Dove, M.R., 1993. The responses of Dayak and bearded pig to mast-fruiting in Kalimantan: an analysis of nature-culture analogies. *East-West Center Reprints No. 7*, 113–123.
- Fielding, D.J., 2004. Intraspecific competition and spatial heterogeneity alter life history traits in an individual-based model of grasshoppers. *Ecol. Model.* 175 (2), 169–187.
- Huise, G., Strand, E., Giske, J., 1999. Implementing behaviour in individual based models using neural networks and genetic algorithms. *Evol. Ecol.* 13, 469–483.
- Illius, A., Gordon, I., 1997. Scaling up from daily food intakes to numerical responses of vertebrate herbivores. In: Olff, H., Brown, V.K., Drent, R.H. (Eds.), *Herbivores: Between Plants and Predators*. Blackwell Science, Oxford, pp. 397–425.
- Kaul, R.B., Abbe, E.C., Abbe, L.B., 1986. Reproductive phenology of the oak family (Fagaceae) in the lowland rain forests of Borneo. *Biotropica* 18 (1), 51–55.
- Leighton, M., Leighton, D.R., 1983. Vertebrate response to fruiting seasonality within a Bornean rain forest. In: Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (Eds.), *Tropical Rain Forest: Ecology and Management*. Blackwell Scientific, Oxford, UK, pp. 181–196.
- Lewis, R.L., Carter, J., 2004. Exploring behaviour of an unusual megaherbivore: a spatially explicit foraging model of the hippopotamus. *Ecol. Model.* 171, 127–138.
- Pfeffer, P., 1959. Biologie et migrations du sanglier de Bornéo (*Sus barbatus* Müller 1869). *Mammalia* 23, 277–303.
- Numata, S., Yasuda, M., Okuda, T., Kachi, N., Noor, N., 2003. Temporal and spatial patterns of mass flowerings on the Malay Peninsula. *Am. J. Bot.* 90 (7), 1025–1031.
- Sakai, S., Momose, K., Yumoto, T., Nagamitsu, T., Nagamasu, H., Hamid, A., Nakashizuka, T., 1999. Plant reproductive phenology over four years including an episode of general flowering in a lowland dipterocarp forest, Sarawak, Malaysia. *Am. J. Bot.* 86 (10), 1414–1436.
- Saether, B.R., 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol. Evol.* 12, 143–149.
- Wich, S.A., van Schaik, C.P., 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. *J. Trop. Ecol.* 16, 563–577.
- Sutherland, W.J., 1996. *From Individual Behaviour to Population Ecology*. Oxford University Press, Oxford.
- Turner, M.G., Wu, Y., Wallace, L.L., Romme, W.H., 1993. A landscape simulation model of winter foraging by large ungulates. *Ecol. Model.* 69, 163–184.
- Walsh, R.P.D., 1996. Drought frequency changes in Sabah and adjacent parts of northern Borneo since the late nineteenth century and possible implications for tropical rainforest dynamics. *J. Trop. Ecol.* 12, 385–407.