

## Linking pasture, livestock productivity and vertebrate pest management

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**Abstract:** The study of pastures, pests (rabbits and caterpillars) and sheep productivity by Barlow (1987; *New Zeal J Ecol* 10: 43–55) is reviewed, updated and extended. Pasture growth was modelled as a dynamic process, though sheep and rabbit abundance were not dynamic. The model predicted that there was a parabolic relationship between sheep productivity and sheep stocking rate with the effects of rabbits being to shift the relationship lower and to the left. The relationship is analogous to a model of sustained harvest of a wild population, and the shape parameter of each has similar numerical values (2 to 3). The Barlow model also predicted a negative relationship between sheep productivity and rabbit abundance, with the relationship being curved with fixed stocking rates. Analysis of data from an independent experimental study shows more support for a negative quadratic (concave down,  $R^2 = 0.509$ ) than a negative linear ( $R^2 = 0.416$ ,  $\Delta\text{AICc} = 2.770$ ) relationship. The Barlow (1987) study assumed a positive linear relationship between the area of denuded pasture and pest abundance. A model selection analysis of a priori models of disturbance by feral pigs provides support for a positive curved relationship ( $R^2 = 0.854$ ) and a positive linear relationship ( $R^2 = 0.357$ ;  $\Delta\text{AICc} = 0.03$ ) between the area of denuded pasture (as disturbed ground) and pig abundance. The general results and their implications are discussed.

**Keywords:** European rabbit; feral pig; functional response; sheep production; vertebrate pest control.

## Introduction

Some wildlife species are pests of agriculture when they impact on the grazing, cropping or other industries. European rabbits (*Oryctolagus cuniculus*) have impacts on pastures (Norbury and Norbury, 1996; Croft *et al.*, 2002) and sheep production (Williams *et al.*, 1995; Fleming *et al.*, 2002). Aspects of the effects of rabbits on sheep production were examined by Barlow (1987), in particular the effects of rabbit grazing on pasture biomass. The effects on sheep productivity of pests denuding pasture were also examined.

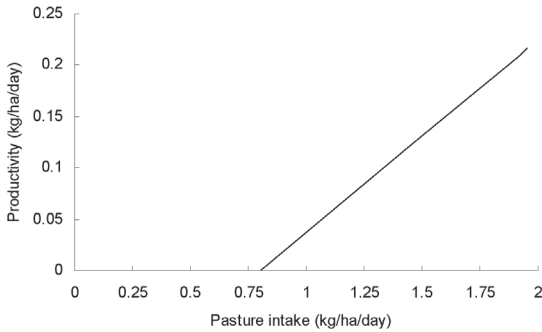
The aim of this paper is to compare the results of the study by Barlow (1987) to results from related rabbit and other studies published subsequently. The results for pests that denude pasture are extended by modelling the process and applying the model to pasture denuded (ground disturbed) by feral pigs. The utilisation in the subsequent literature of the results of Barlow's (1987) study is also examined.

### Original study of Barlow (1987)

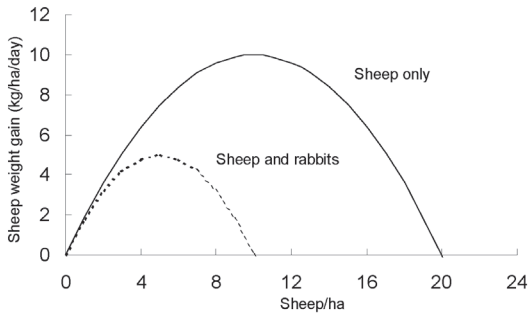
Barlow's study examined, by modelling, the effects of pasture pests on sheep productivity. Two pests, rabbits and porina (*Wiseana* sp.) caterpillars were examined. I will focus on rabbits. A series of equations described

the pasture, sheep and rabbits and examined the equilibrium relationships between them. Rabbits produced impacts because they were a grazing competitor with sheep and reduced pasture availability (kg/ha), whereas the porina caterpillars produced impacts as they reduced (denuded) pasture area. The model's predictions were examined by simulation by Barlow (1987) and key relationships derived by simulation were graphed, so there are often no explicit simple equations (analytical solutions) for the relationships.

Pasture growth was modelled by negative density dependence [a form of generalised logistic growth, though not the theta logistic model used elsewhere, such as by Barlow and Clout (1983) and Barlow (1991)]. The assumption of logistic growth was similar to that assumed in early plant-herbivore models of Caughley (1976a, 1976b, 1977). The sheep and rabbits had no population dynamics. The per capita intakes of pasture by sheep and rabbits were modelled as Type III functional responses (sigmoidal shape). Productivity of sheep, expressed as kilograms of liveweight gain per hectare per day, was assumed to be linearly related to pasture intake (Fig. 1). Seasonal pasture growth reduced productivity compared with constant growth. The stability properties of the grazing system were



**Figure 1.** Positive relationship between sheep productivity (weight gain kg/ha/day) and pasture intake (kg/ha/day) assumed by Barlow (1987).



**Figure 2.** Productivity–sheep stocking rate relationship modelled by Barlow (1987). The solid line shows the relationship in the absence of rabbits and the dotted line the relationship with rabbits. The equation used was Barlow’s equation 5, with  $u = 2$ ,  $v = -0.1$ ,  $\theta = 2$  for sheep only and  $u = 2$ ,  $v = -0.2$ ,  $\theta = 2$  for sheep and rabbits. Note this is an illustrative example of Barlow’s relationship and not a reproduction of any particular figure.

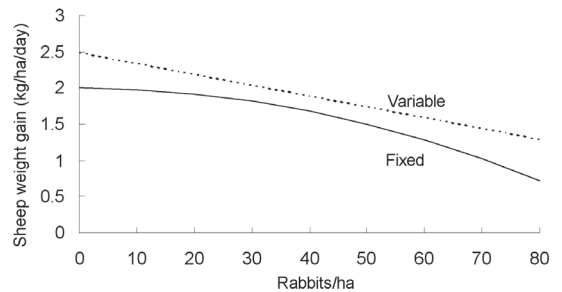
described by Barlow (1987) but will not be examined in detail here.

The main results were that productivity was related to sheep stocking rate in a parabolic-like curved manner (positive then negative). Barlow (1987) suggested his model produced a theoretical basis for the same empirically derived curve described by Jones and Sandland (1974). The effects of rabbits were to shift the productivity–stocking rate relationship down and to the left (Fig. 2). That is, the greatest effects of rabbits occurred at highest stocking rates and effects were lower at lowest stocking rates. At very low stocking rates there may be very little effect of pests (Fig. 2). The effects occurred because of interspecific resource competition as the rabbits ate pasture that would otherwise be eaten by the sheep. In the presence of

rabbits, productivity would be increased by reducing stocking rates. This is not necessarily expected, compared with the simple suggestion of reducing rabbit abundance to increase productivity. However, the suggestion assumes rabbit abundance is constant and does not increase when sheep stocking rate decreases.

The relationship predicted by Barlow (1987) between equilibrium sheep productivity (weight gain (kg)/ha/day) and rabbit density was negative and linear with variable stocking rates (Fig. 3). The relationship was negative and curved (concave down) with fixed stocking rates (Fig. 3). The economic effects of rabbits were estimated at \$1.10 to \$2.50 per rabbit in 1986 NZ dollars. The damage–pest relationship was described as positive, but linear with variable stocking rates or curved (concave up) with fixed stocking rates.

Barlow (1987) also commented briefly on the application of the results to the wider topic of plant–herbivore dynamics. The grazing system of two herbivore species was considered better described by the inferential models rather than the laissez faire models of Caughley (1976b; though cited as 1975). The latter model was considered to contravene the competitive exclusion principle by allowing two competing herbivores to coexist at equilibrium.



**Figure 3.** Predicted linear negative relationship (dotted line) between equilibrium sheep productivity (weight gain kg/ha/day) and rabbit density with variable stocking rates. The equation of the line is that of Barlow (1987, p. 47) solved for  $V = dV/dt = 0$ , and Barlow’s equation 4 (productivity and sheep density), and using parameter values given by Barlow. The predicted relationship (solid line) for fixed stocking rates is also shown. Note that Barlow gave no analytical solution for the curved relationship with fixed stocking rate, so the solid line is an illustrative example of Barlow’s relationship and not a reproduction of any particular equation.

**Table 1.** A comparison of the predictions and observed results for relationships between pest damage and pest (rabbit) density, and between yield of an agricultural activity and pest (rabbit) density. The statistical significances (\* $P < 0.05$ , \*\* $P < 0.01$ ) are from published sources.

Stocking rate		Damage-density relationship	Yield-density relationship
Fixed	Predicted	Positive, curved (concave up) <sup>I</sup>	Negative, curved (concave down) <sup>I</sup>
	Observed	Bare ground* (positive, curved concave up) <sup>II</sup> Loss of pasture height** (positive, linear) <sup>II</sup> % thistles* (humped) <sup>II</sup>	Sheep liveweight** (negative, curved concave down) <sup>III</sup> Fat depth** (negative) <sup>III</sup> Greasy fleece weight** (negative, curved concave down) <sup>III</sup> Pasture biomass** (negative, linear) <sup>IV</sup>
Variable	Predicted	Positive, linear <sup>I</sup>	Negative, linear <sup>I</sup>
	Observed	Not reported	Not reported

I. Barlow (1987)

II. Croft *et al.* (2002)

III. Fleming *et al.* (2002)

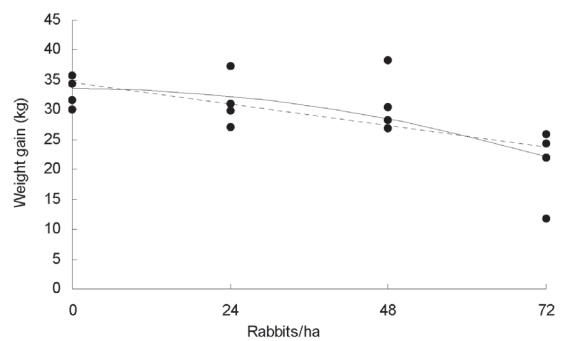
IV. Dendy *et al.* (2003)

### Related rabbit studies

European rabbits were introduced to New Zealand in the 1700s and 1800s (Gibb and Williams, 1995) and into Australia in 1859 (Williams *et al.*, 1995). Much has been written of the agricultural and environmental impacts of rabbits since then. However, there is a paucity of data concerning the impacts of rabbits. A comparison of the predicted (Barlow, 1987) and observed relationships between damage and pest density, and yield and pest density, of several studies are summarised in Table 1 where there is broad but not complete support. A more thorough comparison of the predicted and observed patterns is possible though would require access to the original data.

In a simple comparison of pasture biomass with and without rabbits in central Otago, Norbury and Norbury (1996) reported that biomass was significantly higher when rabbits were absent, though effects differed between pasture species. This is broadly consistent with the relationship between vegetation biomass and pest (rabbit) abundance of Barlow (1987, Fig. 4).

A study of rabbit grazing on pasture in the United Kingdom reported a significant ( $P = 0.001$ ) negative linear relationship between yield and rabbit density (Dendy *et al.*, 2003). This result is analogous to Barlow's (1987) result of the expected negative



**Figure 4.** Relationship between observed mean sheep liveweight gain (kg) over 3 years and rabbit density (rabbits/ha) in the experimental study of Croft (1990) and Fleming *et al.* (2002). Each data point is the mean for the two sheep in each enclosure and data are the differences between the means for spring 1984 and spring 1987, from Croft (1990 Appendix 10). The fitted quadratic regression ( $R^2 = 0.509$ ,  $P = 0.0019$ ) is shown by the solid line, and the fitted linear regression ( $R^2 = 0.416$ ,  $P = 0.0069$ ,  $\Delta AICc = 2.770$ ) is shown by the dotted line.

relationship between vegetation biomass and pest (rabbit) abundance. The study of Dendy *et al.* had rabbits but no sheep grazing pasture, as the focus was on pasture for silage production. The empirical linear relationship of Dendy *et al.* (2003) may be a small part of the curved negative relationships reported by Barlow (1987, Fig. 3a, 3b).

The functional response of rabbits in New South Wales was described by Short (1985, 1987). The 1985 study was not referred to by Barlow (1987). The rabbit study of Short (1985) reported a Type II functional response, compared with the Type III response used by Barlow (1987). However, several aspects of the study should be noted; first, the study of Short (1985) fitted a Type II response, though did not report any statistical measure of goodness of fit such as  $R^2$ . Second, the study did not examine the fit of any other type of functional response. Different types of functional responses, for example types I, II and III, can be fitted to such data (McCallum, 2000). The functional response of wild sheep (*Ovis aries*) has been modelled as a type II relationship (Owen-Smith, 2002).

Short (1987) compared aspects of the functional responses of rabbits and sheep in an arid environment, and estimated that absolute food intakes (not corrected for metabolic liveweight) of rabbits to sheep were in the ratio of 1:12, which equals 0.083. Barlow (1987) assumed the ratio of maximum intakes of rabbits to sheep was 0.1, very close to the estimate of Short (1987), even though pasture availability in New Zealand is higher than in arid Australia. The ratio was assumed to be one rabbit: nine sheep (= 0.111) by Croft *et al.* (2002). The ratio is important as it was an essential component of the equation used by Barlow (1987) to estimate rabbit damage (dollar losses per hectare). The estimates of maximum intake are relevant when pasture availability is high, for example over about 500 kg/ha. When pasture availability is lower, then the estimated rabbit damage would be different.

An analysis of the relationships between yield (such as crop yield, stock liveweight, wool production) and damage and damage and pest density derived a negative relationship between yield and pest density (Hone, 2004). The expected relationships were similar to the relationship described by Barlow (1987) though the details of derivations of the models are slightly different. Both studies incorporated functional responses between intake and food availability. Sheep productivity (weight gain/ha/day) was assumed by Barlow (1987) to be linearly related to pasture intake rate. The rate of weight gain per herbivore was shown empirically to be related to pasture biomass in a positive curved (concave down) manner (Freudenberger *et al.*, 1999) and was modelled as such by Owen-Smith (2002).

The experimental study in New South Wales of

Croft (1990), Croft *et al.* (2002) and Fleming *et al.* (2002) estimated the effects of rabbit density, ranging from 0 to 72/ha, on pasture and sheep production, over a period of three years. It is noteworthy that Barlow (1987) reported results for rabbit density ranging from 0 to 80/ha. The experimental study demonstrated that bare ground increased ( $P < 0.05$ ) and pasture height decreased ( $P < 0.001$ ) with higher rabbit density (Croft *et al.*, 2002). Sheep liveweight ( $P < 0.01$ ), fat depth ( $P < 0.01$ ) and greasy ( $P < 0.001$ ) and clean ( $P < 0.001$ ) fleece weights were negatively related to rabbit density (Fleming *et al.*, 2002). Many other response variables were reported by Croft *et al.* (2002) and Fleming *et al.* (2002) but are not examined here. Many effects of rabbits were most evident in the third (final) year of the study.

The studies of Croft (1990), Croft *et al.* (2002) and Fleming *et al.* (2002) were designed with sheep at a fixed stocking rate. Given that design, the modelling of Barlow (1987) predicted a negative curved (concave down) relationship between sheep productivity and rabbit density (Table 1). The study of Fleming *et al.* (2002) did not test for such a curved relationship. Analysis in Fleming *et al.* (2002, table 1) for sheep liveweight suggests their data support the prediction of Barlow (1987) of a curved relationship. This was further investigated here by analysing the mean weight gain over the three years of the study using data from Croft (1990 Appendix 10). This measure of productivity is analogous to Barlow's (1987) measure of productivity with the only difference being scaling; Barlow's measure was kg/ha/day and here it is kg/3 years. The latter can be converted to per hectare per day by doubling the observed weight gain (as the experiment had two sheep per paddock) and dividing by 365×3 days. The analysis used the computer software SAS (Freund and Little, 1986) and compared models (linear, quadratic and polynomial regressions) using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham and Anderson, 2002). The quadratic relationship (Fig. 4) had most support (AICc = 100.850;  $F = 14.52$ ; d.f. = 1, 14;  $P = 0.0019$ ;  $R^2 = 0.509$ ). The linear relationship (Fig. 4) had less support (AICc = 103.620;  $\Delta$ AICc = 2.770;  $F = 9.99$ ; d.f. = 1, 14;  $P = 0.0069$ ;  $R^2 = 0.416$ ) and the polynomial relationship, with linear and quadratic terms, less support (AICc = 103.882;  $\Delta$ AICc = 3.032;  $F = 7.25$ ; d.f. = 2, 13;  $P = 0.077$ ;  $R^2 = 0.527$ ). The fitted quadratic regression was,

$$y = 33.541 - 0.002(\text{rabbits/ha})^2 \quad (1)$$

where  $y$  = mean sheep liveweight gain over 3 years (Fig. 4). The effects of rabbits on wool production were also examined by Fleming *et al.* (2002) but were not specifically studied by Barlow (1987). Wool

production (\$/ha) was highest at intermediate rabbit density and lowest at the highest rabbit density (Fleming *et al.*, 2002). Such a response was not included in the modelling of Barlow (1987) but was included as a form of compensation in the yield–pest density relationships modelled by Hone (2004).

**Pests denuding pasture**

The model of Barlow (1987) also examined the effects of a pest, such as porina caterpillars or weeds, that reduced pasture area rather than ate the pasture. In the extreme case, such denuding would produce a bare field. Rabbits can denude pasture around their warrens and feral pigs (*Sus scrofa*) by their ground rooting (Hone, 1980, 2002). A detailed model of the processes generating such denuding was not described by Barlow (1987) but an outline of such a model is described here.

Assume pasture of area A ha is initially undisturbed. Disturbance (denuding) creates bare soil of area D. Hence the area A consists of undisturbed (U) and disturbed (D) such that  $A = U + D$ . Barlow (1987) assumed that the lost pasture area was directly proportional to pest density. That assumption can be derived as follows. If undisturbed pasture is changed to disturbed pasture at a rate proportional to pest density (P), and is revegetated at a rate  $\gamma$  then,

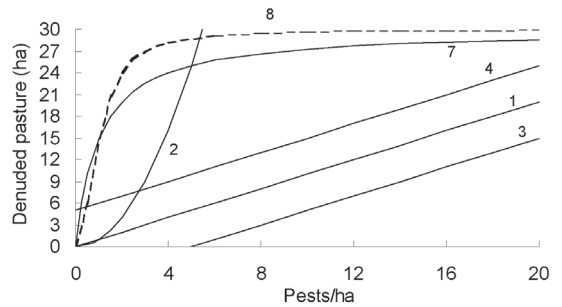
$$dU/dt = -\beta P + \gamma D \tag{2}$$

$$dD/dt = \beta P - \gamma D \tag{3}$$

where the proportionality constant is  $\beta$ . At equilibrium,  $dU/dt = dD/dt = 0$ , and by rearranging either equation, it can be shown that the area of disturbed pasture at equilibrium ( $D^*$ ) is given by,

$$D^* = (\beta/\gamma)P \tag{4}$$

which describes a positive linear relationship between the equilibrium area of disturbed pasture ( $D^*$ ) and pest density (P). The slope of the relationship is the ratio of rates of disturbance ( $\beta$ ) and revegetation ( $\gamma$ ). Hence the area of pasture lost is directly proportional to pest density as assumed by Barlow (1987). The above equilibrium equation infers various features of pests denuding pasture that are important for management. When there are no pests ( $P = 0$ ) then there is no denuded pasture ( $D^* = 0$ ). When there is no behaviour by the pests to denude the pasture then  $\beta = 0$  so  $D^* = 0$ . As the rate of revegetation approaches 0 then the area of denuded pasture increases, and  $D^*$  goes to A; the whole area becomes denuded. Alternatively, as the rate of revegetation becomes very high then the area of denuded pasture goes towards 0, as the ratio ( $\beta/\gamma$ ) goes to 0, and U goes to A.



**Figure 5.** Predicted equilibrium relationships between the area of denuded pasture ( $D^*$ ) and pest density (P). Numbers correspond to models in Table 2. Models 5 and 6 are not shown as the shape of each depends on the value of  $\alpha$ . Parameter values are  $\beta = 0.05$ ,  $\gamma = 0.05$ ,  $A = 30$ ,  $N = 25$ , and  $T = 5$ .

**Table 2.** Assumptions and related predicted equilibrium relationships between the area of pasture denuded by pests ( $D^*$ ) and pest density (P). The model assumption is what determines the rate of change ( $dU/dt$ ) of undisturbed (U) pasture to disturbed (D) pasture. The total area of pasture is  $A (= U + D)$ . In models 3 and 4,  $\delta = (\beta/\gamma)T$ , where T is a threshold pest density. The shape of models 5 and 6 depends on the value of the exponent  $\alpha$ ; the shape is concave down if  $0 < \alpha < 1$ , concave up if  $\alpha > 1$  and if  $\alpha = 1$ , the prediction is linear.

Model	Assumption	Prediction ( $D^*$ )	Interpretation of relationship
1	$-\beta P$	$(\beta/\gamma)P$	Positive, linear
2	$-\beta P^2$	$(\beta/\gamma)P^2$	Positive, curved (concave up)
3	$-\beta(P - T)$	$(\beta/\gamma)P - \delta$	Positive, linear ( $P \geq T$ )
4	$-\beta(P + T)$	$(\beta/\gamma)P + \delta$	Positive, linear
5	$-\beta P^\alpha$	$(\beta/\gamma)P^\alpha$	Positive, curved or linear
6	$-\beta(P \cdot T)^\alpha$	$(\beta/\gamma)P^\alpha + \delta$	Positive, curved or linear
7	$-\beta P U$	$(\beta A)P / (\gamma + \beta P)$	Positive, curved (concave down)
8	$-\beta P^2 U$	$(\beta A)P^2 / (\gamma + \beta P^2)$	Positive, curved (sigmoidal)

Changing the assumption about the determinants of the rate of change of undisturbed pasture to disturbed pasture changes the predicted equilibrium relationships as shown in Table 2 and Figure 5. For example, the study of Croft *et al.* (2002) reported that with higher rabbit density the percentage of bare ground was higher. That observed result could correspond to model 2 in Table 2 and Figure 5. Model 3 has a threshold pest density ( $T$ ) below which there is no denuding of pasture. Model 4 has a background level of bare pasture ( $\delta$ ) even in the absence of pests. Model 6 is a generalisation of the models 1 – 5. Model 7 assumes that the rate of change of undisturbed to denuded pasture is proportional to the product of pest density ( $P$ ) and the area of undisturbed pasture ( $U$ ). Model 8 assumes that the rate of change of undisturbed to denuded pasture is proportional to the product of the square of pest density ( $P^2$ ) and the area of undisturbed

pasture ( $U$ ) (Table 2).

These disturbance models are a set of hypotheses for evaluation as a model selection exercise (Burnham and Anderson, 2002). Data for such an evaluation come from a long-term study of ground disturbance by feral pigs in Namadgi National Park, Australia (Hone, 2002) and extra data collected since that publication. Methods of data collection were described by Hone (2002). Data are the percentage of plots with ground rooting and percentage of plots with dung of feral pigs. The former is positively correlated with the area of ground rooting (Hone, 1988) and the latter with observed density of feral pigs (Hone, 1988, 1995). Data here are from each summer from 1985-86 to 2003-04 inclusive. Any temporal dependence in the ground rooting and dung data was not accounted for in the analysis. During that time period the observed annual instantaneous population growth rate ( $r$ ) of the

**Table 3.** Parameter estimates for models of denuding (also called disturbance) of ground vegetation by feral pigs. Models are listed in Table 2. In some models parameters were fixed at values shown in the table. These fixed values have no standard errors (SE), Student's  $t$  value or probability ( $P$ ) value, and these are shown as NA. Parameters  $\delta$ ,  $(\beta/\gamma)$ , and  $\alpha$  are the intercept, slope and shape parameter (exponent) respectively of models 1 to 6.  $K$  = number of parameters estimated. Note that parameters estimated are formatted differently for models 7 and 8. \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

Model		Parameters				
		$\delta$	$\beta/\gamma$	$\alpha$	AICc	$\Delta$ AICc
1	Estimate	0	9.605	1	126.35	10.11
	SE	NA	1.440	NA	K = 2	
	$t$	NA	6.669***	NA		
	$P$	NA	<0.0001	NA		
2	Estimate	0	3.729	2	139.53	23.29
	SE	NA	1.025	NA	K = 2	
	$t$	NA	3.638**	NA		
	$P$	NA	0.0019	NA		
4	Estimate	6.230	4.840	1	116.27	0.03
	SE	1.530	1.575	NA	K = 3	
	$t$	4.072***	3.073**	NA		
	$P$	0.00079	0.0061	NA		
5	Estimate	0	11.937	0.368	116.24	0
	SE	NA	1.214	0.121	K = 3	
	$t$	NA	9.833***	3.041**		
	$P$	NA	<0.0001	0.0072		
6	Estimate	4.426	7.138	0.665	119.29	3.05
	SE	6.354	7.431	0.758	K = 4	
	$t$	0.696	0.961	0.877		
	$P$	0.496	0.351	0.393		
		$\beta A$	$\gamma$	$\beta$	AICc	$\Delta$ AICc
7	Estimate	17.008	0.361	1.000	117.66	1.42
	SE	3.978	0.239	NA	K = 3	
	$t$	4.276***	1.510	NA		
	$P$	<0.0005	0.146	NA		
8	Estimate	12.428	0.034	1.000	120.19	3.95
	SE	1.796	0.026	NA	K = 3	
	$t$	6.920***	1.308	NA		
	$P$	<0.0005	0.210	NA		

feral pig population was  $-0.050 (\pm 0.038 \text{ SE})$ , which was not significantly different from zero ( $t = -1.31$ , d.f. = 17,  $P = 0.206$ ). The goodness of fit of the data to the models (Table 2) was analysed using the computer software R (R Development Core Team, 2005) and SAS version 8.02 (Freund and Little, 1986). Estimates of all parameters were not possible, for example in models 1–6 the ratio  $\beta/\gamma$  was estimated as the coefficient. Separate estimates of  $\beta$  and  $\gamma$  could not be obtained. Instead estimates of the ratio ( $\beta/\gamma$ ) were obtained. Models were compared by the Akaike's Information Criterion corrected for small sample size (AICc) with the best model, of those compared, having the smallest AICc (Burnham and Anderson, 2002).

Model 5 ( $R^2 = 0.854$ ) had the lowest AICc closely followed by model 4 ( $R^2 = 0.357$ ;  $\Delta\text{AICc} = 0.03$ ) (Table 3). These best models and the data are shown in Figure 6. The other models, except model 7, had larger AICc values to the extent that they would be assessed as being unsupported in comparison (Burnham and Anderson, 2002). Model 3 predicted a threshold on the  $x$ -axis (no denuding until pest density exceeded a threshold value) that corresponds to a negative intercept on the  $y$  axis. The estimated intercept on the  $y$ -axis in model 4 was positive (6.230) and highly significantly so ( $P = 0.00079$ ) (Table 3) and hence model 3 was not supported. The intercept on the  $y$ -axis is interpreted further in Discussion. The model with the lowest AICc was model 5 (Table 3); however, model 6 had the lowest residual sums of squares (334.7) with the next lowest (338.3) being for model 5. Model 6 had an extra parameter, compared with model 5, and so had a higher AICc value.

## Discussion

The various elements of the study by Barlow (1987) are now reviewed in the light of other published studies. In sequence, the modelling and empirical elements then the broader implications are reviewed.

Pasture growth was assumed by Barlow (1987) to be a form of generalised logistic growth. Logistic growth of vegetation has been criticised by Turchin and Batzli (2001) as an unrealistic assumption in many situations. Pasture growth as influenced by pasture biomass was estimated in arid western New South Wales (Robertson, 1987). The relationship was negative and curved (concave down). The fitted relationship lacked the positive relationship between growth and biomass at low pasture biomass of the sort assumed in the model of Barlow (1987). That lack of the positive component of the relationship was noted by Robertson (1987) who suggested it was an artefact of how that study was done (the three-month time period over which growth was estimated). There was a positive

effect of prior rainfall on pasture growth and this effect was stronger than the negative effects of pasture density (Robertson, 1987). A positive effect of rainfall on pasture biomass in semi-arid Australia was also reported by Freudenberger *et al.* (1999).

The productivity–pest density relationship (Fig. 3) examined by Barlow (1987) has also been examined by others using a related relationship (damage–pest density) for a variety of vertebrate pests. The damage–density relationship has been modelled as linear (e.g. Izac and O'Brien, 1991) and as curved (concave up and concave down) (e.g. Braysher, 1993; Hone, 1994, 2004). The yield–density relationship has been estimated empirically mostly as a linear model though with some curved relationships (Hone, 2004).

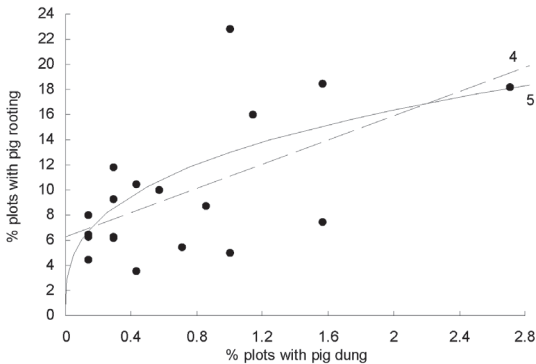
The model of Barlow (1987) had equations for pasture growth but the herbivores (sheep and rabbits) had no dynamics. Models have since been published that have incorporated rabbit dynamics (e.g. Pech and Hood, 1998) and predator dynamics (e.g. Davis *et al.*, 2002). Those subsequent studies have not, however, included sheep as competitive herbivores, so the studies did not examine the effects of rabbits on sheep production. The later studies described pasture growth as a function of pasture biomass and rainfall, after Robertson (1987) and Caughley (1987), and used a type II functional response for rabbits eating pasture, after Short (1985). The effect of simulating the addition of sheep to a kangaroo population was reported by Caughley (1987). Adding sheep had little effect on pasture biomass but reduced kangaroo density.

Barlow's (1987) model developed from an ecological basis the relationship between sheep productivity (relabelled here as  $S$  to avoid confusion with  $P$  as pest density) and sheep stocking rate ( $H$ ) (Fig. 2). Barlow (1987) suggested the model may provide a theoretical basis for the empirical relationship of the same shape reported by Jones and Sandland (1974), which has been criticised (McLeod, 1997) as having no theoretical basis and hence being unable to incorporate variability (stochasticity) in a biologically meaningful manner. The curved relationship between productivity and stocking rate is not universal. In four years of a six-year sheep study in semi-arid Australia, there was a significant linear relationship (two positive, two negative) but no curved relationships (Freudenberger *et al.*, 1999).

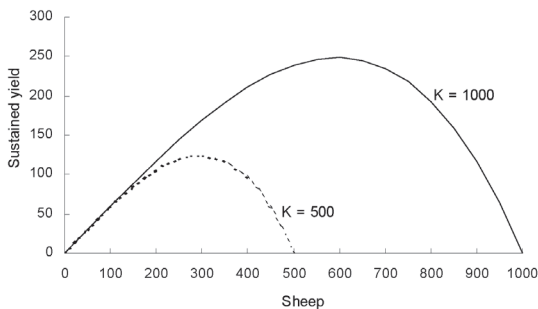
An empirical model of the relationship between productivity ( $S$ ) and stocking rate ( $H$ ) was described by Barlow (1987, equation 5) as well as the theoretical grazing model. The empirical model was,

$$S = uH + vH^w \quad (5)$$

with  $u$ ,  $v$  and  $w$  being model parameters. Barlow (1987) used  $\theta$  not  $w$  but it is relabelled here as  $w$  to



**Figure 6.** Measures of ground disturbance by feral pigs (percentage of plots with pig rooting) and feral pig density (percentage of plots with pig dung). Dots are data for each summer during 1985-86 to 2003-04 inclusive from Namadgi National Park (Australia) and the lines show the fitted regressions for models 4 (dashed line) and 5 (solid line) listed in Table 3.



**Figure 7.** Effect of reducing carrying capacity ( $K$ ) on the annual sustained yield of a sheep population growing according to theta logistic growth. Parameter estimates for  $r_m$  (0.36/year) and  $\theta$  (2.30) are for wild sheep after Lande *et al.* (2003).

avoid confusion with the parameter  $\theta$  in theta logistic population growth. Estimates of the value of  $w$  from agricultural experiments varied from 2 to 3 (Barlow, 1987). By comparison wildlife harvesting studies often model sustained yield (SY) as a function of density (H) (Caughley, 1977) as,

$$SY = aH + bH^w \quad (6)$$

with  $a$ ,  $b$  and  $w$  being model parameters. When  $w = 2$  the model describes logistic growth and  $a = r_m$  and  $b = -r_m/K$ . The corresponding equation for theta logistic growth is,

$$SY = aH + bH^{\theta+1} \quad (7)$$

with  $a = r_m$  and  $b = -r_m/K^\theta$  and  $w = \theta + 1$ .

Equations 5 and 6 are the same as they describe analogous processes. Sheep productivity, as weight gain/ha/day, is an equilibrium solution in the model of Barlow (1987). If the analogy is correct, then the value of  $w$  in equations 5 and 6 should be similar for the same species. Assuming theta logistic population growth, an estimate of  $\theta$  for wild sheep on the island of Hirta off western Scotland is  $\theta = 2.30$  (Lande *et al.*, 2003, p. 41). Hence,  $w = \theta + 1 = 2.3 + 1 = 3.3$ , which is similar to the values of 2 to 3 reported in the agricultural literature (Barlow, 1987).

The analogy can be extended to link to the grazing model of Barlow (1987). The effect of pests on the productivity–stocking rate curve is to lower it and shift it to the left (Fig. 2). Such a change in the sustained yield–density curve occurs when carrying capacity ( $K$ ) is reduced. Carrying capacity has been defined as the ratio of food growth rate divided by food intake rate (Caughley, 1976a, 1977). The inclusion of grazing pests in a grazing system with sheep would increase the food intake rate and hence lower the carrying capacity and the sustained yield (Fig. 7); hence the similarity in equations 5 and 6 and Figures 2 and 7.

The modelling of pests that denude pasture provides most support for models that show a positive relationship between the area of denuded pasture and pest density. There is no clear distinction between positive linear and positive curved (concave down) relationships (models 4 and 5) in the feral pig data (Table 3). Barlow (1987) assumed a positive linear relationship, though he suggested that at high pest density the denuded area per pest may be reduced. This latter possibility would generate a positive curved (concave down) relationship, as described here by models 5 and 6 (with  $\alpha < 1$ ) and model 7. The results of the model selection procedure shown in Figure 6 suggest a need for more data at very high levels of pig density and at very low levels of pig density, to clearly differentiate between alternative models. The estimated positive threshold in model 4 needs interpreting. The threshold could imply that ground rooting (denuding) would be present even when feral pigs are absent. That could occur if the ground rooting was partly caused by other animals, such as wombats (*Vombatus ursinus*) or lyrebirds (*Menura novaehollandiae*). Both species scratch the ground and occur in the study area; however, criteria were developed at the start of the study to differentiate between such disturbance and that caused by feral pigs, so this is considered unlikely. It is more likely that the estimated threshold reflects the lag in disturbed ground revegetating. Disturbance can occur quickly but it may take one or more years to revegetate. That is,  $\beta \gg \gamma$ . If feral pigs were removed the estimated threshold should tend to zero (the origin) or to the background level of disturbed ground if that level is



greater than zero.

The process of pests denuding pasture is analogous to pests trampling vegetation and people trampling vegetation. The latter has been described often in the literature on recreation ecology (Liddle, 1997). The relationship between human use and the extent of trampled vegetation or bare soil is usually positive and curved (concave down) (Liddle, 1997) consistent with the predictions of several models derived here and listed in Table 2.

The study of Barlow (1987) described a variety of predicted relationships. The relationships can be viewed as a priori models for independent evaluation. The evaluation of the models would be aided by results from experimental studies designed with the models in mind. Many of the relationships predicted by Barlow (1987) are non-linear and their evaluation would require a broad range of treatment levels in experiments. For example, evaluation of the curved relationship shown in Figs. 2, 3, 4 and 7 would need at least six to eight levels of the treatment ( $x$  variable). With replication, that suggests a minimum of 12–16 experimental units. The experiment of Croft (1990), Croft *et al.* (2002) and Fleming *et al.* (2002) had four levels of rabbits (the  $x$  variable) each replicated four times for a total of 16 units. If the experiment had eight levels of rabbits each replicated, that would also have used 16 experimental units. Then there would have been greater statistical power to more clearly discriminate between the predictions (linear vs curved relationships).

The broader implications of the Barlow (1987) study are now discussed. In contrast to many other studies, Barlow estimated the economic impact of rabbits on one aspect of sheep production, based on ecological mechanisms and economic concepts. The study developed theoretical predictions of relationships between productivity and rabbits, and the effects of rabbits on the relationship between productivity and sheep stocking rate based on biological mechanisms. The modelling study of rabbit damage to sheep production by Barlow (1987) has been surprisingly overlooked in the subsequent literature on rabbits and rabbit impacts. A search on the Web of Science in July 2004 found the paper had been cited five times. The paper and its results were not cited in related studies of rabbits and sheep production, and hence not used by Croft (1990), Braysher (1993), Brown (1993), Hone (1994), Williams *et al.* (1995), Norbury and Norbury (1996), Olsen (1998), Choquenot *et al.* (1998), Croft *et al.* (2002), Fleming *et al.* (2002), Dendy *et al.* (2003) and Hone (2004). The paper was not cited in studies of sympatric herbivores, such as Choquenot (1994), Freudenberger (1995), Edwards *et al.* (1996), McLeod (1997), Freudenberger *et al.* (1999), McCullough and McCullough (2000) and Choquenot and Ruscoe (2003). There may be several reasons for the lack of citation

and use; “rabbit” was not listed as a keyword in Barlow (1987), maybe the research interest in rabbits focused too much on killing rabbits and not enough on the economic impacts of rabbits, and the Barlow model did not include rabbit dynamics.

The economic analysis used by Barlow (1987) was simple. The dollars lost per hectare of pasture were assumed to be directly proportional to the ratio of the maximum rate of pasture intake by pests divided by that for sheep. If correct, this is a general result, and the value of maximum intake rates for different pests and different livestock could be substituted into the economic equation of Barlow (1987). To do so, requires estimates of the maximum intake rates, and those data could be derived from studies of functional responses. The analysis did not include an estimate of the costs of rabbit control, or of different types of rabbit control, and the effects of those on profitability. More detailed economic analyses of pests and production were described by Hone (1994) and Davis *et al.* (2004). The Barlow study examined one aspect of sheep production, namely liveweight gain, and did not investigate the effects of rabbits on wool production. However, one study should not be expected to do everything. The effects of rabbits on wool production and wool fibre diameter were investigated by Fleming *et al.* (2002).

The study of pasture, pests and productivity by Barlow (1987) was an important study. It demonstrated how the mechanisms underlying the effects of pests such as rabbits could be investigated and it developed theoretical predictions that have been evaluated here by comparison with independent empirical studies. The study has wide practical application for management of other vertebrate pests.

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## References

- Barlow, N.D. 1987. Pastures, pests and productivity: simple grazing models with two herbivores. *New Zealand Journal of Ecology* 10: 43-55.
- Barlow, N.D. 1991. A spatially aggregated disease/host model for bovine Tb in New Zealand possum populations. *Journal of Applied Ecology* 28: 777-793.
- Barlow, N.D.; Clout, M.N. 1983. A comparison of 3-

- parameter, single-species population models, in relation to the management of brushtail possums in New Zealand. *Oecologia* 60: 250-258.
- Braysher, M. 1993. *Managing vertebrate pests. Principles and strategies*. Australian Government Publishing Service, Canberra, Australia.
- Brown, P.R. 1993 (unpublished). *Pasture response following rabbit control on grazing land*. M. Appl. Sc. thesis. University of Canberra, Canberra, Australia.
- Burnham, K.P.; Anderson, D.R. 2002. *Model selection and multimodel inference. A practical information-theoretic approach*. Second edition. Springer Verlag, Berlin, Germany.
- Caughley, G. 1976a. Wildlife management and the dynamics of ungulate populations. In: Coaker, T. H. (Editor), *Applied biology, volume. 1*. Pp. 183-246. Academic Press, London, U.K.
- Caughley, G. 1976b. Plant herbivore systems. In: May, R. M. (Editor), *Theoretical ecology. Principles and applications*. First edition. pp. 94-113. Blackwell, Oxford, U.K.
- Caughley, G. 1977. *Analysis of vertebrate populations*. Wiley, New York, U.S.A.
- Caughley, G. 1987. Ecological relationships. In: Caughley, G.; Shepherd, N.; Short, J. (Editors), *Kangaroos. Their ecology and management in the sheep rangelands of Australia*, pp. 159-187. Cambridge University Press, Cambridge, U.K.
- Choquenot, D (unpublished). 1994. *The dynamics of feral pig populations in the semi-arid rangelands of eastern Australia*. PhD thesis, University of Sydney, Sydney, Australia.
- Choquenot, D.; Ruscoe, W.A. 2003. Landscape complementation and food limitation of large herbivores: habitat-related constraints on the foraging efficiency of wild pigs. *Journal of Animal Ecology* 72: 14-26.
- Choquenot, D.; Druhan, J.; Lukins, B.; Packwood, R.; Saunders, G. 1998. Managing the impact of rabbits on wool production systems in the central tablelands of New South Wales: an experimental study and bioeconomic analysis. *Proceedings of the 11<sup>th</sup> Australian Vertebrate Pest Conference*. pp. 367-374. Bunbury, Western Australia.
- Croft, J.D. 1990 (unpublished). *The impact of rabbits on sheep production*. M.Sc. thesis. University of New South Wales, Sydney, Australia.
- Croft, J.D.; Fleming, P.J.S.; van de Ven, R. 2002. The impact of rabbits on a grazing system in eastern New South Wales. 1. Ground cover and pastures. *Australian Journal of Experimental Agriculture* 42: 909-916.
- Davis, S.A.; Pech, R.P.; Catchpole, E.A. 2002. Populations in variable environments: the effects of variability in a species' primary resource. *Philosophical Transactions of the Royal Society London B* 357: 1249-1257.
- Davis, S.A.; Leirs, H.; Pech, R.; Zhang, Z.; Stenseth, N.C. 2004. On the economic benefit of predicting rodent outbreaks in agricultural systems. *Crop Protection* 23: 305-314.
- Dendy, J.; McKillop, G.; Fox, S.; Western, G.; Langton, S. 2003. The development of a model to assess the effects of rabbit grazing on grass. *Annals of Applied Biology* 142: 317-322.
- Edwards, G.P.; Croft, D.B.; Dawson, T.J. 1996. Competition between red kangaroos (*Macropus rufus*) and sheep (*Ovis aries*) in the arid rangelands of Australia. *Australian Journal of Ecology* 21: 165-172.
- Fleming, P.J.S.; Croft, J.D.; Nicol, H.I. 2002. The impact of rabbits on a grazing system in eastern New South Wales. 2. Sheep production. *Australian Journal of Experimental Agriculture* 42: 917-923.
- Freudenberger, D. 1995. Separating the sheep from the roos: do we know the difference? In: Grigg, G.; Hale, P.; Lunney, D. (Editors), *Conservation through sustainable use of wildlife*, pp. 208-214. Centre for Conservation Biology, University of Queensland, Australia.
- Freudenberger, D.; Wilson, A.; Palmer, R. 1999. The effects of perennial grasses, stocking rate and rainfall on sheep production in a semi-arid woodland of eastern Australia. *Rangeland Journal* 21: 199-219.
- Freund, R.J.; Little, R.C. 1986. *SAS system for regression*. SAS Institute Inc. Cary, N.C., U.S.A.
- Gibb, J.A.; Williams, J.M. 1995. European rabbit. In: King, C.M. (Editor), *The handbook of New Zealand mammals*, pp. 138-160. Oxford University Press, Auckland, N.Z.
- Hone, J. 1980. Effect of feral pig rooting on introduced and native pasture in north-eastern New South Wales. *Journal of the Australian Institute of Agricultural Science* 46: 130-132.
- Hone, J. 1988. Evaluation of methods for ground survey of feral pigs and their sign. *Acta Theriologica* 33: 451-465.
- Hone, J. 1994. *Analysis of vertebrate pest control*. Cambridge University Press, Cambridge, U.K.
- Hone, J. 1995. Spatial and temporal aspects of vertebrate pest damage with emphasis on feral pigs. *Journal of Applied Ecology* 32: 311-319.
- Hone, J. 2002. Feral pigs in Namadgi National Park, Australia: dynamics, impacts and management. *Biological Conservation* 105: 231-242.
- Hone, J. 2004. Yield, compensation and fertility control: a model for vertebrate pests. *Wildlife Research* 31: 357-368.
- Izac, A.-M.; O'Brien, P. 1991. Conflict, uncertainty and risk in feral pig management: the Australian

- approach. *Journal of Environmental Management* 32: 1-18.
- Jones, R.J.; Sandland, R.L. 1974. The relation between animal gain and stocking rate. *Journal of Agricultural Science* 83: 335-342.
- Lande, R.; Engen, S.; Saether, B-E. 2003. *Stochastic population dynamics in ecology and conservation*. Oxford University Press, Oxford, U.K.
- Liddle, M. 1997. *Recreation ecology. The ecological impact of outdoor recreation and ecotourism*. Chapman and Hall, London, U.K.
- McCallum, H. 2000. *Population parameters. Estimation for ecological models*. Blackwell, Oxford, U.K.
- McCullough, D.R.; McCullough, Y. 2000. *Kangaroos in outback Australia. Comparative ecology and behavior of three coexisting species*. Columbia University Press, New York, U.S.A.
- McLeod, S.R. 1997. Is the concept of carrying capacity useful in variable environments? *Oikos* 79: 529-542.
- Norbury, D.C.; Norbury, G.L. 1996. Short-term effects of rabbit grazing on a degraded short-tussock grassland in central Otago. *New Zealand Journal of Ecology* 20: 285-288.
- Olsen, P. 1998. *Australia's pest animals. New solutions to old problems*. Bureau of Resource Sciences and Kangaroo Press, Canberra, Australia.
- Owen-Smith, R.N. 2002. *Adaptive herbivore ecology*. Cambridge University Press, Cambridge, U.K.
- Pech, R.P.; Hood, G.M. 1998. Foxes, rabbits, alternative prey and rabbit calicivirus disease: consequences of a new biological control agent for an outbreaking species in Australia. *Journal of Applied Ecology* 35: 434-453.
- R Development Core Team 2005. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL: <http://www.R-project.org>.
- Robertson, G. 1987. Plant dynamics. In: Caughley, G.; Shepherd, N.; Short, J. (Editors), *Kangaroos. Their ecology and management in the sheep rangelands of Australia*, pp. 50-68. Cambridge University Press, Cambridge, U.K.
- Short, J. 1985. The functional response of kangaroos, sheep and rabbits in an arid grazing system. *Journal of Applied Ecology* 22: 435-447.
- Short, J. 1987. Factors affecting food intake of rangelands herbivores. In: Caughley, G.; Shepherd, N.; Short, J. (Editors), *Kangaroos. Their ecology and management in the sheep rangelands of Australia*, pp. 84-99. Cambridge University Press, Cambridge, U.K.
- Turchin, P.; Batzli, G.O. 2001. Availability of food and the population dynamics of arvicoline rodents. *Ecology* 82: 1521-1534.
- Williams, K.; Parer, I.; Coman, B.; Burley, J.; Braysher, M. 1995. *Managing vertebrate pests: Rabbits*. Australian Government Publishing Service, Canberra, Australia.