

Climate, food, density and wildlife population growth rate

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Summary

1. The aim of this study was to derive and evaluate a priori models of the relationship between annual instantaneous population growth rate (r) and climate. These were derived from the numerical response of annual r and food, and the effect of climate on a parameter in the numerical response. The goodness of fit of a range of such deductive models to data on annual r of Soay sheep and red deer were evaluated using information-theoretic (AICc-based) analyses.

2. The analysis for sheep annual r showed negative effects of abundance and negative effects of the interaction of abundance and climate, measured as March rainfall (and winter NAO) in the best fitting models. The analysis for deer annual r showed a negative effect of deer abundance and a positive effect of climate measured as March rainfall (but a negative effect of winter NAO), but no interaction of abundance and climate in the best fitting models.

3. There was most support in the analysis of sheep dynamics for the ratio numerical response and the assumption that parameter J (equilibrium food per animal) was influenced by climate. In the analysis of deer dynamics there was most support for the numerical responses assuming effects of food and density (Ivlev and density, food and density, and additive responses) and slightly less support for the ratio numerical response. The evaluation of such models would be aided by the collection of and incorporation of food data into the analyses.

Key-words: numerical response, red deer, Soay sheep, trophic models, wildlife population dynamics.

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Introduction

Climate has many effects on wildlife population dynamics. For example, survival rates of Soay sheep *Ovis aries* L. are negatively related to rainfall in March (the end of the northern winter) (Catchpole *et al.* 2000; Coulson *et al.* 2001) and to the winter North Atlantic Oscillation (NAO) (Milner, Elston & Albon 1999; Clutton-Brock *et al.* 2004). Winter mortality of red deer *Cervus elaphus* L. was positively related to rainfall (Clutton-Brock & Albon 1989). Fecundity of sheep and deer are related to climate and density (Coulson, Milner-Gulland & Clutton-Brock 2000). Recruitment of elk *Cervus elaphus* is negatively related to winter snowpack conditions (Garrott *et al.* 2003).

The aim of this paper is to evaluate alternative hypotheses, expressed as models, relating annual wildlife population growth rate (r) to climate. A novel starting point for modelling is the numerical response between annual population growth rate (r) and food availability (Caughley 1977; Bayliss 1987; Choquenot 1998; Sibly & Hone 2003), and the effect of climate on the relationship. Given this starting point, models with no effects of climate and food, such as simple density-dependent models, were not examined. Past studies of climate do not explicitly include effects of food. The study derives and evaluates whole-of-population models of intermediate complexity; that is, intermediate between single species unstructured density-dependent models, and detailed structured demographic models. The latter have much merit, however, the demographic data and food data may not be available in all studies, such as from simple monitoring programmes. The hypotheses are evaluated using data for Soay sheep and red deer on islands off western Scotland.

Table 1. Models of the numerical response between the annual instantaneous rate of population growth (*r*), food availability (*V*) and abundance (*H*), and the derived model relationships between the annual *r*, climate (*W*), abundance (*H*) and food availability (*V*). Also shown is the parameter in each numerical response equation which is assumed to be influenced by climate in a linear manner. The model number is the same between those models that predict the same relationship between *r* and *W*, even though the specific components of each equation's coefficients may differ

Numerical response and source	Parameter influenced	Model relationship	Model no.
Linear $r = -a + bV$ May (1981)	<i>b</i>	$r = (-a + cV) + (dV)W$	1
Quadratic $r = -a + bV - cV^2$ Crawley <i>et al.</i> (2004)	<i>b</i>	$r = (-a + dV - cV^2) + (fV)W$	1
Ivlev $r = -a + c(1 - e^{-dV})$ Bayliss (1987)	<i>c</i>	$r = (-a + b - be^{-dV}) + (f - fe^{-dV})W$	1
Ivlev & density $r = -a + c(1 - e^{-dV}) - bH$ Bayliss & Choquenot (2003)	<i>c</i>	$r = (-a + g - ge^{-dV}) + (f - fe^{-dV})W - bH$	2
Mitscherlich $r = a - be^{-cV}$ Cairns & Grigg (1993)	<i>b</i>	$r = (a - ge^{-cV}) - (fe^{-cV})W$	1
Food & density $r = a - be^{-cV} - dH$ Pech <i>et al.</i> (1999)	<i>b</i>	$r = (a - ge^{-cV}) + (fe^{-cV})W - dH$	2
Additive $r = -a + cV - bH$ Hone & Sibly (2003)	<i>c</i>	$r = (-a + gV) + (fV)W - bH$	2
Ratio $r = r_m(1 - (JH/V))$ May (1974)	<i>J</i>	$r = r_m - (ar_m/V)H - (br_m/V)WH$	3

Models

The positive relationship between population growth rate (*r*) and food availability (*V*) (Table 1) may be modified by climate (*W*). It is postulated that climate may influence, in a linear manner, one parameter in a numerical response (Table 1). For example if a linear numerical response (Table 1) is assumed then climate may influence parameter *b*, the slope of the response relationship and may do so in a linear manner (Table 1). Hence, if

$$r = -a + bV \tag{eqn 1}$$

(Fig. 2a) and

$$b = c + dW \tag{eqn 2}$$

then substituting eqn 2 into eqn 1 and rearranging gives,

$$r = (-a + cV) + (dV)W \tag{eqn 3}$$

which shows a linear relationship between *r* and *W* (Fig. 1a) and the effects of food (*V*) influencing the intercept ($-a + cV$) and slope (dV) of the relationship (Table 1). The negative ($d < 0$) effect of climate could occur through effects of, for example, low temperatures on survival. The positive ($d > 0$) effects could occur through a lessening of climate stress. Equation 3 is

described in the text as model 1 (Table 1). The derivation highlights the usefulness of food data in estimating determinants of annual population growth. It also highlights that an analysis of annual *r* and climate can occur even in the absence of food data though the conclusions may be weakened by the extra unaccounted for variation in the data. The approach can be extended to other forms of the numerical response and converted into alternative relationships between annual *r* and climate (Table 1, Fig. 1a–c). Model 2 with additive effects of climate and density is equivalent to the density-dependent rainfall model of Dennis & Otten (2000). However, model 2 has an explicit parameter for food availability (*V*) that was not explicit in the Dennis and Otten model. The models are multiple working hypotheses in the sense of Chamberlin (1965).

Three models of the numerical response (Table 1; Ivlev and density, food and density, and additive) assume that annual population growth rate (*r*) is related to food availability (*V*) and an extra effect of density (*H*). The ecological mechanism generating the extra effect of density is not clear, but it is assumed that it is not food. The extra effects have been described as caused by social processes, predation or pathogens (Choquenot & Ruscoe 2000), interference competition (Hone & Sibly 2003; Sibly & Hone 2003), density dependence (Bayliss & Choquenot 2003) and possible effects of pathogens (Ruscoe *et al.* 2005). Internal parasites of Soay sheep may lower survival rates (Gulland 1992).

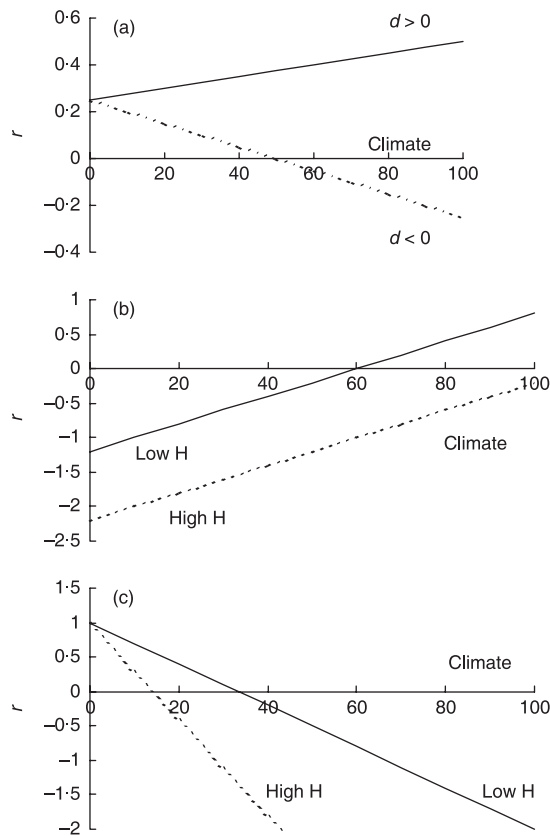


Fig. 1. (a) Derived linear relationships in model 1 between annual population growth rate (r) and climate (W) for negative ($d < 0$) and positive ($d > 0$) effects of climate (W) on parameter b the slope in the linear numerical response. (b) Derived linear relationships in model 2 between annual population growth rate (r) and climate (W) and effects of density (H) on the relationship when climatic effects are positive. (c) Derived linear relationships in model 3 between annual population growth rate (r) and climate (W) and effects of density (H) on the relationship when climatic effects are negative.

Methods

Data on abundance of Soay sheep on Hirta and red deer on the island of Rum off western Scotland are examined. The data for sheep are from 1985 to 2000 inclusive and are total numbers (males and females combined) of sheep for the intensively studied area around the Village Bay. The data on red deer are from 1974 to 2000 inclusive and are for total numbers (males and females combined) on the North Block of Rum. The sheep are censused in August and the deer in May (Tim Coulson pers. comm.). Details have been described of the history of the sheep population (Clutton-Brock & Pemberton 2004) and the deer population (Clutton-Brock *et al.* 1997). The sheep population can suffer starvation between January and March (Milner & Gwynne 1974). Median dates of deaths of deer are in February and March (Clutton-Brock *et al.* 1997). The annual instantaneous population growth rate (r) was estimated as $r = \ln(N_{t+1}/N_t)$ (Caughley 1977). Over the duration of each study the sheep population averaged 405 animals (range = 211–591) with a mean annual r of $-0.007 (\pm 0.116 \text{ SE})$.

The deer population averaged 310 animals (range = 201–397) with a mean annual r of $0.021 (\pm 0.022 \text{ SE})$. There are no mammalian predators on the two study islands. The sheep (Clutton-Brock *et al.* 1997) and deer (Coulson *et al.* 2004b) populations show little net movement into and out of each study site.

Based on results in the above literature, climate was measured as March rainfall (mm) and the winter (December–March) NAO (Hallett *et al.* 2004; Stenseth & Myserud 2005). Broad scale climate measures, such as NAO, have been used in other ecological studies (Almaraz & Amat 2004a,b). Data on rainfall on Hirta were based on rainfall recorded at Benbecula and for Rum were from the weather station on Rum (Tim Coulson pers. comm.). Data on the station-based winter NAO were obtained from the Jim Hurrell website (<http://www.cgd.ucar.edu/~jhurrell>). Rainfall in March is positively correlated with the value of the winter NAO (Catchpole *et al.* 2000). High NAO values are associated with wet and windy weather and low NAO values are associated with dry and cold weather (Forchhammer *et al.* 2001).

The regressions were calculated using linear least squares and nonlinear least squares regressions in computer software R (Ihaka & Gentleman 1996) and SAS version 8.2 (Freund & Little 1986). Model selection was based on identifying the model with the lowest Akaike Information Criterion corrected for small samples (AICc) (Burnham & Anderson 2002). Models with ΔAICc of less than 2 are quite similar (Burnham & Anderson 2002) so were examined closely. The two data sets are each from one site and extend over many years. Any temporal correlations in the data sets have not been estimated or incorporated into the analyses. The results may therefore overestimate the probability of relationships if positive correlations occur over time.

Results

SOAY SHEEP

The analysis of sheep dynamics and both March rainfall and winter NAO showed that the model with the lowest AICc was model 3 (Table 2), which had negative, linear terms for sheep abundance and a negative interaction of abundance and March rainfall (Fig. 2a) or winter NAO (Fig. 2b). Model 3 reconstructed the broad patterns in the dynamics of the sheep population (Fig. 3). However, in 1987, 1990 and 1998 the model predicted abundance to decrease when it was observed to increase (Fig. 3). The proportion of variation in sheep abundance accounted for between years, as estimated by the relationship between observed and predicted abundances, was 49%.

RED DEER

The best fitting model (model 2) had a positive effect of March rainfall and a negative effect of deer abundance

Table 2. Parameter estimates for models of dynamics of Soay sheep and climate. The y variable is annual instantaneous population growth rate (r), and the parameters are the intercept (β_0), regression coefficient (β_1) for climate as measured by March rainfall (mm) (or winter NAO), regression coefficient (β_2) for sheep abundance, and the regression coefficient (β_3) for the interaction of March rainfall (or winter NAO) and sheep abundance. Model numbers refer to models in Table 1. AICc, Δ AICc and Akaike weights (w_i) for each model are also shown. The number of parameters (K) equals 3 in model 1 and 4 in models 2 and 3

Model	Parameters			
	β_0	β_1	β_2	β_3
March rainfall				
1	E	0.726	-0.0052	0
	SE	0.345	0.0023	NA
AICc = 20.97, Δ AICc = 11.62, $w_1 = 0.002$				
2	E	1.556	-0.0043	-0.0024
	SE	0.316	0.0016	0.0006
AICc = 12.23, Δ AICc = 2.88, $w_2 = 0.191$				
3	E	0.857	0	-0.00013
	SE	0.234	NA	0.00093
AICc = 9.35, Δ AICc = 0, $w_3 = 0.807$, $R^2 = 0.742$				
Winter NAO				
1	E	0.114	-0.074	0
	SE	0.141	0.052	NA
AICc = 23.63, Δ AICc = 10.40, $w_1 = 0.004$				
2	E	1.166	-0.074	-0.0026
	SE	0.274	0.035	0.00064
AICc = 14.35, Δ AICc = 1.12, $w_2 = 0.362$				
3	E	1.078	0	-0.0024
	SE	0.258	NA	0.00063
AICc = 13.23, Δ AICc = 0, $w_3 = 0.634$, $R^2 = 0.665$				

E = parameter estimate, SE = standard error and NA = not applicable.

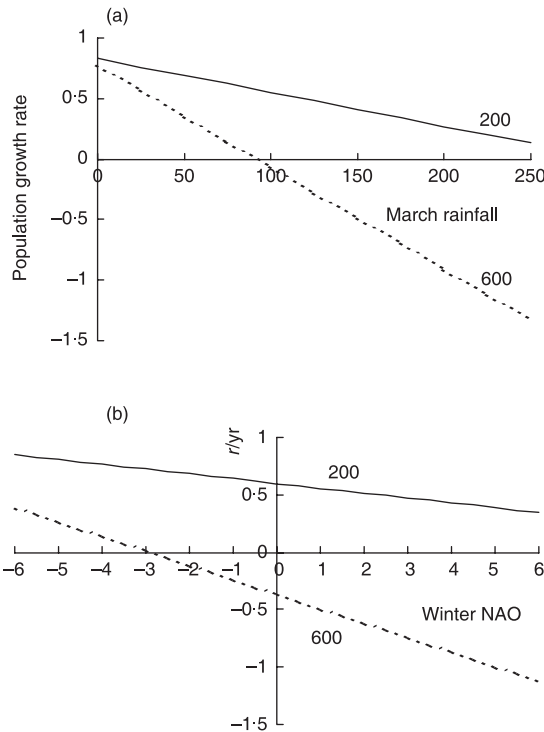


Fig. 2. Fitted regressions between annual population growth rate (r) of Soay sheep and (a) March rainfall (mm) and abundance of sheep ($H = 200, 600$) in August at the start of the 12-month period, and (b) winter NAO and abundance of sheep ($H = 200, 600$) in August at the start of the 12-month period. Estimates are from model 3 in Table 2.

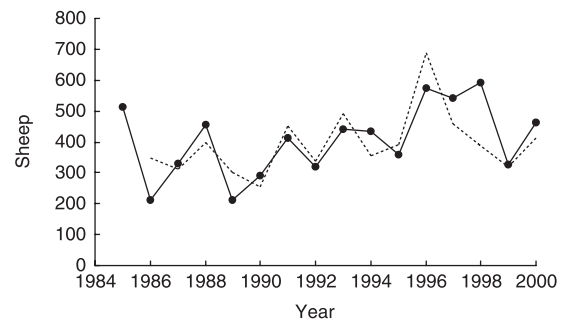


Fig. 3. Observed data (dots and solid line) and reconstructed estimates of Soay sheep abundance from model 3 (dotted line) of Table 2. Estimates are for August of a particular year (year t) based on sheep abundance in August of the previous year (year $t - 1$) and the rainfall measured in March in year t .

(Table 3, Fig. 4a). The proportion of variation in deer abundance accounted for between years, as estimated by the relationship between observed and predicted (from model 2 using March rainfall) abundances, was 43%. The model with the second best fit (Δ AICc = 0.02) was model 3, which had a negative effect of deer abundance and a positive interaction of rainfall and deer abundance (Table 3). Akaike weights (w_i) were similar for models 2 and 3 whether climate was measured as March rainfall or winter NAO (Table 3). With climate measured as winter NAO model 2 (Table 3) had negative

Table 3. Parameter estimates for models of dynamics of red deer and climate. The y variable is annual instantaneous population growth rate (r), and the parameters are the intercept (β_0), regression coefficient (β_1) for climate as measured by March rainfall (mm) (or winter NAO), regression coefficient (β_2) for deer abundance, and the regression coefficient (β_3) for the interaction of March rainfall (or winter NAO) and deer abundance. Model numbers refer to models in Table 1. AICc, Δ AICc and Akaike weights (w_i) for each model are also shown. The number of parameters (K) equals 3 in model 1 and 4 in models 2 and 3

Model	Parameters				
	β_0	β_1	β_2	β_3	
March rainfall					
1	E	0.048	-0.0001	0	0
	SE	0.076	0.0003	NA	NA
AICc = -34.28, Δ AICc = 8.46, $w_1 = 0.007$					
2	E	0.464	0.00013	-0.0016	0
	SE	0.133	0.00023	0.00044	NA
AICc = -42.74, Δ AICc = 0, $w_2 = 0.499$, $R^2 = 0.300$					
3	E	0.495	0	-0.0017	0.0000004
	SE	0.135	NA	0.0005	0.0000007
AICc = -42.72, Δ AICc = 0.02, $w_3 = 0.494$					
Winter NAO					
1	E	0.033	-0.0099	0	0
	SE	0.026	0.011	NA	NA
AICc = -35.03, Δ AICc = 7.77, $w_1 = 0.010$					
2	E	0.472	-0.0055	-0.0014	0
	SE	0.131	0.0091	0.0004	NA
AICc = -42.80, Δ AICc = 0, $w_2 = 0.508$, $R^2 = 0.301$					
3	E	0.467	0	-0.0014	-0.00002
	SE	0.133	NA	0.0004	0.00003
AICc = -42.69, Δ AICc = 0.11, $w_3 = 0.481$					

E, parameter estimate; SE, standard error; NA, not applicable.

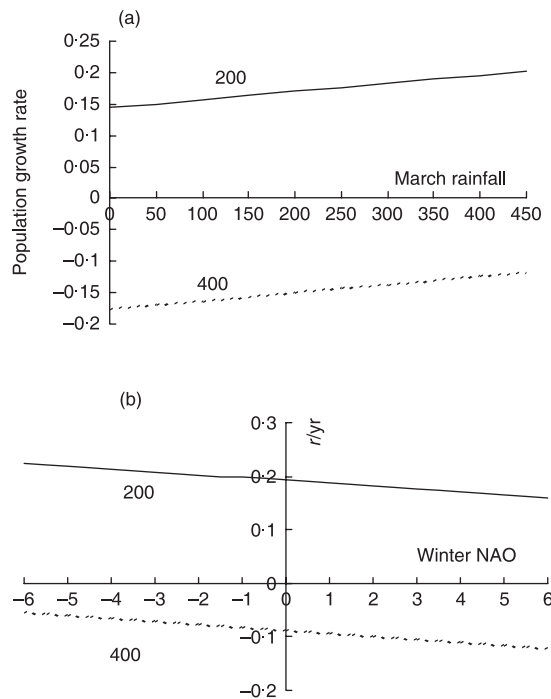


Fig. 4. Fitted regressions between annual population growth rate (r) of red deer and (a) March rainfall (mm) and abundance of deer ($H = 200, 400$) in May at the start of the 12-month period, and (b) winter NAO and abundance of deer ($H = 200, 400$) in May at the start of the 12-month period. Estimates are from model 2 in Table 3.

effects of climate and deer abundance (Fig. 4b). The proportion of variation in deer abundance accounted for between years, as estimated by the relationship between observed and predicted (from model 2 using winter NAO) abundances, was 46%.

Discussion

Evaluation of the deductive trophic models (Table 1) showed that the population dynamics of Soay sheep are consistent (model 3, Table 2) with the reported (Coulson, Rohani & Pascual 2004a; Hallett *et al.* 2004) interaction of climate and density on trends in abundance. The novel feature of the models and analyses reported here is that an ecological mechanism for that interaction is shown; the direct effect of climate on a parameter (J) in the ratio numerical response. The interaction ($W * H$) term is actually a $W * H/V$ interaction (Table 1) and can be rewritten as $W/(V/H)$. That is, climate (W) divided by per capita food availability (V/H). The term will become larger when food (V) is reduced and become smaller when food (V) increases. If the reported climate and density interaction assumes density is a surrogate for food then the interpretations are compatible. However, this new derivation highlights that there may be an extra effect of density, such as pathogens, beyond an effect of food that generates what is actually a climate \times food \times density interaction. The results infer support for the ratio

model (Table 1) and for a ratio-dependent approach of the type suggested by Arditi & Ginzburg (1989). Greater evaluation of prey-dependent and ratio-dependent models has been encouraged (Abrams & Ginzburg 2000). The results for red deer are not so clear with prey-dependent and ratio-dependent models having similar support (Table 3) which suggests a need for extra data to more clearly distinguish between these approaches.

The results for sheep but not for deer were very similar whether climate was measured as March rainfall or winter NAO. This is in contrast to Hallett *et al.* (2004) who reported winter NAO may be a better descriptor of ecological processes than local climate. The results suggest that climate change involving increases in March rainfall could have negative effects on the sheep and positive effects on the red deer populations.

The proportion of variation in sheep abundance accounted for by model 3 in the present study was 49% as estimated from the relationship between observed and predicted abundance. That model, of intermediate complexity, accounted for more variation than the density-dependent models of sheep abundance (*c.* 20%; Grenfell *et al.* 1998) but less than the 90% accounted for by the best demographic model (Coulson *et al.* 2001). Hence the goodness of fit in trends in Fig. 3 is intermediate between those shown in fig. 13·8(c,d) of Clutton-Brock & Coulson (2003).

The parameter r_m was estimated as the intercept in model 3; however, such estimates are likely overestimates associated with the lack of abundance data below 200 animals. The sheep estimates (0·857 and 1·078; Table 2) are higher than an estimate (0·36), derived from population counts, of annual r_m of Soay sheep for the whole island of Hirta (Lande, Engen & Saether 2003, fig. 2·7). The estimates of r_m for red deer (0·467 and 0·495, model 3 Table 3) were higher than those (0·270 and 0·383) reported by Sinclair (1996) and the difference may also be a result of extrapolation.

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