

Of sheep and rain: large-scale population dynamics of the red kangaroo

NICLAS JONZÉN*†, ANTHONY R. POPLÉ†, GORDON C. GRIGG† and HUGH P. POSSINGHAM‡

†Department of Zoology and Entomology, University of Queensland, St. Lucia 4072 QLD, Australia, and

‡Department of Mathematics, University of Queensland, St. Lucia 4072 QLD, Australia

Summary

1. We analysed time-series data from populations of red kangaroos (*Macropus rufus*, Desmarest) inhabiting four areas in the pastoral zone of South Australia. We formulated a set of *a priori* models to disentangle the relative effects of the covariates: rainfall, harvesting, intraspecific competition, and domestic herbivores, on kangaroo population-growth rate.

2. The statistical framework allowed for spatial variation in the growth-rate parameters, response to covariates, and environmental variability, as well as spatially correlated error terms due to shared environment.

3. The most parsimonious model included all covariates but no area-specific parameter values, suggesting that kangaroo densities respond in the same way to the covariates across the areas.

4. The temporal dynamics were spatially correlated, even after taking into account the potentially synchronizing effect of rainfall, harvesting and domestic herbivores.

5. Counter-intuitively, we found a positive rather than negative effect of domestic herbivore density on the population-growth rate of kangaroos. We hypothesize that this effect is caused by sheep and cattle acting as a surrogate for resource availability beyond rainfall.

6. Even though our system is well studied, we must conclude that approximating resources by surrogates such as rainfall is more difficult than previously thought. This is an important message for studies of consumer-resource systems and highlights the need to be explicit about population processes when analysing population patterns.

Key-words: consumer-resource dynamics, environmental stochasticity, herbivores, population dynamics spatial correlation, herbivores, time-series analyses, environmental stochasticity, spatial correlation

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Introduction

Since the pioneering work by the Australian statistician P.A.P. Moran in the early 1950s (e.g. Moran 1953), the spatial dimension of population dynamics and especially large-scale synchrony in population fluctuations has received a lot of attention from ecologists (Royama 1992; Ranta *et al.* 1995; Bjørnstad, Ims & Lambin 1999; Koenig 1999). There is a growing interest in extending

the analysis of ecological dynamics to include the spatial dimension (e.g. Bascompte & Solé 1997; Tilman & Kareiva 1997; Dieckmann, Metz & Law 2000).

The spatial distribution of individuals can be important when the primary interest is to understand temporal dynamics. For instance, populations at different spatial locations may differ in terms of demography (LaMontagne, Irvine & Crone 2002) and how they respond to environmental fluctuations, i.e. averaging across space can be misleading. The driving environmental variables may also vary across space. Hence, to be able to analyse space–time series data in a rigorous way, population models should allow for spatial variation in growth-rate parameters and environmental

*Correspondence and current address, Niclas Jonzén, Department of Theoretical Ecology, Ecology Building, Lund University, SE-223 62 Lund, Sweden. E-mail: niclas.jonzén@teorekol.lu.se. Tel. +46 46 222 4828, Fax: +46 46 222 3766.

variability, as well as spatially correlated error terms (Dennis, Kemp & Taper 1998). In some cases, the populations may also be connected by dispersal, which has turned out to be challenging to estimate, but possible, from space–time series data (Lele, Taper & Gage 1998). Failure to account for spatial patterns may sometimes lead to very different conclusions about an organism's ecology, such as when estimating environment–abundance relationships (Keitt *et al.* 2002).

In this paper, we use a multivariate maximum likelihood framework to study spatio-temporal population dynamics in the red kangaroo (*Macropus rufus*, Desmarest) inhabiting the pastoral zone of South Australia. We are primarily interested in finding out to what extent kangaroo dynamics are affected by rainfall, intraspecific competition, interspecific competition with sheep and cattle, and whether there are any spatial differences in these interactions between different management areas. Previous kangaroo studies have highlighted the importance of the interactions listed above, but no attempt has been made to put them all together in a unified statistical framework.

Because kangaroos interact with sheep via resource competition (Caughley 1987; Edwards 1989) and are harvested for meat and skins (Ramsay 1994; Pople & Grigg 1998; Grigg & Pople 2001), there is a clear need for population models that can be used to evaluate alternative decisions under uncertainty. There is also a need to sort out how the different processes identified above translate into observable kangaroo dynamics and that is our major goal here. Such knowledge is important to be able to make reasonable management decisions, such as optimal harvesting in response to predicted grazing pressure and rainfall. It is also valuable on a more general level because different population processes can give rise to the same patterns in time-series data (Jonzén *et al.* 2002a; Jonzén, Ripa &

Lundberg 2002b). However, the system dealt with in this paper is relatively well studied, which minimizes the risk of ignoring key processes governing a population's dynamics (Jonzén *et al.* 2002a).

It has previously been assumed that the red kangaroos inhabiting the study area make up a single large and uniform population (McCarthy 1996), but there are other studies suggesting that there may be differences between at least the western and the central and eastern regions in terms of the numerical response to rainfall (Cairns & Grigg 1993). Furthermore, the study area has been divided by the government management agency into different management regions, each with its own annual harvest quota (SADEH 2002). Hence, there are ecological as well as management reasons to increase the spatial resolution of current understanding and to study the temporal dynamics of the red kangaroo in the different management areas rather than across South Australia as a whole.

STUDY AREA AND DATA

The pastoral zone of South Australia covers approximately 282 000 km² in area and comprises a range of different landforms and vegetation types (Laut *et al.* 1977). The aerial survey of kangaroos in the pastoral zone of South Australia was initiated in 1978 and has been conducted annually each winter. Survey methods are described elsewhere (Caughley & Grigg 1981; Cairns & Grigg 1993).

Data on red kangaroo densities (individuals km⁻²) in six management regions of South Australia (Fig. 1) were collected by winter aerial survey (Caughley & Grigg 1981; Grigg *et al.* 1999) between 1978 and 2002. To reduce the number of parameters that we had to estimate, we amalgamated data from pairs of similar regions, resulting in the following four major areas:

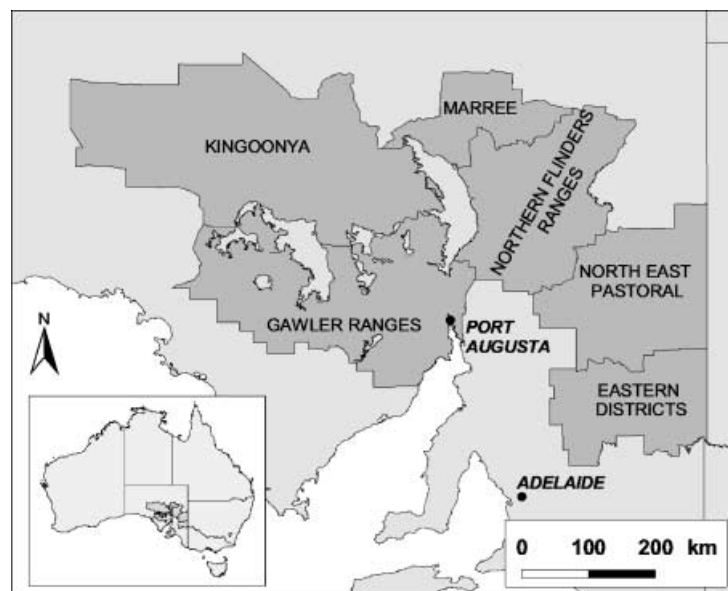


Fig. 1. Map showing the six management regions of South Australia where the analysed data were collected.

Eastern Districts, Gawler, Kingoonya/Maree, and North Flinders Ranges/North-east Pastoral, referred to as areas 1, 2, 3 and 4, respectively. The pooled regions border each other and have similar rainfall statistics.

Kangaroos are shot throughout the year and the carcasses are brought to nearby refrigeration units or dealer sites throughout the pastoral zone. The density (individuals km⁻²) of kangaroos harvested on properties in South Australia each year were determined from shooter and dealer returns collated by the South Australian government conservation agency (currently the Department for Environment and Heritage). Records of harvested kangaroos were available only for the State as a whole in 1978 and 1979. Therefore, the proportion of the State total that was shot in each region in 1980 was used to apportion the State total in 1978 and 1979. The number of red kangaroos harvested in each region between consecutive aerial surveys was used in the analysis.

We used rainfall data from each of the management areas collected during the 12-month period prior to the start of the winter census. Rainfall during this period has been found to have the best positive correlation with the population rate of change of red kangaroos between two censuses following this 12-month period of rain, at least on the broad spatial scale of the whole pastoral zone in South Australia (McCarthy 1996).

Sheep are the predominant domestic stock in the South Australian pastoral zone, with cattle run mostly on properties in the north of the zone. Mean annual numbers of sheep and cattle on properties in the pastoral zone were determined from graziers' stock returns collated by the South Australian government department responsible for primary industries (currently Department of Water, Land and Biodiversity Conservation). Cattle numbers were converted to dry sheep equivalents by multiplying by eight, the conversion factor recommended by the Department of Water, Land and Biodiversity Conservation in South Australia (Reid 1990). Henceforth, we refer to the combined mean as Dry Sheep Equivalents (DSE), which will be expressed as a density (km⁻²).

METHODS OF ANALYSIS

(a) Background to kangaroo modelling research

Several different models of macropod populations have been developed (reviewed by Cairns 1989) and the focus of most studies has been to document a general impact of (time-lagged) rainfall on population rate of change in the red kangaroo (e.g. Caughley, Bayliss & Giles 1984; Bayliss 1985a,b; Cairns & Grigg 1993; McCarthy 1996). Rainfall is a proxy for pasture growth and biomass and is important for predicting fluctuations in kangaroo populations. In the pastoral zone of South Australia, initial data analysis (Cairns & Grigg 1993) found that red kangaroo populations respond to rainfall at short time-lags on the scale of single management areas of 20 000–40 000 km⁻². However, a

longer lagged effect of rainfall was found using a longer time series on a broad scale across the entire South Australian pastoral zone (McCarthy 1996).

Statistical density dependence (i.e. a relationship between population rate of change and density) was detected on a broad scale covering the entire pastoral zone of South Australia (McCarthy 1996), but the processes underlying that pattern are not fully understood. Whereas intraspecific competition for food may seem to be a logical explanation, one must also consider that kangaroos compete with sheep and cattle (Edwards 1989). The conventional wisdom is that domestic livestock density has a marked influence on the long-term density of kangaroos, but only a negligible effect on their short-term dynamics (Caughley 1987). In other words, domestic herbivore density should not affect the rate of change of kangaroos. However that has not been shown statistically. In this paper we explore different models for the impact of domestic herbivore density on kangaroo population dynamics at the regional scale.

(b) Models

Let $N_{i(t)}$ be the kangaroo population density (individuals km⁻²) in area i at time t for $i = \{1,2,3,4\}$ corresponding to Eastern Districts, Gawler, Kingoonya/Maree, and North Flinders Range/North-east Pastoral, respectively. We assume the mapping of density from one year to the next is described by a multivariate stochastic Ricker model (Dennis *et al.* 1998) including harvesting (H), rainfall (R) and the DSE density (S) as covariates. Hence, the full model can be written

$$N_{i(t)} = N_{i(t-1)} e^{(a_i + b_i N_{i(t-1)} + c_i R_{i(t-1)} + d_i S_{i(t-1)} - H_{i(t)} + E_{i(t)})}, \quad \text{eqn 1}$$

where a_i and b_i are constants for each area i , often referred to as a drift or location parameter and statistical density dependence, respectively. We assume the dynamics are influenced by a regionally and time-dependent environmental random variable $E_{i(t)}$ that is drawn from a multivariate normal distribution with mean zero and variance-covariance matrix Σ . The parameters c_i and d_i capture the local response to rainfall and DSE in each area. To be able to compare the response to kangaroo density, rainfall and DSE across the areas, we standardized these time series to zero mean and unit variance.

$H_{i(t)}$ is the instantaneous harvest mortality in area i between winter in year $t - 1$ and winter in year t calculated as

$$H_{i(t)} \approx -\ln \left(1 - \frac{C_{i(t)}}{\sqrt{N_{i(t-1)} N_{i(t)}}} \right), \quad \text{eqn 2}$$

where $C_{i(t)}$ is the total number of harvested animals per km² in each area i between consecutive aerial surveys. To approximate the annual harvest fraction, we have to divide $C_{i(t)}$ by the geometric mean of population density in year $t - 1$ and t because harvesting is not a

discrete event and population density is estimated only once every year (see Cairns & Grigg 1993). By not fitting a coefficient to the harvest term, we are assuming that the effect of harvesting is constant for a given population-growth rate, and the population-growth rate was simply adjusted for harvest rate (i.e. we assumed the coefficient was one). Estimating a coefficient (other than 1) would be seeking the level of compensation (< 1) or perhaps superadditivity (> 1) in harvesting in addition to the density dependence that was modelled, and the effect of harvesting is not the focus of this paper.

Finally, we also consider a different model structure motivated by the theory of ratio-dependent consumer–resource interactions (Arditi & Ginzburg 1989) and a previous study on red kangaroo dynamics in South Australia (McCarthy 1996). This second model is

$$N_{i,t} = N_{i,t-1} e^{\left(a_i + b_i \frac{N_{i,t-1}}{R_{i,t-1}} + d_i \frac{S_{i,t-1}}{R_{i,t-1}} - H_{i,t} + E_{i,t} \right)}, \quad \text{eqn 3}$$

where b_i is now the regression coefficient with respect to the ratio of kangaroo density and rainfall (i.e. not standardized as above), d_i is the regression coefficient with respect to the ratio of DSE and rainfall. These ratios were standardized to mean zero and unit variance to facilitate the comparison across areas.

(c) *Parameter estimation and model selection*

The stochastic multivariate Ricker model with covariates (equation 1) can be considered a hybrid between an ecological and a statistical model in the sense that the parameters have an ecological interpretation, but the model can be expressed as a statistical time-series model on a logarithmic scale. If we define $\ln(N) \equiv X$, we can write equation 1 as a multivariate first-order nonlinear autoregression (NLAR) model (Tong 1990) with linear covariates on the log-scale:

$$\mathbf{X}_{(t)} = \mathbf{X}_{(t-1)} + \mathbf{a} + \mathbf{N}_{(t-1)}\mathbf{b} + \mathbf{R}_{(t-1)}\mathbf{c} + \mathbf{S}_{(t-1)}\mathbf{d} - \mathbf{H}_{(t)} + \mathbf{E}_{(t)}, \quad \text{eqn 4}$$

where the boldface indicates that the parameters and data have vector (\mathbf{a} , \mathbf{b} , \mathbf{c} , \mathbf{d} , $\mathbf{H}_{(t)}$ and $\mathbf{E}_{(t)}$ are column vectors) or matrix ($\mathbf{N}_{(t-1)}$, $\mathbf{R}_{(t-1)}$ and $\mathbf{S}_{(t-1)}$ are diagonal matrices) structure. The likelihood function for a multivariate NLAR with Gaussian error structure is presented in Dennis *et al.* (1998) and the log-likelihood, which was used for estimating the unknown parameters, can be written as

$$\ln L(\mathbf{a}, \mathbf{b}, \mathbf{c}, \mathbf{d}, \Sigma) = -0.5mq \ln(2\pi) - 0.5q \ln(|\Sigma|) - 0.5 \sum_{t=1}^q \mathbf{Z}'_t \Sigma^{-1} \mathbf{Z}_t, \quad \text{eqn 5}$$

where \mathbf{Z}_t is a vector of residuals at time t , m is the number of areas ($m = 4$) and all sums are from time $t = 1$ to $t = q$ ($= 25$). We obtain maximum-likelihood estimates of the unknown parameters by minimizing

the negative log-likelihood ($-\ln L(\mathbf{a}, \mathbf{b}, \mathbf{c}, \mathbf{d}, \Sigma)$) using the Nelder–Mead simplex algorithm (Press *et al.* 1994). For a more detailed explanation of the multivariate normal likelihood function, see Dennis *et al.* (1998).

We calculate the likelihood for each of a set of candidate models where equations 1 and 3 describe the full models assuming either additive (equation 1) or ratio-dependent (equation 3) effects of density and rainfall. We confront models with and without a term for density dependence and/or DSE, but harvesting, rainfall and a location parameter were included in all models. Each model could be further classified as having population-specific or global parameter values and the variance-covariance matrix had either zero or non-zero off-diagonal elements. Model selection was guided by the information-theoretic approach and we used the Akaike Information Criteria corrected for small sample size, AIC_c (Burnham & Anderson 1998; p. 51) to rank the alternative models. We ignored observation error because we have no *a priori* reason to assume that the magnitude of the observation error should differ among the alternative models, and relative differences should therefore remain similar (LaMontagne *et al.* 2002).

Finally, we undertook a residual analysis of the best model as determined by the smallest AIC_c value to make sure that the residuals were approximately normally distributed and not strongly serially correlated. For this purpose, one can treat the residuals from the four areas as approximately independent (Tong 1990). We performed Lilliefors test for goodness of fit to a normal distribution at the $\alpha = 5\%$ level (Conover 1980), and we analysed the residuals for autocorrelation by estimating the partial autocorrelation function. The critical value of the partial autocorrelation coefficient is considered significantly differently from zero at the 5% level if it is greater than $|2/\sqrt{n}| = 0.408$, where n is the length of the residual vector (Chatfield 1999).

Results

Inspection of the time series of kangaroo density in the four regions (Fig. 2a) shows that the four populations do not fluctuate independently. However, they are not as correlated to each other as their biotic and abiotic environments are correlated across regions, as indicated by the temporal dynamics of DSE (i.e. sheep and cattle), rainfall and the annual harvest fraction (Fig. 2b–d, Table 1). When confronting a set of alternative models, the most parsimonious model turned out to have a drift parameter and a parameter for statistical density dependence common to all areas, dry sheep equivalents as a covariate, and a variance-covariance matrix with non-zero off-diagonal elements (Table 2). Remember that rainfall and harvest were included in all models. This model provided a reasonable fit (see Fig. 3) and the assumption of normally distributed errors could not, according to Lilliefors test, be rejected in any of the four areas: Area 1 ($D^* = 0.12$, $P > 0.2$), Area 2 ($D^* =$

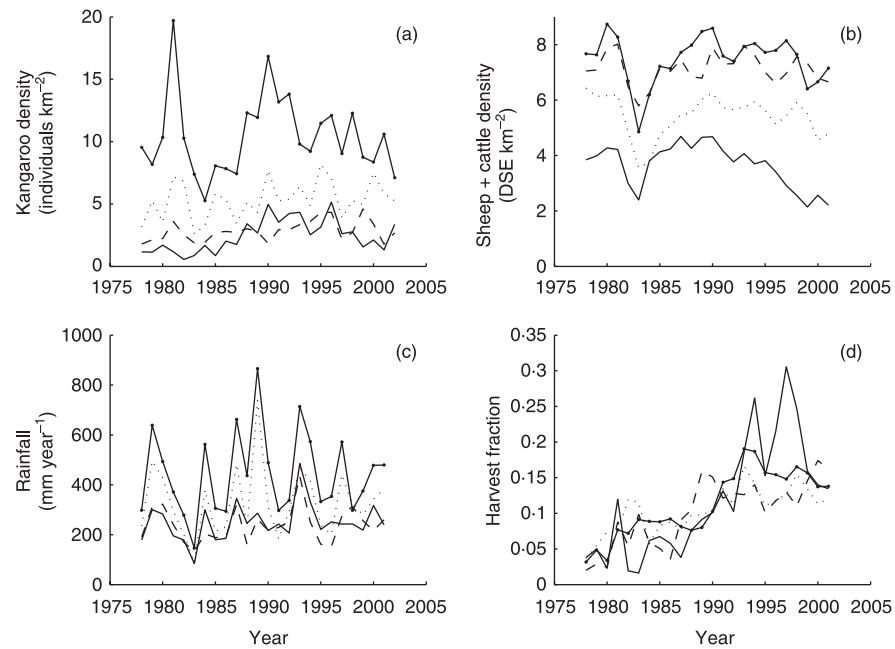


Fig. 2. The observed dynamics of (a) red kangaroo density (individuals km^{-2}), (b) sheep plus cattle density as dry sheep equivalents (DSE km^{-2}), (c) rainfall during the 12-month period prior to the first winter census of kangaroo, and (d) the annual harvest fraction. The four areas are Eastern Districts (solid lines), Gawler (dashed lines), Kingoonya/Maree (dotted lines), and North Flinders Range/North-east Pastoral (solid lines with dots).

Table 1. Spatial correlation of red kangaroo density, domestic herbivore density (as Dry Sheep Equivalent, DSE), rainfall and harvest fraction. $\text{Corr}(i, j)$ refers to the correlation between the time series in area i and j . Area 1–4 correspond to Eastern Districts, Gawler, Kingoonya/Maree, and North Flinders Range/North-east Pastoral, respectively

	Corr(1,2)	Corr(1,3)	Corr(1,4)	Corr(2,3)	Corr(2,4)	Corr(3,4)
Kangaroo density	0.32	0.38	0.39	0.49	0.19	0.51
Sheep + cattle (as DSE)	0.44	0.47	0.62	0.78	0.71	0.84
Rainfall	0.75	0.66	0.78	0.67	0.63	0.94
Harvest fraction	0.58	0.68	0.82	0.67	0.70	0.86

Table 2. Alternative models, number of estimated parameters (K), log-likelihood ($\log L$), Akaike Information Criteria corrected for small sample size (AIC_c), AIC_c differences ($\Delta_i = \text{AIC}_{c_i} - \min \text{AIC}_c$) and Akaike weights (w_i) for the models where $w_i > 0.01$. The Σ sign (variance-covariance matrix) refers to models where the covariance in error structure is estimated. All other models assume that the variance-covariance matrix is diagonal (i.e. no covariances)

Model	Log L	K	AIC_c	Δ_i	w_i
$a + bN + cR + dS - H, \Sigma$	44.6	14	-56.1	0	0.53
$a + bN + cR + dS - H$	35.7	8	-53.7	2.4	0.16
$a + bN + cR + d_i S - H, \Sigma$	47.5	17	-53.1	2.9	0.12
$a + bN + cR + d_i S - H$	38.4	11	-51.6	4.4	0.06
$a + bN + c_i R + dS - H, \Sigma$	46.2	17	-50.5	5.6	0.03
$a + bN + c_i R + dS - H$	37.3	11	-49.5	6.6	0.02
$a + b_i N + cR + dS - H, \Sigma$	45.2	17	-48.5	7.6	0.01

0.07, $P > 0.2$), Area 3 ($D^* = 0.12$, $P > 0.2$), Area 4 ($D^* = 0.09$, $P > 0.2$). There were no indications of serially correlated residuals in areas 1, 2 or 3, but the second order partial autoregressive coefficient, r_2 , in area 4 exceeded the critical value: Area 1 ($r_1 = -0.24$, $r_2 = 0.11$), Area 2 ($r_1 = 0.14$, $r_2 = -0.022$), Area 3 ($r_1 = -0.037$, $r_2 = -0.27$), Area 4 ($r_1 = -0.13$, $r_2 = -0.44$). However, the proportion of the variation, R^2 , explained by the

best model varied from 0.07 in Kingoonya/Maree to 0.6 in Northern Flinders/North-east Pastoral, with intermediate values, 0.2, in Eastern Districts and Gawler.

The second best model was identical to the best model except that the variance-covariance matrix was diagonal (i.e. the populations were considered to be independent). The sum of the Akaike weights for the two most parsimonious models was about 0.7; hence,

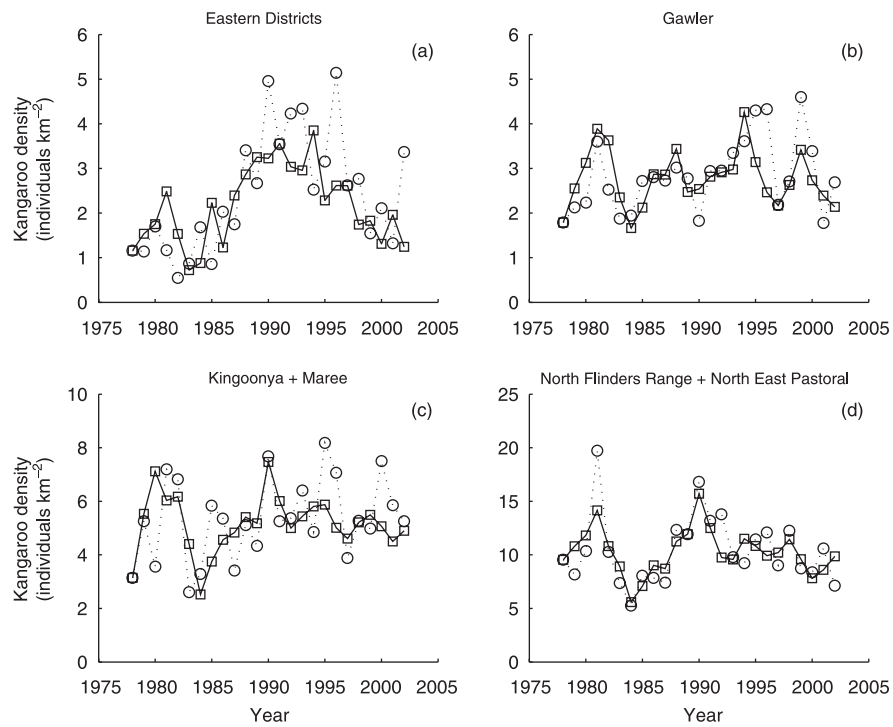


Fig. 3. The observed time series of red kangaroo density (dotted lines with circles) and the fit of the most parsimonious model (solid line with squares) for the 4 different areas.

Table 3. Maximum likelihood estimates, 95% confidence intervals, and the variance-covariance matrix when fitting the most parsimonious model $\ln\{N_{i,t}\} - \ln\{N_{i,t-1}\} = a + bN_{i,t-1} + cR_{i,t-1} + d\Sigma_{i,t-1} - H_{i,t} + E_{i,t}$ to time-series data on red kangaroo density (individuals km^{-2}) in each area i between 1978 and 2002. The parameter a is the drift parameter, b is the strength of density dependence, c is the regression coefficient with respect to rainfall, and d is the regression coefficient with respect to the density of dry sheep equivalents. All predictor variables were standardized to zero mean and unit variance. We assume that the process error has a multivariate normal distribution with a mean vector of zero and a variance-covariance matrix Σ . Correlations are given in boldface in the lower triangular of Σ

Area	a	b	c	d	Σ			
E districts	0.10	-0.25	0.088	0.13	0.26	0.05	0.01	-0.01
Gawler	0.10	-0.25	0.088	0.13	0.40	0.05	0.03	0.01
Kingoonya/Maree	0.10	-0.25	0.088	0.13	0.11	0.51	0.08	0.02
N Flinders R/NE Pastoral	0.10	-0.25	0.088	0.13	-0.11	0.16	0.50	0.03
Boundary of 95% CI								
Upper	0.038	-0.30	0.011	0.061				
Lower	0.16	-0.20	0.16	0.21				

there was strong evidence of a common dynamic structure across areas as well as an impact of DSE on the population-growth rate in the red kangaroo. Unexpectedly, the regression coefficient with respect to DSE was positive rather than the negative we would expect for competing species. Because both rainfall and DSE were standardized we can compare the corresponding regression coefficients. The positive effect of DSE on the kangaroo population-growth rate was in fact even stronger than the effect of rainfall. The maximum likelihood estimates of all parameters in the best model are given in Table 3. There was no support for ratio-dependence (Akaike weights = 0); in fact, there were 10 alternative additive models that were more parsimonious than the best ratio-dependent model.

Discussion

The sheep rangelands of southern Australia constitute a grazing system where the erratic fluctuations of rainfall and kangaroo abundance have influenced the way many ecologists think about population dynamics in large herbivores. This system has provided the inspiration for the 'mechanistic paradigm' of population-growth rate (Sibly & Hone 2002) and an emphasis on the relationship between population-growth rate and resource availability (Caughley 1976, 1987; Cairns & Grigg 1993). The general idea is that density-dependent mortality regulates population density through food-shortage (Sinclair, Dublin & Borner 1985) and, hence, the only effect of population density is to reduce the amount of available resources (see review by Bayliss & Choquenot

2002). This idea has sparked a research programme where per capita population-growth rate is assumed to be a function of available resources rather than previous population densities; the latter being the approach in classical studies of density dependence (e.g. Turchin 1999). In this paper we attempted to blend the mechanistic paradigm and classical studies of density dependence, using a time series longer than previously available for kangaroos.

Despite some model uncertainty (Table 2), there was no evidence of ratio-dependence. Models without a separate term for density dependence were not supported at all. Instead, there was strong support for region-independent density dependence (b) and the same location parameter (a). The lagged rainfall, which has been used as a surrogate for resources in previous studies, did not account for the observed feedback structure. This is in agreement with McCarthy (1996) who studied the effect of density dependence and rainfall assuming that the red kangaroos inhabiting South Australia's pastoral zone make up a single large and uniform population. The strong support for global parameter values across the four areas (i.e. no area-specific parameter values) suggests that the spatial difference in average kangaroo density between the areas (Fig. 2a) is most likely due to spatial variation in the average level of the covariates (Fig. 2b–c). Hence, rainfall, sheep and cattle density vary between areas, but populations respond to that variation in a similar way. This in turn suggests that the population structure in the four regions is not different enough to generate spatial variation in the demographic response to variation in resource abundance. What did differ among the regions, however, was the proportion of the variation explained by the best model. We conclude that a 'best model' is not necessarily a good model, but it is not clear why we explained as much as 60% in one area and only 7% in another area.

When we initiated this study, we believed that sheep and cattle densities would have a negative effect on the rate of change of red kangaroos, generating an effect not accounted for by the resource proxy. However, the effect of sheep and cattle on population rate of change in kangaroos was positive rather than negative. Does this mean that grazing by sheep and cattle has facilitative effects? No, not necessarily. One has to realize that pastoralists control sheep and cattle densities and it makes perfect sense for them to increase the sheep and cattle densities when grazing conditions are favourable. If rainfall is a good surrogate for resources, then we should be able to pick up the effect of competition. The positive effect of DSE on kangaroos suggests the contrary, and it seems that we do not yet have a clear understanding of how resource availability should be modelled in this system. This view is further supported by our results showing the occurrence of density dependence obviously not captured by the rainfall data, and the fact that there was still evidence of spatially correlated residuals (Table 2) despite the inclusion of all known sources of population synchrony in this grazing system

(Table 1). Dispersal could potentially generate spatially correlated residuals, but there is no evidence of dispersal of the magnitude required for the spatial scale studied here (Priddel 1987; Croft 1991; Norbury, Norbury & Oliver 1994). More likely, we have missed an aspect of resource dynamics that is not captured by the rainfall included in the models. Future studies may show that including another rain period will solve the problem but that remains to be proven. Also, future work should explore the possibility of nonlinear effects of rainfall. How abiotic conditions work their way through the individuals to the dynamics of a population is indeed a general problem, and potentially important to our understanding of population declines observed in, for example, South African large herbivores (Ogutu & Owen-Smith 2003).

Given that kangaroo dynamics in the sheep rangelands have been studied for a long time and there exists a theory for how rainfall drives the kangaroo dynamics by generating fluctuations in the resource abundance (Caughley 1987), the conclusion that we still do not know how to approximate resource availability may seem a bit surprising. However, previous studies have focused on one or a few processes at a time, which sometimes give the false impression that we understand more than we do, especially if different processes can generate identical patterns in data (Jonzén *et al.* 2002a; Jonzén, Ripa & Lundberg 2002b). Our conclusions should alert ecologists working in less well-known systems to think carefully about what demographic and environmental processes are operating and how these processes could be expressed in mathematical terms. Only then can we get an idea about whether our models and hypotheses are supported by empirical observations.

We find ourselves in the crossfire between the proponents of models that explicitly consider resource–herbivore interactions (e.g. Choquenot & McLeod 1997) and the more pragmatic view motivated by the difficulties of measuring the resources and estimating functional relationships between the two trophic levels (e.g. Sæther 1997). We have followed the more pragmatic view, but our results indicate that we must think more carefully about the mechanistic relationships between sheep, cattle, kangaroos and their resources. Hence, if we are ever going to understand how demographic processes interact with environmental fluctuations, we need to go much further than simply model patterns in data. This calls for rigorous treatment of the problems, an understanding of the stochastic nature of the phenomena we are studying, and an embracing of flexible stochastic models with strong theoretical underpinning that can be confronted with all available relevant data.

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