

## SHORT COMMUNICATION

## INTRINSIC RATE OF INCREASE FOR A BRUSHTAIL POSSUM POPULATION IN RATA/KAMAHI FOREST, WESTLAND

**Summary:** An estimate of intrinsic rate of increase ( $r_m$ ) of a brushtail possum (*Trichosurus vulpecula*) population was calculated from the measured increase in possum numbers after a poisoning operation in Westland rata/kamahi forest. Our empirical estimate of  $r_m$  (0.22- 0.25) was lower than published estimates for this species (0.30, 0.34, 0.59). Consequently, the control operation was effective for longer than predicted by population models that used these published values. We suggest reasons why the rates of fecundity and juvenile survival used in other modelling studies may have been inappropriate for this population.

**Keywords:** population dynamics; brush tail possums; *Trichosurus vulpecula*; control; survival; fecundity; rata/kamahi forest.

## Introduction

Intrinsic rate of increase ( $r_m$ ) is the maximum rate of increase that a population can achieve in the absence of crowding and of shortage of resources (Caughley, 1977: p. 109).  $r_m$  is not constant for a species, but is specific to the particular population in which it is measured. Estimates of  $r_m$  for brushtail possums (*Trichosurus vulpecula*) have been incorporated into models of population growth used to predict the response of this species to control operations (Spurr, 1981), harvesting (Clout and Barlow, 1982; Barlow and Clout, 1983; Keber, 1985), and infection with bovine tuberculosis (N.D. Barlow, pers. comm.).

Intrinsic rate of increase can be calculated from schedules of survival and fecundity using Lotka's equation (in Caughley, 1977):

$$\sum l_x e^{(r_m - d)x} m_x = 1.0 \quad (\text{Eqn.1})$$

where:  $x$  = age class

$l_x$  = maximum probability of surviving to age  $x$

$m_x$  = maximum number of female offspring/female of age  $x$ .

For a seasonally breeding population in which survival is constant for all age classes, and fecundity is constant except for young of the year (which are assumed not to breed), the integral form of Lotka's equation can be used to approximate  $r_m$  using instantaneous rates of birth ( $b$ ) and death ( $d$ ):

$$r_m \approx (b - d) \quad (\text{Eqn. 2})$$

where:  $b = \ln(1 + \text{maximum female offspring/ female/year})$

$d = \ln(\text{maximum annual survival})$ .

We know of two estimates of  $r_m$  for possums in New Zealand calculated by these equations: 0.59 (Equation 1; Keber, 1985) and 0.30 (Equation 2; Clout and Barlow, 1982).

$r_m$  can also be calculated by fitting a growth model to the increase in size over time of a recently

established population or one where density has been artificially reduced (Caughley and Birch, 1971). Bamford (1972, 1973) calculated a third estimate of  $r_m$  (0.338) by applying this curve-fitting technique to data derived from the geographic spread of possums in the Taramakau Valley during 1970 and 1971; this estimate was subsequently adopted by Spurr (1981) for use in his population model.

Two studies (Clout and Efford, 1984; Green and Coleman, 1984) have monitored the recovery of possum populations after numbers had been artificially reduced, but these involved small blocks of forest (24 ha and 100 ha, respectively) subject to immigration of possums from surrounding areas. In this study we assess the accuracy with which published estimates of  $r_m$  predicted the recovery of possum numbers after a control operation covering an area of rata/kamahi forest in Westland that was large enough to minimise the contribution of immigration to the subsequent increase in numbers. We then used a simple population growth model to derive an empirical estimate of  $r_m$  for this population.

## Methods

*Recovery of possum numbers after control*

In June 1974, carrot baits loaded with compound 1080 (sodium monofluoroacetate) were aerially sown to kill possums on a 19 km length of forested frontal faces on the north bank of the Taramakau River, Westland. Details of the area and the poison operation are given in Pekelharing (1979). In this paper, we assess changes in possum numbers in a block of rata/kamahi forest (Block A in Pekelharing, 1979) 8 km in length within the poison area.

A trial poison operation in 1970 had killed some possums in the western half of this rata/kamahi block (Bamford, 1972), but at the time of the 1974 poison operation a faecal pellet survey revealed no significant east-west difference in relative numbers of possums (Pekelharing and Batcheler, in press). The kill achieved by the 1974 operation, and the subsequent recovery of possum numbers, were assessed by further pellet surveys in 1975, 1977, 1981 and 1985 (Pekelharing and Batcheler, in press). Each survey provided an index of possum numbers on the block, and we scaled these so that the survey immediately before the 1974 operation had an index value of 10. Despite the preliminary operation in 1970, the rate of recovery of possum numbers did not differ significantly for the eastern and western halves of the block (Pekelharing and Batcheler, in press). Consequently, we pooled the data for both halves before calculating a mean and 95% confidence interval for each pellet survey.

#### Modelling the recovery of possum numbers

An asymmetric growth equation is a better model of resource-limited population growth in mammals than is the standard logistic equation (Fowler, 1981; Barlow and Clout, 1983). We used a  $\alpha$ -logistic equation recommended by Barlow and Clout (1983) to model the recovery of the Taramakau possum population:

$$\frac{dN}{dt} = r_m N (1 - N/K)^\theta \quad (\text{Eqn. 3})$$

where:  $N$  = population density at time  $t$   
 $K$  = equilibrium density  
 $\theta = 2$ .

We calculated the recovery in possum numbers predicted by this model for the three published estimates of  $r_m$ . We then obtained an empirical estimate of  $r_m$  from the Taramakau data by determining the value that minimized the error sums of squares between predicted and observed numbers of possums. As variance was dependent on the mean, the survey data were log-transformed before this analysis.

## Results and Discussion

Comparison of pre- and post-poison pellet surveys indicated that the 1974 operation killed 85(±8)% of the possum population on the rata/kamahi block. The subsequent recovery of possum numbers can be estimated from the series of pellet surveys between 1975 and 1985 (Fig. 1). If the population was near equilibrium density before poisoning (i.e.,  $K \approx 10$ ), the line of the best fit for these data would correspond to an  $r_m$  of 0.22 in Equation 3.

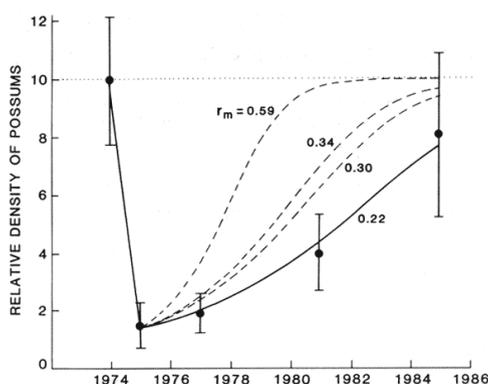


Figure 1: Changes in relative numbers of possums in rata/kamahi forest after aerial 1080 poisoning in the Taramakau catchment in 1974. Predicted curves were fitted using  $r_m$  values of 0.59 (Keber, 1985), 0.34 (Bamford, 1972), 0.30 (Clout and Barlow, 1982), and 0.22 (empirical). The possum population was assumed to be at equilibrium density prior to control. Pellet-count survey data is presented  $\pm 95\%$  C.L.

The population may have been above its equilibrium density in 1974 (Pekelharing and Batcheler, in press), but our estimate of  $r_m$  was relatively insensitive to the value of  $K$  in the model. Reducing  $K$  to 8 or 6 resulted in a small increase in  $r_m$  (to 0.23 or 0.25, respectively). We rejected the possibility of  $K$  being much below 6 as this would predict possum densities below the 95% confidence interval for the 1985 pellet survey estimate. Thus, the range 0.22-0.25 provides an empirical estimate of  $r_m$  for a non-colonising population of possums in Westland rata/kamahi forest.

Our simple model did not explicitly consider the response of forest vegetation to changing levels of browsing by possums (cf. Caughley, 1977: p. 128). Barlow and Clout (1983) show, however, that Equation 3 is a suitable replacement for a herbivore/vegetation model provided an appropriate value of  $\theta$  has been selected. These authors regarded 2 as a conservative estimate of  $\theta$  for possums, but our survey data are too variable to enable both  $a$  and  $r_m$  to be estimated simultaneously. Increasing  $\theta$  to 3 produced a marginally better fit of the model to the survey data ( $R^2 = 0.52$ , vs  $R^2 = 0.51$  for the empirical curve in Fig. 1), but this required a corresponding reduction in  $r_m$  (e.g., to 0.20 for

$K = 10$ ). The possibility that we have underestimated  $\theta$  does not, therefore, explain why we overestimated the rate at which possum numbers increased when we used any of the three published values of  $r_m$  in Equation 3 (Fig. 1).

An assumption of our model was that large-scale immigration of possums into the rata/kamahi block did not occur after the poison operation (cf. Clout and Efford, 1984; Green and Coleman, 1984). The rata/kamahi block was relatively large, and poisoning extended for several kilometres to the east and west of its boundaries (Pekelharing, 1979). Moreover, substantial immigration of possums would have caused a more rapid increase in numbers than our model predicted. Thus, the absence of immigration as a factor in our model does not explain the discrepancy between the survey results and published estimates of  $r_m$ .

We conclude, therefore, that the published values of  $r_m$  are too high for the Taramakau population. There are several possible explanations for this population having an apparently low rate of increase. Both Keber (1985) and Clout and Barlow (1982) calculated  $r_m$  using estimates of survival that were valid only for adults. Juvenile mammals typically have lower rates of survival than adults (Caughley, 1966), and juvenile survival has a marked effect on the rate of increase of a population. If estimates of maximum adult fecundity and survival given by Clout and Barlow (1982) apply to the Taramakau population, our empirical estimate of  $r_m$  would suggest that maximum juvenile survival was about 20% lower than that of adults.

The assumption that breeding rates are constant among age classes (Clout and Barlow, 1982; Keber, 1985) is probably invalid, as field studies suggest that yearlings are consistently less likely to breed than older females (references in Green, 1984). Furthermore, Keber (1985) assumed that all adult females breed twice a year in populations at low density (i.e., a maximum fecundity of 1.0 female offspring/female/year). Frequency of double breeding could be related to population density (Kean, 1971), but also depends on habitat quality (Kean, 1971; Triggs, 1982). Double breeding is found in populations colonising native forest (e.g. Fraser, 1979), but as such populations become well-established the relative abundance of palatable plant species in the forest is reduced (Kean, 1971; Green, 1984). This long-term change in the plane of nutrition may greatly reduce the potential for increased fecundity at low population densities. For example, a population in the

Copland Valley that reached peak density and has since declined no longer exhibits the double breeding common when it was at similar pre-peak densities (K. W. Fraser, pers. comm.). Extensive trapping of an established population in the Orongorongo Valley did not stimulate double breeding (Kean, 1971). Consequently, we suggest that the maximum fecundity of most noncolonising populations in native forests will be  $< 0.5$  female offspring/female/year. The very high fecundity assumed by Keber (1985) caused his estimate of  $r_m$  (0.59) to be much higher than the other estimates discussed.

Bamford's (1972) estimate of  $r_m$  was derived by curve-fitting with a standard logistic equation for population growth. The difference between his estimate and ours is largely due to our use of a 8-logistic model. Applying Equation 3 to Bamford's (1972) data gives an estimate of  $r_m$  similar to the value we report here.

Large sums of money are spent by the Department of Conservation and Ministry of Agriculture and Fisheries on possum control (Coleman, 1981), and commercial harvesting provides substantial economic returns in many areas (Clout and Barlow, 1982). Although predictive models may be useful for cost-benefit analyses of control and harvesting operations, our study shows the importance of carefully assessing the validity of the values selected for the parameters in such models. For example, if the selected value of  $r_m$  is too high (as in the published estimates discussed), the models will underestimate the effectiveness of control and overestimate the sustainable harvest from a population. Therefore, we believe that more effort should be made to monitor possum populations after large-scale control operations. These operations provide opportunities to estimate habitat-specific values of  $r_m$  (and perhaps  $\theta$ ), and to assess the contribution of changes in double breeding, age at sexual maturity, and age-specific survival to density-dependent population growth in this species.

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