

Demographic, mechanistic and density-dependent determinants of population growth rate: a case study in an avian predator

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Identifying the determinants of population growth rate is a central topic in population ecology. Three approaches (demographic, mechanistic and density-dependent) used historically to describe the determinants of population growth rate are here compared and combined for an avian predator, the barn owl (*Tyto alba*). The owl population remained approximately stable ($r \approx 0$) throughout the period from 1979 to 1991. There was no evidence of density dependence as assessed by goodness of fit to logistic population growth. The finite (λ) and instantaneous (r) population growth rates were significantly positively related to food (field vole) availability. The demographic rates, annual adult mortality, juvenile mortality and annual fecundity were reported to be correlated with vole abundance. The best fit ($R^2 = 0.82$) numerical response of the owl population described a positive effect of food (field voles) and a negative additive effect of owl abundance on r . The numerical response of the barn owl population to food availability was estimated from both census and demographic data, with very similar results. Our analysis shows how the demographic and mechanistic determinants of population growth rate are linked; food availability determines demographic rates, and demographic rates determine population growth rate. The effects of food availability on population growth rate are modified by predator abundance.

Keywords: barn owl; demography; population growth rate; predation; numerical response

1. INTRODUCTION

The empirical estimation of the determinants of how quickly or slowly population density increases or decreases, has used a variety of approaches. Krebs (1995, 2002) suggested that, historically, two approaches (paradigms) have been used: a density paradigm, which focuses on the effects of density on population growth rate, and a mechanistic paradigm, which focuses on the effects of trophic factors such as food, predators and parasites on population growth rate. These paradigms, and a related approach, the demographic paradigm (Sibly & Hone 2002) that focus on the effects of demographic rates (fecundity and survival) on population growth rate, have been widely used, though rarely compared and contrasted.

This paper demonstrates the application of the various approaches to identify the determinants of population growth rate in a closed population. A range of alternative hypotheses, as expressed in mathematical models, are described and evaluated empirically. Data from Taylor's exemplary (1994) study of the barn owl (*Tyto alba*) are used to illustrate the approaches.

2. MODELS

The patterns described in five ecological models, and the field data, are compared. The first four models are specific examples of the general discrete-time population model of Dennis & Otten (2000; eqn (2.1)). The general model is

$$N_{t+1} = N_t e^{a + bN_t + cv}, \quad (2.1)$$

where abundance at time $t + 1$ (N_{t+1}) is related to abundance at time t (N_t) and food availability (v) at time $t + 1$. Coefficients a , b , c are parameters to be estimated. The model of Dennis & Otten (2000) has been modified here to be a deterministic model, and by substituting food availability (v) for their weather term (W).

The first *a priori* model is exponential growth, which occurs in density-independent growth. Abundance at time $t + 1$ (N_{t+1}) is related to abundance at time t (N_t) by

$$N_{t+1} = N_t \lambda^t = N_t e^{rt}, \quad (2.2)$$

where the finite population growth rate is λ ($= N_{t+1}/N_t$) and the instantaneous population growth rate is r ($= \ln \lambda$). Exponential growth occurs in equation (2.1) when $b = c = 0$, and $a = r$ and there is a time-step of 1 yr. This and other models assume the population is closed, with no emigration or immigration. The barn owl population studied by Taylor (1994) was sedentary with very little movement into and out of the population.

The second *a priori* model is logistic growth, as a form of density-dependent population growth. Logistic growth

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is described by equation (2.1) when $c=0$. Evidence of logistic growth is an example of the density paradigm of Krebs (1995, 2002).

The third *a priori* model is a numerical response. Two types of numerical response were estimated: (i) a Solomon-type, after Solomon (1949), relating predator (owl) abundance to prey (vole) abundance (v); and (ii) a Caughley-type relating the predator (owl) population growth rate (λ or r) to food availability (vole abundance). The types of numerical responses are reviewed briefly by Sibly & Hone (2002), and Bayliss & Choquenot (2002). The Caughley-type numerical response using r is described by equation (2.1) when $b=0$. Use of the numerical response is an example of the mechanistic paradigm of Krebs (1995, 2002). Alternative hypotheses were, that there was a positive linear relationship between λ and vole abundance, and a positive linear relationship between r and vole abundance. The latter relationship is the linear assumption in the original Lotka–Volterra model (May 1981; table 5.1). The linear regression of λ and voles is the finite difference analogue of the linear Lotka–Volterra model. The Caughley-type numerical responses were examined with, and without, a time-lag of 1 year in the vole data, to examine whether there was any evidence of lagged effects of food on owl dynamics.

The fourth *a priori* model is the full Dennis–Otten model (2000) as described in equation (2.1). In that model, there are additive effects of food and of owl abundance.

The fifth *a priori* model is the two-stage Euler–Lotka equation,

$$\lambda^\alpha(1 - s/\lambda) = lb, \quad (2.3)$$

where α is the age at first reproduction, s is annual adult survival, l is survival from birth to age at first reproduction, and b is annual fecundity (mean female young per female) (Lande 1988; Sibly *et al.* 2000). When the age at first reproduction equals 1.0 then the equation can be rearranged to give

$$\lambda = s + lb, \quad (2.4)$$

which states that the finite population growth rate (λ) equals the sum of annual adult survival (s) and recruitment (lb).

The implementation of equations (2.3) or (2.4) is an example of the demographic paradigm. It can be combined with the ideas in the mechanistic paradigm by assuming or demonstrating that one or more of the demographic rates in equations (2.3) or (2.4) are determined by mechanistic factors, such as food. In the study of barn owls in southern Scotland (Taylor 1994), the demographic rates, s , l and b , were shown to be correlated with the abundance of the main food of the owls, field voles (*Microtus agrestis*). If it is assumed that the demographic parameters in equations (2.3) or (2.4) are related to food availability, then it follows that the finite population growth rate (λ) must be determined by food availability.

In the analyses described here, model fit is assessed firstly by statistical significance and then by the coefficient of determination (R^2). An information-theoretic analysis, such as Akaike's information criterion, was not used as the x - and y -terms in analyses were not consistent.

Burnham & Anderson (1998) advised against use of Akaike's information criterion with such analyses.

(a) *Parameter estimation*

(i) *Population growth rates (λ , r)*

The finite population growth rate (λ) was estimated as the ratio of successive annual estimates of abundance of pairs of barn owls. Data on abundance of pairs of barn owls (Taylor 1994; fig. 15.1; Newton 1998; fig. 7.4) were used. Total abundance of pairs was the sum of the number of breeding pairs and the number of non-breeding pairs. The mean annual population growth rate (r) was estimated by the regression of the natural logarithm of abundances over time (Caughley 1980).

(ii) *Intrinsic population growth rate (r_m) and carrying capacity (K)*

Evidence of logistic growth was assessed by the regression of observed instantaneous growth rate ($r = \ln(N_{t+1}/N_t)$) on total owl abundance (N_t) (Caughley 1980). The fitted regression has an intercept on the y -axis of the intrinsic rate of population growth (r_m), and on the x -axis of carrying capacity (K).

(iii) *Numerical responses*

The Solomon-type numerical response was estimated as the linear regression of abundance of pairs of owls in year t on vole abundance in year t , following Solomon (1949). The Caughley-type numerical response relationships between the finite population growth rate (λ) and vole abundance, and the instantaneous growth rate (r) and vole abundance were estimated by linear regression. The abundance of pairs of barn owls was estimated by the minimum number known to be alive in the breeding season (spring and summer) each year during intensive observation and mark–recapture of owls. An index of abundance of field voles (v) was estimated annually by trapping in spring (Taylor 1994).

(iv) *Age at first reproduction (α)*

Taylor (1994) reported that owls fledged in spring and summer first bred the following spring or summer. Hence, it was assumed that $\alpha = 1$ year.

(v) *Annual adult survival (s)*

Annual survival is the complement of annual mortality. Taylor (1994) reported that annual mortality of adult owls ranged from 15 to 55%, and was strongly negatively correlated (correlation coefficient = -0.78 , d.f. = 9, $p < 0.01$) with vole abundance (Taylor 1994; fig. 14.5). The linear regression was estimated to be,

$$\text{annual adult mortality} = 1 - s = 0.44 - 0.0071v, \quad (2.5)$$

where vole abundance is v .

(vi) *Juvenile survival (l)*

Survival from birth to age at first reproduction (l) was significantly negatively correlated (correlation coefficient = -0.78 , $p < 0.01$) with vole abundance (Taylor 1994; p. 210). It was assumed, for analysis, that in the absence of voles many, but not all, owls died so survival was low (0.1). When vole abundance was high (30) it was assumed

Table 1. The coefficients of determination (R^2) and statistical significance (p) of each model of barn owl dynamics. Also shown is the dependent variable ($\ln N_t$, λ , r or N_t) in each analysis.

model	λ , r or N_t	R^2	p
exponential	$\ln N_t$	0.30	0.053
logistic	r	0.21	0.137 (NS)
Solomon-type numerical response (no time-lag)	N_t	0.44	0.014
Caughley-type numerical response (no time-lag)	λ	0.72	0.0005
Caughley-type numerical response (1 year time-lag)	λ	0.05	0.476 (NS)
Caughley-type numerical response (no time-lag)	r	0.72	0.0005
Caughley-type numerical response (1 year time-lag)	r	0.01	0.720 (NS)
Caughley-type numerical response (vole and owl effects with no time-lag: full model)	r	0.82	0.0004

that survival was 0.3. The linear regression was then estimated to be

$$l = 0.1 + 0.007v. \tag{2.6}$$

Equation (2.6) estimates that when mean vole abundance is 20, then survival is 0.24, and therefore juvenile mortality equals 0.76. This is similar to the higher juvenile survival estimates reported (Taylor 1994; p. 207).

(vii) *Annual fecundity (b)*

The clutch size (correlation coefficient = 0.87, d.f. = 11, $p < 0.001$) (Taylor 1994; fig. 11.8) and the number of young fledging (correlation coefficient = 0.72, $p < 0.01$) (Taylor 1994; fig. 12.9), varied positively with vole abundance. The estimated linear regression relating the number of female young fledged per female per year to vole abundance was

$$b = 1.02 + 0.03v. \tag{2.7}$$

(viii) *Sensitivity analysis*

The effects of a small change in each demographic parameter (α , s , l or b) on the finite population growth rate (λ) were estimated in a sensitivity analysis using the equations of Lande (1988). The assumed parameter values, based on data in Taylor (1994) were as follows: age at first reproduction (α) was 1 year, mean annual adult survival (s) was 0.65, mean juvenile survival (l) was 0.3 and mean annual fecundity (b) was 1.5 females per female. These values provide an estimated annual finite population growth rate (λ) of 1.1 and a generation interval of 2.4 years.

3. RESULTS

(a) *Exponential growth*

The regression of the natural logarithms of owl abundance over time, was not quite statistically significant ($F = 4.69$, d.f. = 1,11, $p = 0.053$, $R^2 = 0.30$) (table 1). The slope of the regression, an estimate of mean r , was -0.06 yr^{-1} with 95% CI of -0.115 to 0.001 . Hence, there was no strong evidence against the proposal that $r = 0$; however, with additional data that conclusion would be reinforced. The observed trends in abundance of barn owls and field voles are illustrated in figure 1, showing apparently linked oscillations over time.

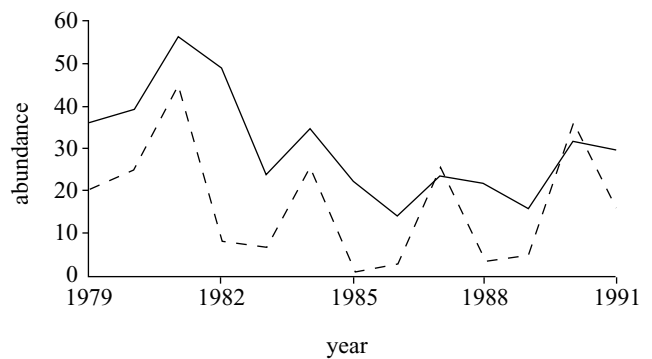


Figure 1. Observed trends in abundance of pairs of barn owls (solid line) and field voles (dashed line) in southern Scotland. Modified from Taylor (1994).

(b) *Logistic growth*

The analysis for evidence of logistic growth showed a non-significant result ($F = 2.62$, d.f. = 1,10, $p = 0.137$, $R^2 = 0.21$) (table 1). Hence, there was no strong evidence supporting the proposal of logistic growth. Therefore, there were no estimates of r_m or K estimated by the regression analysis. Given the observed trend in owl abundance (figure 1) it was not surprising that there was no empirical support for logistical growth.

(c) *Numerical responses*

The Solomon-type numerical response of the relationship between the number of pairs of owls and vole abundance was significant ($F = 8.52$, d.f. = 1,11, $p = 0.014$, $R^2 = 0.44$) (table 1). The relationship and the fitted regression are shown in figure 2.

The Caughley-type numerical response of the annual finite population growth rate (λ) and vole abundance (v) was highly significant ($F = 25.16$, d.f. = 1,10, $p = 0.0005$, $R^2 = 0.72$) (table 1). The fitted regression was

$$\lambda = 0.607 + 0.028v, \tag{3.1}$$

which is illustrated in figure 3. The regression estimates that owl abundance declines when vole abundance drops below 14, and when voles are absent the annual growth rate (λ) of the owl population equals 0.607. The numerical response using vole abundance in the previous year as the independent variable was not significant ($F = 0.55$, d.f. = 1,10, $p = 0.476$, $R^2 = 0.05$) (table 1).

The Caughley-type numerical response of the annual

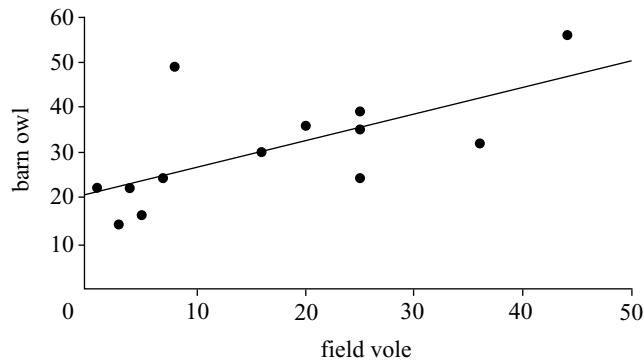


Figure 2. The Solomon-type numerical response of pairs of barn owls in year t to variation in field vole abundance in year t . Data are estimated from Taylor (1994) and Newton (1998) and are based on censuses.

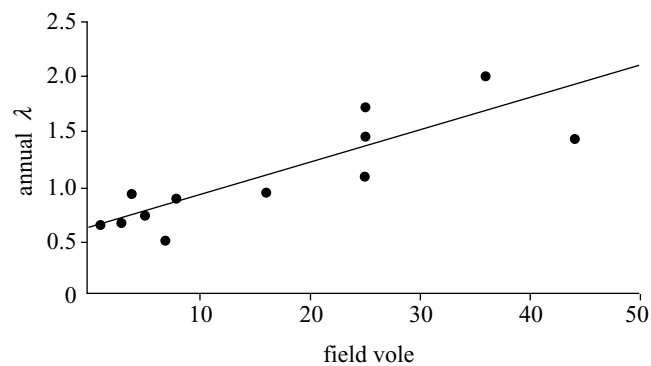


Figure 3. The Caughley-type numerical response of a barn owl population to variation in field vole abundance. The response variable is the annual finite population growth rate (λ) of the owl population. Data are estimated from Taylor (1994) and Newton (1998) and are based on censuses.

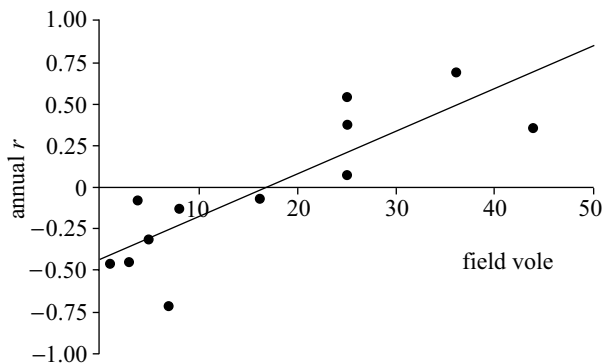


Figure 4. The Caughley-type numerical response of a barn owl population to variation in field vole abundance. The response variable is the annual instantaneous population growth rate (r) of the owl population. Data are estimated from Taylor (1994) and Newton (1998) and are based on censuses.

instantaneous population growth rate (r) and vole abundance (v) was highly significant ($F = 25.12$, d.f. = 1,10, $p = 0.0005$, $R^2 = 0.72$) (table 1). The fitted regression was

$$r = -0.446 + 0.026v, \tag{3.2}$$

which is illustrated in figure 4. The regression estimates

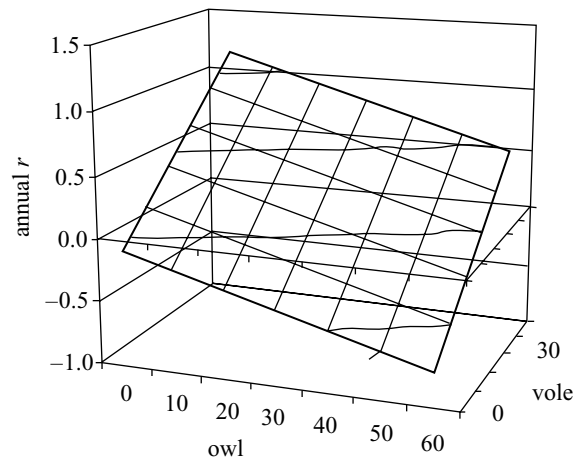


Figure 5. The Caughley-type numerical response of a barn owl population to variation in field vole abundance and owl abundance (equation (3.3)). The response variable is the annual instantaneous population growth rate (r) of the owl population.

that owl abundance declines when vole abundance drops below 17, and when voles are absent, r of the owl population equals -0.446 yr^{-1} . The numerical response using vole abundance in the previous year as the independent variable was not significant ($F = 0.14$, d.f. = 1,10, $p = 0.720$, $R^2 = 0.01$) (table 1).

The Caughley-type numerical response of the annual instantaneous population growth rate (r) and vole abundance (v) and owl abundance in year t (equation (2.1)) was highly significant ($F = 20.82$, d.f. = 2,9, $p = 0.0004$, $R^2 = 0.82$) (table 1).

The fitted regression was

$$r = -0.069 - 0.011 \text{ owls} + 0.024v, \tag{3.3}$$

which is illustrated in figure 5. The population growth rate increased when vole abundance increased and decreased as owl abundance increased. The standard errors, and associated t -values, on each parameter (a , b , c in equation (2.1)) were 0.1871 ($t = -0.37$, NS), 0.0049 ($t = -2.33$, $p = 0.045$) and 0.0044 ($t = 5.49$, $p = 0.0004$), respectively. These indicate the intercept (a) was not different to $r = 0$, but the coefficient for the effect of owl abundance (b) was significant and for the effect of vole abundance (c) was highly significant. The observed (dashed line) and reconstructed (using equation (3.3), solid line) abundance of barn owls are shown in figure 6, showing the close agreement.

(d) Demographic and mechanistic determinants of population growth rate

The relationship between the finite population growth rate (λ) and vole abundance was estimated by substituting equations (2.5) to (2.7) into equation (2.4). The resultant equation showed a positive relationship between λ and vole abundance (figure 7). The estimated regression was

$$\lambda = 0.662 + 0.0172v + 0.00021v^2. \tag{3.4}$$

The estimated relationship is slightly curved being upwardly concave, though this is not obvious in figure 7. Because of the substitution of equations, a quadratic equa-

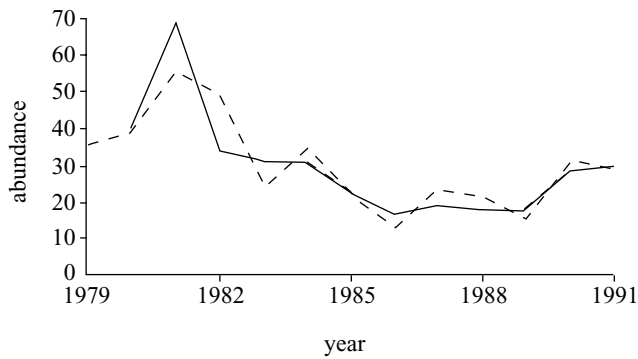


Figure 6. The observed (dashed line) and reconstructed (solid line) abundance of pairs of barn owls over years. There is no estimate of owl abundance in 1979 because of the absence of data on owl abundance in the prior year.

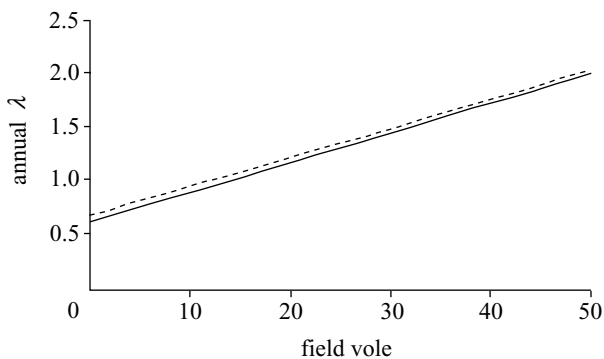


Figure 7. A comparison of the Caughley-type numerical responses, estimated by two methods, of a barn owl population to variation in field vole abundance. The numerical response estimated from census data (equation (3.1) and shown in figure 3) is shown by the solid line and the numerical response estimated from demographic data (equation (3.4)) is illustrated by the dotted line. The response variable is the annual finite population growth rate (λ) of the owl population.

tion with a positive intercept and positive regression coefficients for the linear and quadratic terms is produced.

The demographic numerical response relationship shown in figure 7 is compared with that estimated from the annual census data (figure 3). The two numerical response relationships are very similar (figure 7) with that derived from demographic and mechanistic data giving slightly higher estimates of λ than that estimated from the census data.

(e) Sensitivity analysis

The sensitivity analysis showed that the largest effect on λ was produced by a small change in annual adult survival (1.7), followed by survival to age at first reproduction (1.5), annual fecundity (0.3) and age at first reproduction (−0.2).

4. DISCUSSION

The population growth rate of a closed population is determined by demographic rates and the influence of extrinsic mechanistic factors, such as food, and intrinsic factors, such as spacing behaviour. The results reported

here show that for the avian predator, the barn owl, changes in abundance are closely related to the variation in food supply (especially of field voles). The Caughley-type numerical response, as estimated by the finite population growth rate (λ), to food supply can be estimated directly from a field census of owls (figure 3). The Caughley-type numerical response can also be estimated indirectly (figure 7) from empirically estimated relationships between demographic rates and food supply. Hence, use of the demographic and mechanistic approaches to estimating the determinants of population growth rate can yield similar and complementary results.

The ecological model (equation (3.3)) with the best fit, as assessed by the coefficient of determination R^2 , was the Caughley-type numerical response of population growth rate, as r , on vole abundance and owl abundance (table 1). That relationship accounted for 82% of the variation in population growth rate. The model combined the mechanistic and density paradigms of Krebs (1995, 2002). The additive and negative effect of owl abundance of population growth rate (r) in the barn owl study may have been associated with some form of density-dependent competition for food and possibly breeding sites. The barn owls have overlapping home ranges but do defend nesting sites (Taylor 1994).

The numerical response relationships showed that the barn owls responded to variation in food availability within a year. The analyses using lagged vole data were non-significant. This result occurred through within-year changes in survival and fecundity of owls. With higher vole abundance, owls laid their first egg earlier in the breeding season (Taylor 1994; fig. 9.3b), mean clutch size was higher (Taylor 1994; fig. 11.8) and the mean number of young fledged per pair increased (Taylor 1994; fig. 12.9). Such a quick response, with no time-lag, has also been recorded in Tengmalm's owl (*Aegolius funereus*) (Korpimäki & Norrdahl 1989) and red kangaroo (*Macropus rufus*) and western grey kangaroo (*M. fuliginosus*) populations (Bayliss 1987) in response to variation in food availability.

Variation in prey availability has been shown to be related to demographic rates of predatory wildlife in several studies. For example, microtine rodent abundance was related to fecundity in Tengmalm's owls (Korpimäki & Norrdahl 1989), variation in lifetime reproductive success in male Tengmalm's owl (Korpimäki 1992), survival of male Tengmalm's owl (Hakkarainen *et al.* 2002) and survival of breeding females and age at first reproduction in Ural owl (*Strix uralensis*) (Brommer *et al.* 1998). Fecundity in kit fox (*Vulpes macrotis*) was positively related to leporid abundance (White & Garrott 1999).

The Solomon-type numerical response of predators (barn owl) and prey (voles) was positive (figure 2). Such a positive relationship has also been reported for Tengmalm's owl and *Microtus* spp. (Korpimäki & Norrdahl 1989).

The results reported here suggest that approaches used in other studies of the determinants of population growth rate may be usefully modified. For example, the demographic studies of population growth rate in northern spotted owl (*Strix occidentalis caurina*), such as those of Lande (1988) through to Seamans *et al.* (2001), focused on using demographic rates to estimate population growth rate, but did not estimate food availability or a numerical response

relationship. In contrast, studies of kangaroos, such as those of Bayliss (1987), Caughley (1987), Cairns & Grigg (1993) and McCarthy (1996), focused on estimating a Caughley-type numerical response without any detailed data on demographic rates. The study here shows that such different approaches can be combined. Such a combination of demographic and mechanistic approaches occurred in a graphical, not quantitative, form in the study of Himalayan thar (*Hemitragus jemlahicus*) of Caughley (1970; fig. 5).

The models and analyses described in the present study have strengths and limitations. The estimated numerical responses reported here (figures 3, 4, 5 and 7) are linear. Over a broader range of food availability, such numerical responses should be curved with the population growth rate approaching a maximum, the intrinsic rate of growth (r_m). The estimated relationships between the demographic rates and food availability should also be curved relationships, as survival clearly has a maximum value of 1.0 and fecundity has a maximum value determined by genotype. There was no clear evidence of curved relationships in the data; however, perhaps such curves would be evident if food (vole) availability occurred at higher levels than reported in the study by Taylor (1994).

The numerical response may also be influenced by other mechanistic factors. For example, fecundity may be partly determined by the availability of nest sites, as well as food. If that occurred then a modified version of equation (2.7) would need to be estimated showing the effects of food and nest sites. Expressing the effects of food and nest sites on population growth rate would be similar to the description of ecological niche given by Sibly & Hone (2002) and the modelling of the effects of two obligate resources on population growth rate by Tilman (1982). Similarly, effects of pesticides on owl abundance, or wildlife generally, could be incorporated into the modelling by evaluating whether adult and/or juvenile survival are affected by food and pesticide exposure. In many studies of birds, including avian predators, the effects of nest sites and pesticides have been reported (Newton 1998).

Most models of the numerical response had no explicit effects of density, though the full model (equations (2.1) and (3.3)) did. Future research could evaluate whether one or more demographic rates (such as adult survival and fecundity) are density dependent, as has been reported in wildebeest (*Connochaetes taurinus*) in which annual adult survival was negatively related to per capita food availability (Mduma *et al.* 1999).

The numerical response relationship of r versus food, could be used in a model of trophic interactions, such as described by a modified Lotka–Volterra model (Caughley 1987). That has not been done here as the data in the original study do not allow description of vole dynamics in the absence of owls, and the functional response of owls to a variation in food supply was not described in the original study by Taylor (1994). Such use of the numerical response in a modified Lotka–Volterra model would include a density-dependent response of the owls and their food supply. That could occur in one of two ways: an increase in vole abundance would cause an increase in owl abundance that would cause, in the following year, an increase in predation of voles by owls that may lower vole abundance; hence, there would be negative feedback on

vole abundance. Alternatively, use of the full model in equation (3.3) describes an instantaneous effect of owl abundance on r within a year.

The sensitivity analysis indicated that a change in annual adult survival had the greatest effect on finite population growth rate (λ). That is similar to the results reported for the northern spotted owl (Lande 1988). The sensitivity analyses for both species ranked the demographic parameters in the same descending order of effects on finite population growth rate: s , l , b and α . The sensitivity of population growth rate to juvenile survival was higher for barn owls, and was presumably associated with the shorter life expectancy for that species. The results of the sensitivity analysis and of the demographic and numerical response analysis demonstrate an important result from this study. The demographic and numerical response analyses show the causes of changes in demographic rates, while the sensitivity analysis shows the effects of changes in demographic rates. Those distinctions show why it is useful to combine aspects of the mechanistic and demographic paradigms in identifying the determinants of population growth rates.

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