Statistical modelling of the population dynamics of a raptor community in a semi-desert environment

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Summary
1. We performed an extensive statistical modelling study on the population fluctuations and population growth rates of 15 raptor species in the Kalahari desert in South Africa.
2. The correlation pattern between rainfall and population abundance changed systematically with raptor body weight and diet type. The abundance of heavier raptors feeding on larger prey-items had lower correlations with rainfall than lighter raptors feeding on small prey-items. Whereas raptor species feeding on small prey-items were more affected by immediate rainfall, species feeding on large prey-items were more affected by rainfall in the previous year.
3. Population abundances were explained most parsimoniously by direct and delayed density dependence and rainfall during the current and previous breeding season. Interspecific competition was never a predictor variable. Population abundances of species best described by rainfall fed on larger prey-items than population abundances of species best described by density dependence.
4. Population growth rates were always best described by direct density dependence. The strength of density dependence was positively correlated with reproduction rate, due mainly to Falconiform species having higher reproduction rates than Accipitrid species.
5. Shifting from the species to the guild level, we found that abundance and biomass shares of feeding guilds did not vary significantly over time, supporting the hypothesis of guild constancy.

Key-words: community, density dependence, population abundance and growth rate, rainfall, raptor, statistical modelling.

Introduction
A central theme in ecology is to understand the factors causing temporal fluctuations in the population density of organisms (Elton 1927; Nicholson 1933; Andrewartha & Birch 1954; Lack 1954, 1966; Royama 1992; Begon, Harper & Townsend 1996). Population fluctuations can be caused by density-dependent factors in a direct or delayed manner (May 1986; Dennis & Taper 1994; Ellner & Turchin 1995; Ferrer & Donazar 1996; Stenseth 1999), competition with other species (Hansen et al. 1999a) or density-independent factors such as weather (Andrewartha & Birch 1954; Kostrzewa & Kostrzewa 1990; Post & Stenseth 1999), or a complex combination of factors (Steenhof, Kochert & McDonald 1997; Lewellen & Vessey 1998a,b; Krüger & Lindström 2001a). The relative importance and type of effect these factors exert on populations has important implications for theoretical ecologists as well as conservation biologists (Ginzburg, Ferson & Akçakaya 1990; Allen, Schaffer & Rosko 1993; Krüger & Lindström 2001a,b). For example, the strength and type of density dependence will have a profound influence on the survival time of a given population (Stacey & Taper 1992).

A substantial literature exists on population dynamics in relation to density dependence and weather (Hörnfeldt 1994; Leirs et al. 1997; Forchhammer et al. 1998; Coulson, Milner-Gullard & Clutton-Brock 2000), especially on small rodents (Bjørnstad, Falck & Stenseth 1995; Hansen et al. 1999a; Hansen, Stenseth...
& Henntonen 1999b; Lima, Keymer & Jaksic 1999; Madsen & Shine 1999; Stenseth 1999). Notably, very few studies have addressed the dynamics of predator populations (but see Steenhof et al. 1997, 1999; Fryxell et al. 1999; Stenseth et al. 1999; Krüger & Lindström 2001a) and these studies focused on single species.

This long-term study of population fluctuations of an entire raptor community has several advantages besides the fact that long-term data sets for predator communities are scarce. First, annual data might not be appropriate to reveal processes for species with several generations per year (Lewellen & Vessey 1998a), but all raptor species breed only once per year. In addition, the detection of density dependence is usually easier in species with long life-spans (Holyoak & Baillie 1996). Raptors are also more likely to be affected by interspecific competition, due to their trophic level (Schoener 1983), a factor which has been largely ignored in modelling studies on population dynamics (Hansen et al. 1999a). Finally, rainfall has been shown to affect the principal prey species of many raptors (especially in semi-arid areas, Sheppe 1972; Crowe 1978; Cheeseman & Delany 1979; Jaksic et al. 1997; Madsen & Shine 1999; Steenhof et al. 1999), hence rainfall might be an appropriate surrogate for food abundance. Overall, there are good a priori reasons to expect all three factors, intra- and interspecific competition and weather, to be important for the population abundance and population growth rate of a given raptor species.

Data for an entire community also offer the possibility to assess the relative importance of these factors on population fluctuations. This tackles not only the question of which factors influence the dynamics of a given species, but also which factors drive the dynamics of the whole community. Thiollay (2000) has proposed several hypotheses affecting population abundances in a West African raptor community, but in the semi-arid Kalahari it is believed that rainfall is the overly dominant factor driving many processes (Liversidge 1994).

Here we modelled the population dynamics of each raptor species separately by an information-theoretic approach. We then looked if there is a pattern emerging across species. A priori, we formulated predictions based on general ecological theory:

1. Migrant raptor species should be more likely to be affected by rainfall than resident species, because they are not territorial and move with the fluctuating food abundance.

2. Species with many competitors should be more likely to be affected by interspecific competition than species with few competitors (Schoener 1983).

3. The scope and strength of density dependence should be higher in species with a high reproduction rate, because density dependence can ultimately only operate via changes in birth and death rates (Bjornstad et al. 1995).

4. Systematic changes in relation to diet: (a) larger prey-items show a longer lag between abundance and rainfall, thus species feeding on larger prey-items are more prone to be affected by delayed rainfall and species feeding on small prey-items are more likely to be affected by direct rainfall; (b) larger prey-items are more mobile and hence have a greater ability to move with rainfall, thus species feeding on larger prey-items are more prone to be affected by rainfall than species feeding on small prey-items.

Materials and methods

Data collection

The study was undertaken in Kalahari National Park, South Africa (25°17’S and 20°32’E) from 1973 to 1992. This southern section of the vast Kalahari ecosystem is the most arid part and receives 200–250 mm of rainfall per year, but this with high variability. The area experiences a hot, wet summer season (October–April) and a cold, dry winter season (May–September). The habitat is an undulating terrain of red sand dunes covered with sparse grass and shrubs and Acacia erioloba as the dominant tree species. For a detailed description of the area, see Liversidge (1984). The abundance of 15 raptor species (11 resident and four migrant species, see Table 1) was determined annually in the wet season by road counts totalling 11 141 km, performed always by the same observer over the same route. Each year, at least 1 week was spent in the area and counts were made over several days (3–20 days each year) with transect distances of 500 km each year. Driving speed was around 20 km/h and all raptors within 500 m of the road were included. The exceptionally good visibility in the open habitat facilitated very accurate identification of raptors (Liversidge 1984). We also used the monthly precipitation from January to April recorded within the park.

Statistical analysis

Before analysis, the abundances of all raptor species were transformed (logX + 0.1). Because no data were available for 1987 and 1990, we replaced these missing years by the overall species-specific mean. This avoids the problem of strengthening an existing pattern, which happens with moving averages. We also checked the robustness of our results by performing the analyses including the first 14 years only and results did not change qualitatively. Before modelling, we explored the time-series and looked for correlations with rainfall and statistical density dependence using the randomization test of Pollard, Lakhani & Rothery (1987).

As population abundances are generally governed by birth and death processes which operate in a multiplicative manner (Bjornstad et al. 1995), these processes will therefore be additive on a log scale, allowing the application of additive statistical models. To check whether the time-series were stationary (Royama 1992; Chatfield 1996), we looked at trends and changes in

variation over time. None of the 15 species showed a significant linear or non-linear trend over time (rank correlation coefficients, \( r \), between population abundance and time were all far from significance), so we did not detrend the data. Also, the amplitude of all time-series did not fluctuate greatly over time.

We modelled the population abundance \( X_t \), using previous densities \((X_{t-1}, X_{t-2})\) as well as population growth rate \( R_t = (X_{t+1} - X_t) \), also using previous population densities \((X_t, X_{t-1})\). Other explanatory variables included rainfall \((\text{Rain}_{t-1}, \text{Rain}_{t-2})\) and the abundance of interspecific competitors \((C_{t-1}, C_{t-2})\). The model for population abundance did not include an intercept. For each raptor species, a diet value was calculated using information for South Africa given in Brown, Urban & Newman (1982) and del Hoyo, Elliott & Sargatal (1994). The diet value was calculated as a weighted average between six categories (1 = insects, 2 = reptiles, 3 = rodents, 4 = birds, 5 = larger mammals and birds, 6 = game carrion), aligned to reflect ascending prey size. We used non-parametric analyses based on rank for this variable. According to the main prey category, each species was also assigned to one ecological feeding guild (see Table 1). The number of interspecific competitors was hence calculated as the sum of all other raptor species in the same feeding guild. This approach is simplistic, as it does not consider the effect of dominance hierarchies on a species within a feeding guild, related normally to body size (Basset 1996). We also could not consider predation adequately as none of the 15 species is caught regularly by any other raptor species surveyed.

For candidate model selection, we looked at the autocorrelation structure in each time-series. Autocorrelation coefficients were never significant after lag two, hence we included only direct and delayed density dependence. The same was carried out for rainfall and interspecific competitors, so we used six explanatory variables. We also identified one important interaction term \((\text{weather}_{t-1} \times \text{density}_{t-1})\) resulting in 126 candidate models for each species for both population abundance and population growth rate. Model performances were compared using the Akaike Information Criterion (Akaie 1973) corrected for small sample sizes and referred to as AICc (Hurvich & Tsai 1989; Burnham & Anderson 1998), calculated from least square regression residuals. As AICc penalizes the model for every free parameter used, it renders it possible to compare models of different complexity and hence avoid overfitting (Burnham & Anderson 1998). The autocorrelation structure of residuals was checked using Box–Pierce tests (Cromwell, Labys & Terraza 1994); models with residuals differing from the assumption of a white noise process were invalid (Pindyck & Rubinfeld 1991).

Finally, we looked at the entire community, performing a hierarchical cluster analysis to look for synchrony between raptor time-series. The dendrogram was based on a squared Euclidian distance matrix in SPSS. We also tested whether the different feeding guilds fluctuated significantly over time. We used an ANOVA model with the 20 years as repeated measures and tested whether the abundance or biomass share (both arcsin squareroot transformed prior to analysis) fluctuated significantly between feeding guilds and over time.

### Results

#### Abundance Patterns

The abundance of the entire raptor community fluctuated between 10 and 131 raptor individuals per 100 km survey distance. The total abundance showed no trend over time \((r = -0.004, \text{d.f.} = 18, P = 0.993)\) or a correlation with rainfall \((r = -0.003, \text{d.f.} = 18, P = 0.994)\). The two most common species were *Gyps africanus* and *Accipitridae*.
Melierax canorus. The mean number of individuals per 100 km transect distance is given in Table 1 with the standard deviation. Mean abundances were not related to body weight \((r = 0.015, \text{d.f.} = 13, P = 0.159)\) or diet value \((r = 0.424, n = 15, P = 0.116)\) and there was also no difference in mean abundance between resident and migrant species \((F_{1,13} = 1.258, P = 0.282)\). As can be seen from Table 1, variation between years was marked in some species. However, the amount of interannual variation was not related to body weight \((r = 0.016, P = 0.955)\) or diet value \((r = 0.017, P = 0.952)\), but migrant species showed a significantly higher interannual variability than resident species \((F_{1,13} = 6.513, P = 0.024)\).

Of the 15 species, two \((Polihierax semitorquatus\) and \(Falco rupicoloides\)) showed a significant positive correlation between abundance and rainfall and three others \((Melierax canorus, Circaetus cinereus and Aquila nipalensis\) exhibited a positive trend. The abundance–rain correlation changed in a systematic manner with body weight and diet value (Fig. 1a,b). The heavier the raptor species, the weaker and more negative the abundance–rain correlation became \((r = -0.608, P = 0.016)\). This might be due to diet value, because the larger the prey items, the weaker and more negative the abundance–rain correlation became \((r = -0.516, P = 0.048)\). Of the 15 species, three \((M. canorus, C. cinereus\) and \(A. nipalensis\) showed a significant positive correlation between abundance and rainfall in the previous year. Differences between the correlation coefficients between abundance and direct and delayed rainfall were not random: for species feeding on small prey-items the correlation was higher with direct rainfall, whereas it was higher for delayed rainfall in species feeding on large prey-items (Fig. 1c, \(r = 0.750, P = 0.001\)). There was no significant association with body weight \((r = 0.459, P = 0.086)\), and the correlation between diet type and rainfall correlation difference was not caused by body weight (partial correlation controlling for body weight \(r = 0.539, \text{d.f.} = 12, P = 0.048\)). Resident and migrant species did not differ in the strength of the abundance–rainfall correlation \((F_{1,13} = 0.261, P = 0.618)\).

The randomization test showed that 14 of 15 species exhibited negative statistical density dependence, that is years with a high density were followed by years with a lower density and vice versa. The fifteenth species, \(A. nipalensis\), showed a negative trend \((P < 0.1)\). The strength of the density dependence was not related to body weight \((r = 0.122, P = 0.666)\) or diet value \((r = 0.036, P = 0.899)\) and there was also no difference between resident and migrant species \((F_{1,13} = 0.942, P = 0.349)\).

**Fig. 1.** Scatterplots between the correlation coefficient between rain and population abundance and body weight \((a)\) and diet type \((b)\). Scatterplot between the difference in the correlation coefficients between abundance and direct and delayed rain and diet type \((c)\).

**Modelling population abundances**

Modelling the population abundance produced most parsimonious models, explaining between 16% and 78% of the variation in population abundances (as indicated by \(R^2\)). Neither body weight \((r = -0.288, P = 0.298)\) nor diet value \((r = 0.199, P = 0.476)\) or reproduction rate \((r = 0.369, P = 0.176)\) were correlated with the amount of variation explained, so models did not become weaker for heavier species or species feeding on larger prey items. In addition, there was no correlation between mean abundance and the amount of variation explained \((r = 0.075, P = 0.792)\) nor between the interannual variation and the amount of variation explained \((r = 0.141, P = 0.615)\). Thus, models did not become systematically weaker for scarcer species or species showing lower interannual variation. The quality of models (as indicated by \(R^2\) also did not differ between resident and migrant species \((F_{1,13} = 0.568, P = 0.464)\). Models always included only one explanatory variable (Table 2). Direct density dependence was selected for three, delayed density dependence for four, direct rainfall for one and delayed rainfall for seven species. The abundance of interspecific competitors was never selected as the most parsimonious model explaining population abundances. For some species,
Table 2. Results of the autoregressive modelling of population abundance $X_t$ and population growth rate $R_t$ for each species. $\Delta \text{AICc (min)}$ is the minimal Akaike Information Criterion value and $\Delta \text{AICc}$ gives the difference to the second best model. The term $1 + \beta_1$ gives the coefficient of direct density dependence affecting $R_t$.

<table>
<thead>
<tr>
<th>Species</th>
<th>Best model $X_t$</th>
<th>$\Delta \text{AICc (min)}$</th>
<th>$\Delta \text{AICc}$</th>
<th>$R_t^2$</th>
<th>Best model $R_t$</th>
<th>$\Delta \text{AICc (min)}$</th>
<th>$\Delta \text{AICc}$</th>
<th>$1 + \beta_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$S. serpentarius$</td>
<td>$X_{t-1}$</td>
<td>$-9.293$</td>
<td>1.967</td>
<td>0.658</td>
<td>$X_{t-1}$</td>
<td>$-10.570$</td>
<td>1.703</td>
<td>$-0.939$</td>
</tr>
<tr>
<td>$P. semitorquatus$</td>
<td>$X_{t-2}$</td>
<td>$-9.512$</td>
<td>2.052</td>
<td>0.559</td>
<td>$X_{t-1}$</td>
<td>$-7.962$</td>
<td>1.185</td>
<td>$-1.237$</td>
</tr>
<tr>
<td>$P. bellicosus$</td>
<td>$\text{Rain}$</td>
<td>$-9.267$</td>
<td>1.337</td>
<td>0.520</td>
<td>$X_{t-1}$</td>
<td>$-6.482$</td>
<td>1.831</td>
<td>$-0.877$</td>
</tr>
<tr>
<td>$M. canorus$</td>
<td>$\text{Rain}$</td>
<td>$-7.068$</td>
<td>0.080</td>
<td>0.700</td>
<td>$X_{t-1}$</td>
<td>$-4.330$</td>
<td>1.289</td>
<td>$-0.736$</td>
</tr>
<tr>
<td>$G. afric anus$</td>
<td>$\text{Rain}$</td>
<td>$3.416$</td>
<td>0.180</td>
<td>0.440</td>
<td>$X_{t-1}$</td>
<td>$0.806$</td>
<td>2.949</td>
<td>$-1.182$</td>
</tr>
<tr>
<td>$T. trachelol tus$</td>
<td>$\text{Rain}$</td>
<td>$-2.438$</td>
<td>0.029</td>
<td>0.180</td>
<td>$X_{t-1}$</td>
<td>$0.364$</td>
<td>2.267</td>
<td>$-0.091$</td>
</tr>
<tr>
<td>$F. rupicoloides$</td>
<td>$\text{Rain}$</td>
<td>$-10.296$</td>
<td>0.820</td>
<td>0.367</td>
<td>$X_{t-1}$</td>
<td>$-7.393$</td>
<td>2.488</td>
<td>$-1.040$</td>
</tr>
<tr>
<td>$T. ecaudatus$</td>
<td>$\text{Rain}$</td>
<td>$-12.159$</td>
<td>0.530</td>
<td>0.501</td>
<td>$X_{t-1}$</td>
<td>$-8.656$</td>
<td>1.408</td>
<td>$-0.980$</td>
</tr>
<tr>
<td>$A. rapax$</td>
<td>$\text{Rain}$</td>
<td>$-5.913$</td>
<td>0.050</td>
<td>0.478</td>
<td>$X_{t-1}$</td>
<td>$-6.814$</td>
<td>2.853</td>
<td>$-1.097$</td>
</tr>
<tr>
<td>$E. caeruleus$</td>
<td>$X_{t-2}$</td>
<td>$-4.005$</td>
<td>2.185</td>
<td>0.275</td>
<td>$X_{t-1}$</td>
<td>$0.825$</td>
<td>1.151</td>
<td>$-1.205$</td>
</tr>
<tr>
<td>$C. pectoralis$</td>
<td>$X_{t-2}$</td>
<td>$-6.084$</td>
<td>0.016</td>
<td>0.160</td>
<td>$X_{t-1}$</td>
<td>$-3.486$</td>
<td>0.616</td>
<td>$-0.961$</td>
</tr>
<tr>
<td>$F. biarmicus$</td>
<td>$\text{Rain}$</td>
<td>$-4.862$</td>
<td>0.772</td>
<td>0.400</td>
<td>$X_{t-1}$</td>
<td>$-1.583$</td>
<td>1.891</td>
<td>$-1.053$</td>
</tr>
<tr>
<td>$F. tinnunculus$</td>
<td>$X_{t-2}$</td>
<td>$-12.081$</td>
<td>1.597</td>
<td>0.783</td>
<td>$X_{t-1}$</td>
<td>$-10.265$</td>
<td>2.016</td>
<td>$-1.425$</td>
</tr>
<tr>
<td>$C. cinereus$</td>
<td>$X_{t-1}$</td>
<td>$-7.344$</td>
<td>1.282</td>
<td>0.473</td>
<td>$X_{t-1}$</td>
<td>$-5.571$</td>
<td>0.105</td>
<td>$-0.590$</td>
</tr>
<tr>
<td>$A. nipalensis$</td>
<td>$X_{t-1}$</td>
<td>$-1.785$</td>
<td>0.300</td>
<td>0.418</td>
<td>$X_{t-1}$</td>
<td>$-0.497$</td>
<td>0.124</td>
<td>$-0.662$</td>
</tr>
</tbody>
</table>

The second most parsimonious model was nearly as good as the best model (Table 2), as indicated by the $\Delta \text{AICc}$ value (a value of two in $\Delta \text{AICc}$ is considered to be statistically significant, Burnham & Anderson 1998). However, in most cases, the second best model also involved the variable of the best model plus a second one.

We grouped species into the density dependence pool (combining direct and delayed density dependence) or the rain pool (combining direct or delayed rain affecting population abundances) in order to look for differences explaining why some species were rainfall affected whereas others were density-driven. The best model type was not related to phylogeny (excluding *Sagittarius serpentarius*, $F_{1,12} = 0.101$, $P = 0.756$), hence differences between species affected by rain or by density are not an artefact of phylogeny. These two groups did not differ significantly in body weight (Fig. 2a, $F_{1,11} = 1.711$, $P = 0.214$), but did in diet (Fig. 2b, $U$-test, $Z = 2.269$, $P = 0.021$). Species with abundance fluctuations best described by density dependence fed on smaller prey types than those species whose abundance fluctuations were best described by rain. Reproduction rate did not differ between the two groups (Fig. 2c, $F_{1,13} = 0.016$, $P = 0.902$). Also, there was no difference between residents and migrants in the type of most parsimonious model ($F_{1,13} = 1.727$, $P = 0.212$).

**MODELLING POPULATION GROWTH RATES**

Before modelling population growth rates, we constructed a log-linear autoregressive model of order two (see Fig. 3 legend for equation details). The dynamic properties of this model are well understood (Brochwell & Davis 1991; Royama 1992; Stenseth 1999). Parameter combinations outside the triangle lead to extinction, those within indicate population persistence. Above the semicircle and to the left of the vertical line, populations exhibit strong direct density dependence and to the right of the vertical line they are stable. Below the semicircle, populations exhibit a multi-annual cycle (Royama 1992; Bjørnstad et al. 1995;...
Stenseth 1999). As can be seen from Fig. 3, all raptor species were located above the semicircle and to the left of the vertical line, which indicates strong direct density dependence affecting the population growth rate when other variables such as weather and competition are not included.

For all 15 species, the most parsimonious model explaining population growth rate was indeed direct density dependence. These models explained between 31 and 70% of the variation in population growth rate. In comparison with the models explaining population abundances, those for population growth had significantly higher $\Delta AICc$ values ($F_{1,28} = 4.257, P = 0.047$).

The strength of the direct density dependence parameter $1 + \beta_1$ was not significantly correlated with either body weight ($r = 0.152, P = 0.589$) or diet value ($r = 0.094, P = 0.739$), but was significantly negatively correlated with reproduction rate (Fig. 4a, $r = -0.583, P = 0.023$). Inspecting Fig. 4a indicates that the distribution of reproduction rates is rather bimodal. This is caused by phylogeny; the four species with the highest reproduction rates belong to the family Falconidae, whereas the other (except for S. serpentarius) belong to the family Accipitridae. Comparing the strength of the direct density dependence parameter of the 15 species with regard to the two families reveals a significant difference ($F_{1,12} = 4.829, P = 0.048$) and the two taxonomic groups also differ in reproduction rate ($F_{1,28} = 180.985, P < 0.0001$). The difference in the direct density dependence parameter was not significant between resident and migrant species ($F_{1,13} = 0.393, P = 0.542$).

COMMUNITY-LEVEL ANALYSIS

At community level, we looked first at synchrony between population fluctuations. The dendrogram in Fig. 5 shows that time-series of species were clustered with no reference to phylogeny. However, three of the four migrant species were closely clustered and $F_{1,12} = 4.829, P = 0.048$ and the two taxonomic groups also differ in reproduction rate ($F_{1,28} = 180.985, P < 0.0001$). The difference in the direct density dependence parameter was not significant between resident and migrant species ($F_{1,13} = 0.393, P = 0.542$).

Within the park (R. Liversidge, unpublished observation). The two existing main clusters did not differ in body weight ($t_{13} = 0.973, P = 0.348$), feeding guild ($t_{13} = 1.490, P = 0.160$) or reproduction rate ($t_{13} = 0.087, P = 0.932$).

A breakdown of abundance and biomass shares by feeding guild is given in Table 3. The dominating guilds in terms of abundance were rodent- and carrion-feeders, while the carrion-feeders were by far the dominating guild in terms of biomass share (because of the two vulture species being both abundant and, more important, very heavy). As can be seen from Table 3, mean abundance and biomass shares differ mainly between the insectivores and carrion-feeders, while the other three guilds have similar abundance and biomass shares. Fluctuations over time are marked in the five feeding guilds and are shown in Fig. 6. However, there was no significant difference in abundance share among the feeding guilds ($F_{4,10} = 0.881, P = 0.508$) and none of the guilds showed significant differences over

### Table 3. Mean abundance and biomass shares (SE in parentheses) of the five feeding guilds

<table>
<thead>
<tr>
<th>Feeding guild</th>
<th>Abundance share</th>
<th>Biomass share</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insects</td>
<td>6.3 (1.1)</td>
<td>0.7 (0.2)</td>
</tr>
<tr>
<td>Reptiles</td>
<td>15.8 (2.2)</td>
<td>18.5 (3.7)</td>
</tr>
<tr>
<td>Rodents</td>
<td>30.0 (3.3)</td>
<td>14.8 (2.9)</td>
</tr>
<tr>
<td>Birds and mammals</td>
<td>16.0 (2.0)</td>
<td>10.4 (1.4)</td>
</tr>
<tr>
<td>Carrion</td>
<td>32.0 (5.3)</td>
<td>55.6 (5.9)</td>
</tr>
</tbody>
</table>

time (insectivores: $F_{19,19} = 1.21, P = 0.299$, reptilivores: $F_{19,57} = 1.21, P = 0.353$, rodent-feeders: $F_{19,57} = 1.11, P = 0.366$, bird- and mammal-feeders: $F_{19,38} = 1.47, P = 0.153$, carrion-feeders: $F_{19,19} = 1.61, P = 0.155$). With regard to biomass share, there was also no significant difference between guilds ($F_{4,10} = 3.311, P = 0.057$).

With the exception of the bird- and mammal-feeders ($F_{19,38} = 2.01, P = 0.033$), there was no significant difference over time in biomass share (insectivores: $F_{19,19} = 1.49, P = 0.144$, reptilivores: $F_{19,57} = 1.26, P = 0.265$, rodent-feeders: $F_{19,57} = 1.53, P = 0.122$, carrion-feeders: $F_{19,19} = 0.92, P = 0.573$). Thus, although there are fluctuations over time, the overall guild structure is constant. To test for an effect of rainfall on the guild constancy over time, we calculated correlations between the abundance and biomass shares and rainfall levels. Rainfall levels were only significantly correlated with the abundance and biomass share of rodent-feeders ($r = 0.538, P = 0.014$ and $r = 0.446, P = 0.049$, respectively) but not with any of the other guilds.

**Discussion**

The results of our analyses have supported some but not all of our a priori predictions. Migrant species were not more likely to be described best in their population abundances by rainfall than by density dependence (Prediction 1) and also they did not differ in the strength of density dependence affecting the population growth rate. There seems to be some similarity in their population fluctuation however, as indicated by the cluster analysis. They were also more variable between years than resident species, which is predicted by ecological theory. As interspecific competition was never chosen as a explanatory variable for any of the species, our prediction that the number of competing species should be correlated with the importance of interspecific competition (Prediction 2) is not supported either.

In contrast, our prediction that the strength of density dependence should be inversely related to reproduction (Prediction 3) is strongly supported by our results. The direct density dependence parameter was highly significantly correlated with reproduction rate, due very probably to phylogenetic inertia. As closely related species tend to be more similar in terms of life history or ecology (Harvey & Pagel 1991), the difference in reproduction rate we found between the two families Accipitrinae and Falconidae might reflect their evolutionary past rather than a present ecological adaptation (see also Krüger 2000).

With regard to predictions concerning the interplay between diet type and rainfall our first prediction (Prediction 4a), that species feeding on small prey-items should be affected by direct rainfall whereas species feeding on large prey-items are more affected by previous rainfall, is not unequivocally supported. The differences between the correlation patterns between abundance and rainfall in the first year and between abundance and the previous year lent support to the prediction, but the modelling has shown that only in one species (*Polemaetus bellicosus*) was rainfall of the same year chosen, and this raptor hunts the largest prey of any species (Brown *et al.* 1982). In the other seven species where rainfall was the most parsimonious model, it was always the rainfall of the previous year and the species span the entire range of prey sizes. This finding is in contrast to Korpimäki (1994), who found that avian predators in Fennoscandia tracked the changing abundance of their prey with no time lag and Fryxell *et al.* (1999), who found no time lag between Marten (*Martes americana*) population growth rate and prey abundance.
We found clear support for our last prediction (Prediction 4b) that species feeding on large prey-items are more rainfall-driven than species feeding on small prey-items which are more likely to be density-driven. It is well known that in many African semi-arid ecosystems, bird and mammal populations move with rainfall over vast distances (Sinclair & Arcese 1995). In contrast, many of the raptor species feeding on large prey-items are territorial and hence rainfall within their territory will increase their food supply dramatically. Although this is also true for the food sources of raptor species capitalizing on smaller prey, they are fluctuating in their abundance much more than species feeding on large prey-items, due probably to higher reproduction and mortality rates (see also Fig. 4). Hence they have a much higher scope for population regulation through density dependence. Indeed, two common strategies for birds in semiarid regions are nomadism or rapid reproduction (Liversidge 1984). Although territoriality limits nomadism in many raptor species (but see the social system of vultures), many species feeding on large prey-items have very large territories and select suitable hunting patches within them. Korpimäki (1994) also found that the numerical response of avian predators to prey abundance took place via immigration and emigration. Small species might respond by

Fig. 6. Abundance (a) and biomass (b) share fluctuations of the five feeding guilds over time with rainfall data as a comparison (c).
rapid and high reproduction, which might trigger density-dependent effects via increased adult mortality or reduced chick survival which has been shown in raptors (Sulkava, Huhtala & Tornberg 1994; Ferrer & Donazar 1996).

Another overall feature of all models for population abundances and population growth rates was simplicity. None of the models had more than one explanatory variable. It is generally acknowledged that semi-arid ecosystems have a much lower degree of complexity than, i.e. tropical forests (Begon et al. 1996). Surprisingly for a semi-arid ecosystem, not all population abundances and no population growth rates seem to depend strongly on rainfall but on previous population density. We are the first to admit, however, that our approach relies on correlational support and cannot directly demonstrate density dependence (Royama 1992).

Another encouraging aspect of our model results is that there is no relationship between model quality and abundance, body weight or diet. Therefore a systematic bias due to these factors causing artefacts is unlikely to explain the patterns we have reported here. However, population fluctuations in some of the resident species might be caused largely by non-breeding individuals moving around, rather than density dependence. The strong territoriality of resident raptors make it unlikely that this is a sufficient explanation.

Finally, our results seem to indicate that although ecological feeding guilds fluctuate in their abundance and biomass share over time, there is a degree of guild constancy, i.e. overall, a particular feeding guild abundance or biomass share is not increasing or decreasing over time. We have to admit, however, that the statistical power of our guild analysis was limited due to only 15 species surveyed and we were only able to detect large fluctuations with our analyses. The guild constancy might be explained by the fact that all prey species are positively affected by rainfall and hence relative food abundance will be similar. The concept of guild constancy over spatial and temporal scales has been intensively debated, some studies suggesting that guilds are stable (Heatwole & Levins 1972; Lawton & Gaston 1989; Southwood 1996; Krüger & McGavin 2001), and some suggesting that they are not (Root 1973; Southwood, Moran & Kennedy 1982; Cornell & Kahn 1989). Some of these studies have also found constancy in biomass as we did, which is more important for resource partitioning in communities than abundance (Basset 1996). Although unpredictable rainfall is likely to cause variation over time, this study strengthens the idea of the importance of intrinsic processes in communities upon which weather stochasticity acts as a modifier (Southwood 1980).

Acknowledgements

Permission to carry out this study was kindly granted by the National Parks Board of South Africa. Financial support came from the McGregor Museum, South Africa, a Marie Curie Fellowship of the European Union and a Junior Research Fellowship from Churchill College, Cambridge to O.K. We are grateful for comments made by T. Coulson, M. Fowle and two anonymous referees which improved the manuscript.

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Population dynamics of a semi-desert raptor community


Received 7 August 2001; accepted 12 February 2002