

Rainfall in arid zones: possible effects of climate change on the population ecology of blue cranes

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Summary

1. Understanding the demographic mechanisms through which climate affects population dynamics is critical for predicting climate change impacts on biodiversity. In arid habitats, rainfall is the most important forcing climatic factor. Rainfall in arid zones is typically variable and unpredictable, and we therefore hypothesise that its seasonality and variability may be as important for the population ecology of arid zone animals as its total amount.
2. Here we examine the effect of these aspects of rainfall on reproduction and age specific survival of blue cranes (*Anthropoides paradiseus* Lichtenstein) in the semi-arid eastern Nama Karoo, South Africa. We then use our results to predict the effect of changes in rainfall at the population level.
3. Using combined capture-mark-resighting and dead-recovery models, we estimated average survival of cranes to be 0.53 in their first year, 0.73 in their second and third year, and 0.96 for older birds.
4. We distinguished between three seasons, based on the blue cranes' breeding phenology: early breeding season, late breeding season and nonbreeding season. Cranes survived better with increasing rainfall during the late but not early breeding season. Based on road counts and success of monitored nests, reproduction was positively associated with rainfall during the early but not late breeding season.
5. A matrix population model predicted that population growth rate would increase with increasing rainfall. A stochastic analysis showed that variation in early breeding season rainfall increased population growth slightly due to the nonlinear relationship between rainfall and reproduction. This effect was opposed by the effect of variation in late breeding season rainfall on survival and overall, variation in rainfall had a negligible effect on population growth.
6. Our results allow predictions to be made for a range of climate-change scenarios. For example, a shift in seasonality with drier springs but wetter summers would likely decrease reproduction but increase survival, with little overall effect on population growth.

Key-words: capture-mark-recapture, climate forcing, environmental stochasticity, Leslie matrix, ring recovery

Introduction

Many animal populations are clearly affected by climatic variability (e.g. Sæther *et al.* 2000; Coulson *et al.* 2001; Altwegg *et al.* 2005; Grosbois *et al.* 2008). However, relatively little is known about environmental forcing in arid regions, where variable and unpredictable rainfall is the dominating environmental variable (Noy-Meir 1973). In a recent review of bird

studies, Sæther *et al.* (2004) found that rainfall during the breeding season was an important determinant of population size in the few arid zone birds that have been studied. Survival of migratory birds can depend on rainfall in their dry wintering grounds (e.g. Cave 1983; Kanyamibwa *et al.* 1990; Dugger *et al.* 2004), and breeding activity in resident arid-zone birds depends on rainfall (Maclean 1970; Immelmann 1973; Lloyd 1999). Beyond this, the demographic mechanisms that relate climatic variation to population dynamics in arid zone birds are poorly understood.

To improve such an understanding, two interconnected issues need to be considered. (i) It may not only be important

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Fig. 1. Blue crane (*Anthropoides paradiseus* Lichtenstein) in the semi-arid eastern Nama Karoo, South Africa. Photographer: Mark Anderson.

how much rain falls, but also during which season it falls and how variable it is. These three aspects of rainfall, amount, seasonality and variability are all changing under climate change (Easterling *et al.* 2000; Tadross *et al.* 2005). A change in seasonality may be important for population dynamics if rainfall affects different fitness components depending on season. Variability generally decreases the population growth rate (Tuljapurkar 1982), but this depends on the exact relationship between the environmental variable (in our case rainfall) and the population growth rate (Drake 2005). (ii) The effect of the environment on populations can be buffered by a species' life-history if the most susceptible fitness components are least important for population growth (Pfister 1998; Morris *et al.* 2008). For populations of long-lived birds, for example, rainfall is more important if it affects adult survival than if it affects reproduction.

Here we examine the effect of the different aspects of rainfall on reproduction and age-specific survival in the eastern Nama Karoo population of blue cranes (*Anthropoides paradiseus*) (Fig. 1). Since survival and reproduction are not equally important for blue cranes' population dynamics, we gauge the overall effect of rainfall on population growth using a matrix population model. We then use the model to predict the response of blue cranes to different scenarios of climate change. The Nama Karoo is semi-arid and rain predominantly falls during the summer months (Desmet & Cowling 1999). Under climate change, our study area is predicted to receive slightly increased rainfall during the austral summer months, December to March (downscaled predictions of six General Circulation Models). Rainfall is also predicted to become more variable during this season. For the rest of the year the climate models either predict no change or disagree in their predictions (M. A. Tadross, personal communication; Midgley *et al.* 2005).

Material and methods

SPECIES AND STUDY AREA

The blue crane, a southern African endemic, has a distribution which is centred on South Africa's grassland, eastern Nama Karoo

and Overberg regions (Allan 2005). The eastern Nama Karoo population has been estimated to number *c.* 5800 birds (Allan 1993). The population has recently probably remained stable (Allan 2005), even though mortality due to poisoning and collision with power lines has kept it below historic levels (Anderson & Taljaard 2003).

Little is known about the age at first breeding in blue cranes. They probably reach sexual maturity at 3–5 years, but may start breeding later (Wilkinshaw 1963; McCann & Wilkins 1995). They usually lay two eggs, mainly between October and December (Allan 2005). Incubation lasts 30 days and the chicks fledge at about 12 weeks but remain near their parents for several months thereafter (Allan 2005). There is no previous information available on recruitment rates in the blue crane.

Our study took place in an area of *c.* 30 000 km² in the eastern Nama Karoo at the eastern end of the Northern Cape Province, South Africa (roughly between 29°45' S to 31°30' S and 23°30' to 25° E, Anderson & Taljaard 2003). Our study area is large in relation to movements of individual cranes (McCann *et al.* 2001), and only one bird has been resighted outside our study area (this record is not included in our analyses). The vegetation type of our study area is the Eastern Mixed Nama Karoo that reflects an extensive ecotone between the Nama Karoo Biome in the west and the Grassland Biome to the east (Low & Rebelo 1996). The Karoo is predominantly used for small stock farming, particularly sheep, and game farms.

RAINFALL

We examined rainfall effects during three distinct periods, characterised by the blue cranes' breeding phenology. (i) August to November leads up to the breeding season and includes mating and incubation. We expect weather during this time to affect the birds' body condition and possibly their decision whether or not to breed in a given year, and how many eggs to lay. We call this period the 'early breeding season'. (ii) The period from December to March covers the time of hatching, fledging and the early post-fledging period. In our study area, this is the main rainfall season and we expect this time to be critical for survival, especially of fledglings. We call this period the 'late breeding season'. (iii) The remainder of the year, April to July, is the nonbreeding season. Early-breeding-season rainfall ranged from 27.4 to 167.8 mm, late-breeding-season rainfall from 51.2 to 260.6 mm and nonbreeding season rainfall from 28.6 to 110.0 mm. There was no significant correlation among these rainfall variables (all $P > 0.4$). Rainfall was measured at the meteorological station at De Aar (30°40' S, 24° E) near the centre of our study area.

SURVIVAL

We estimated survival of blue cranes using combined capture-mark-resighting and ring recovery models (Burnham 1993). These methods separate the local survival rate from the probability of resighting an individual that is alive at a given time (resighting rate, Lebreton *et al.* 1992) and the probability of recovering a ring after the bird dies (recovery rate, Brownie *et al.* 1985).

A total of 451 cranes were ringed in the Northern Cape Province, South Africa, between 10 February 1997 and 12 April 2008. Seventeen of these birds were ringed as moulting adults, whereas the rest were ringed as chicks before they could fly. All birds were captured between November and early March, and we therefore estimated survival for the period from 1 November until 31 October in the following year. The first and the last year of the study were only 9 and 5 months long, respectively, and we adjusted the estimates so

Table 1. Summary of model selection for blue crane survival in the eastern Nama Karoo

	Model	QAICc	Δ QAICc	QAICc Weights	K	QDeviance
1	S(a3)P(y)r()	791.969	2.202	0.138	15	202.197
2	S(a2)P(y)r()	793.284	3.517	0.071	14	205.632
3	S(a4)P(y)r()	794.088	4.322	0.048	16	202.187
4	S(a3 + y)P(y)r()	803.836	14.070	0.000	26	190.176
5	S(a3)P(y)r(y)	806.638	16.871	0.000	26	192.978
6	S(a4)P(y)r(y)	808.862	19.095	0.000	27	192.978
7	S()P(y)r()	819.669	29.903	0.000	13	234.129
8	S(a3 + rain_{late breeding})	789.767	0.000	0.414	16	197.866
9	S(a3 × rain _{late breeding})	791.523	1.757	0.172	18	195.340
10	S(a3 + rain _{early breeding})	793.646	3.879	0.059	16	201.745
11	S(a3 + rain _{nonbreeding})	794.076	4.309	0.048	16	202.175
12	S(a3 × rain _{nonbreeding})	794.300	4.533	0.043	18	198.116
13	S(a3 × rain _{early breeding})	797.830	8.064	0.007	18	201.647

The models consist of three parts describing survival (S), resighting (P) and recovery (r) probabilities. We examined the effects of year (y) on all three components, and in addition the effect of age (four age classes: a4, three age classes: a3, two age classes: a2) on survival. Models 8–13 examine survival in relation to rainfall during three seasons. We consider rainfall to affect the two age classes equally (+), or differently (×, interaction between age and rain). The structure of the remaining components is as in model 1, which was the best model excluding rain. Model selection was based on Akaike's Information Criterion adjusted for overdispersion ($\hat{c} = 1.15$) and sample size (QAICc). A smaller value indicates a better model. Δ QAICc is the difference in QAICc between the current model and the best (in bold). QAICc weights give the relative support each model has compared to the others, and K is the number of parameters.

that they also correspond to annual survival rates. All birds were ringed with a numbered metal ring (South African Bird Ringing Unit) and a unique combination of colour rings, except for 17 small chicks, which only received a metal ring. The latter individuals could not be identified from resightings, but their rings could still be retrieved if they died. We therefore set the resighting probability for this group to zero, but otherwise treated them like the rest. During our study, 29 cranes were found dead and 51 cranes were resighted at least once.

We examined the effects of year on resighting, and recovery probabilities, and the effects of year and age on survival. We examined three alternative age effects, distinguishing between two age classes (1–3, 4 years and older), three age classes (1, 2–3, and 4 years and older) and four age classes (1, 2, 3, and 4 years and older). The adult birds ringed during moult were assumed to be 4 years or older. Burnham's (1993) approach also allows an estimation of site fidelity if recoveries are made outside the study area where individuals can be sighted or captured (e.g. Altwegg *et al.* 2003). In our case, however, recoveries and resightings were made in the same area. Accordingly, the fidelity parameter was estimated to be 1 and we did not further investigate it.

We started model selection from the model with age-dependent survival and year-dependent resighting and recovery rates, which was the most general model supported by our data (Model 6, Table 1). A year effect on survival was then examined with a simpler representation for the resighting and recovery rates. A goodness-of-fit test using the median- \hat{c} approach in program MARK 4.3 (White & Burnham 1999) showed that the starting model fitted our data well and overdispersion was low (estimated $\hat{c} = 1.15$, SE = 0.02). Nonetheless, we used this estimate to correct the confidence intervals of our parameter estimates and based model selection on Akaike's Information Criterion adjusted for overdispersion and sample size (QAICc, Burnham & Anderson 2002). All models were run in program MARK 5.1 (White & Burnham 1999). We then took the QAICc selected best model as a starting point, and examined a pos-

sible relationship between rainfall and survival by adding the rainfall covariates to the model (Lebreton *et al.* 1992).

REPRODUCTION

We examined the relationship between reproduction and rainfall using two separate data sets. The first data set consisted of standardised road counts along 36–72 (median = 55) transects of 20 km length each, and surveyed annually during the last Saturday in January, from 1997 to 2007. Observers counted and aged (as chick, fledged young or adult) all blue cranes seen along their route. Fledged young birds can be identified by their short tertiary feathers (adults have conspicuously long tertiaries), and are in their first year. We used the proportion of young and chicks in the total count as an index of reproduction. Young birds may be more difficult to detect than adults, and we therefore limited our analysis to observations made within 300 m to either side of the road. In the open habitat of our study area, cranes of all ages are clearly visible within this distance. The total count of cranes observed ranged from 30 to 301 per year.

The second data set consisted of observations of blue crane pairs with large chicks, 1–3 weeks from fledging. Ten to 87 of these crane families were observed per year in our study area. Blue cranes fledge either one or two chicks (Allan 2005), and we examined the proportion of broods fledging two chicks in relation to rainfall. One pair was observed with three chicks but we omitted this observation because the third chick may have been adopted from another pair.

We examined reproduction in relation to rainfall during the early and late breeding seasons, as used in the survival analysis. We analysed both data sets using generalised linear models with logit link function and binomial errors, implemented in procedure glm in program R 2.7.1 (R Development Core Team 2008). These methods implicitly account for the yearly variation in sample sizes. For each of the two data sets and rainfall variables we considered two models: (i) a linear (on the logistic scale) relationship, and (ii) a

quadratic relationship, and compared them to a model assuming no relationship between rainfall and reproduction. We used AICc to select the best models.

POPULATION GROWTH

We examined the population level effects of rainfall using a matrix population model. We assume a pre-breeding census, a 1-year projection interval, and that all cranes breed at 5 years of age (McCann & Wilkins 1995). The model is

$$n_{t+1} = An_t \quad \text{eqn 1}$$

where n_t is a vector holding the number of individuals in each stage at time t , and A is the population projection matrix:

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & F \times S_1 \\ S_2 & 0 & 0 & 0 & 0 \\ 0 & S_2 & 0 & 0 & 0 \\ 0 & 0 & S_3 & 0 & 0 \\ 0 & 0 & 0 & S_3 & S_3 \end{bmatrix} \quad \text{eqn 2}$$

In A we used the estimated survival rates for three age classes (s_1 , s_2 , s_3) from the best supported capture-mark-resighting model without rainfall covariates (Model 1, Table 1). F is the number of young (y) per adult (a) observed in the road counts, which we obtained from the fitted logistic regression. The logistic regression gives the proportion (P) of young in the total number ($y + a$) of cranes, rather than the number of young per adult. We calculated F as follows:

$$\frac{p}{1-p} = \frac{[y/(y+a)]}{[1-(y/(y+a))]} = \frac{y}{a} = F \quad \text{eqn 3}$$

The dominant eigenvalue of A is the asymptotic population growth rate λ , and we estimated the sensitivity of λ to variation in survival and reproduction at the mean observed values (Caswell 2001). We calculated confidence intervals for λ and the sensitivities using bootstrap methods as described in Altwegg *et al.* (2005). These confidence intervals evaluate the uncertainty in the estimates of λ due to the uncertainty in the time-constant survival and fecundity estimates. Then we calculated deterministic λ for combinations of summer rainfall and winter rainfall within the observed range and using the observed relationships between rainfall and the fitness components.

Our model does not include density dependence because we have no data on how the fitness components relate to density. However, blue crane densities in our study area were historically much higher (Anderson & Taljaard 2003), and we do not expect density dependence to be strong in this population at present.

To evaluate the effect of variation in rainfall on λ , we conducted stochastic simulations using the matrix model described in eqns 1–3. Following Morris and Doak (2002), we created matrix A_t by randomly selecting one of the 11 study years with complete data with probability 1/11 and by calculating the matrix entries from the observed relationships between fitness components and rainfall for that year. This retained the correlation structure among fitness components. There was no significant temporal autocorrelation in rainfall and we therefore did not consider such correlations, despite their potential importance in other cases (Tuljapurkar & Haridas 2006). We started the simulations with a population vector of $n_0 = 1$. This vector was left-multiplied 20 000 times by A_t . After discarding the first 2000 steps to eliminate transient dynamics, we calculated the stochastic population growth rate from total population sizes N as,

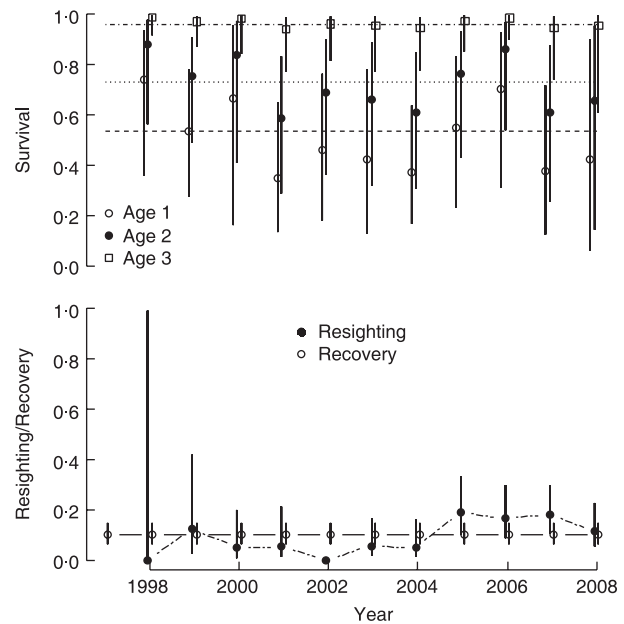


Fig. 2. Upper panel: survival of three age classes of blue cranes in the eastern Nama Karoo. The age classes are first year (1), second year and third year (2), and fourth year or older (3). The lines show average survival according to the best model excluding rainfall (Model 1, Table 1): age classes 1 (dashed line), 2 (dotted line), and age class 3 (dash-dotted line). The estimates from the more general year- and age-dependent model 4 (Table 1) are given with their 95% confidence intervals. Lower panel: resighting and recovery rates according to model 1. No resightings were made in 1998 and 2002.

$$\log \hat{\lambda}_s = \frac{1}{18\,000} \sum_{i=2001}^{20\,000} \log \left(\frac{N_{i+1}}{N_i} \right) \quad \text{eqn 4}$$

We examined three scenarios. In the first scenario, both survival and reproduction varied with rainfall. In scenarios two and three, only either survival or reproduction varied with rainfall, respectively, while the other fitness component was held constant at its mean. All three stochastic scenarios used the same sequence of the randomly chosen years. We compared the stochastic λ_s to the deterministic λ obtained by using the mean values for all fitness components. The whole procedure was repeated 100 times with a different sequence of randomly chosen years. All matrix calculations were performed in program R 2.7.1 (R Development Core Team 2008).

Results

SURVIVAL

Among the models without rainfall, model selection favoured a model that distinguished survival between three age classes, year-dependent resighting and constant recovery rate (Model 1, Table 1, Fig. 2). Models 2 and 3, distinguishing between two and four age classes, respectively, were also well supported. According to the best model, average survival of age class 1 (first year) cranes was 0.53 (95% confidence interval: 0.37 to 0.69), that of age class 2 (second and third year) cranes was 0.73 (0.59 to 0.84) and that of older cranes was 0.96 (0.88 to 0.99). The estimates from the model with

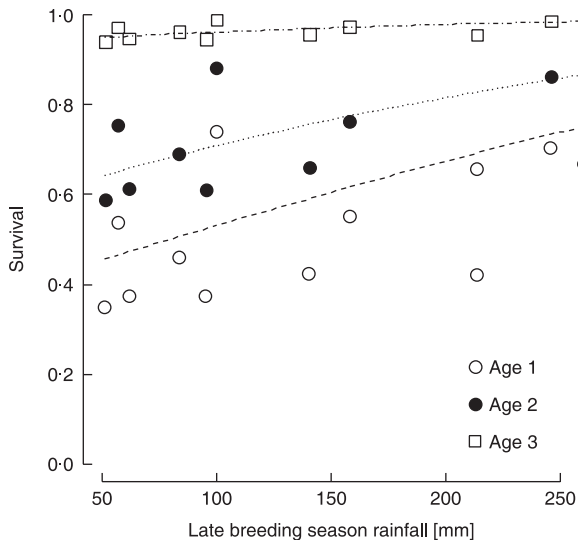


Fig. 3. Survival of blue cranes in relation to summer rainfall. The lines show the best fitting linear (on the logit scale) relationship between rainfall and survival (from model 8, Table 1). The relationship was $\text{logit}(\text{survival}) [\text{se}] = -0.484 [0.446] + 0.766 [0.483] \times \text{age2} + 3.100 [0.696] \times \text{age3} + 0.006 [0.003] \times \text{rainfall}$, where the indicator variable $\text{age2} = 1$ for age class 2, and $\text{age3} = 1$ for age class 3, and $\text{age2} = \text{age3} = 0$ otherwise. Note that these lines are parallel on the logit scale. For reference, we plot the annual survival estimates for the three age classes from model 4 (Table 1), which allowed for full year dependence.

lowest AICc value lead to a life expectancy at birth of 9.2 years (calculation followed Caswell 2001, p. 119).

Next, we examined survival in relation to rainfall. Including rainfall during the late breeding season as a covariate improved the model clearly (Model 8, Table 1), suggesting that blue cranes survived better in wetter years (Fig. 3). An analysis of deviance showed that rainfall during the late breeding season explained 36% of the yearly variation in survival ($F_{1,10} = 5.63$, $P = 0.039$). There was little evidence that the age classes reacted differently to late breeding season rainfall (model 9) and there was no evidence for an effect of rainfall during the other seasons on survival (models 10–13).

REPRODUCTION

More rainfall during the early breeding season was associated with a higher proportion of young cranes among the road counts during the subsequent year (Fig. 4, quadratic model AICc = 87.6, linear model AICc = 91.9 and constant model AICc = 142.0), and a higher proportion of broods with two chicks (Fig. 4, linear model AICc = 64.7, quadratic model AICc = 66.5 and constant model AICc = 68.5), even though the wettest year strongly influenced these results. We found no clear relationship between late breeding season rainfall and reproduction, where the constant model was nearly as good as or better than the models with rainfall as a covariate (Fig. 5, road counts: quadratic model AICc = 140.8, constant model AICc = 142.0, linear model AICc = 142.8; brood size: constant model AICc = 68.5, quadratic model AICc = 69.2 and linear model AICc = 70.2).

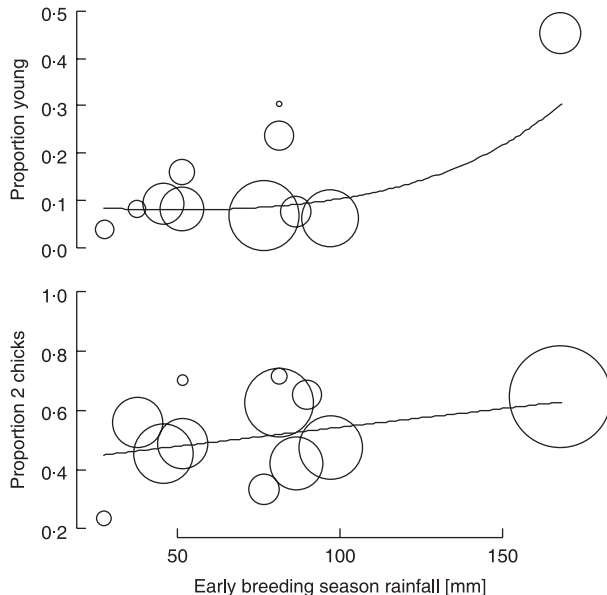


Fig. 4. Reproduction in blue cranes in relation to spring rainfall. The upper panel shows the proportion of young birds among cranes counted during road counts. The lower panel shows the proportion of broods with two chicks in a sample of broods close to fledging. Broods in our study area fledged either one or two chicks. The diameter of the circles is proportional to sample size, and the lines show the best fitting logistic regression lines. The equations were as follows: $\text{logit}(\text{proportion of broods with 2 young}) [\text{se}] = -0.32 [0.21] + 0.005 [0.002] \times \text{rainfall}$, and $\text{logit}(\text{proportion of young}) [\text{se}] = -2.16 [0.462] - 0.016 [0.010] \times \text{rainfall} + 0.00012 [0.00005] \times \text{rainfall}^2$.

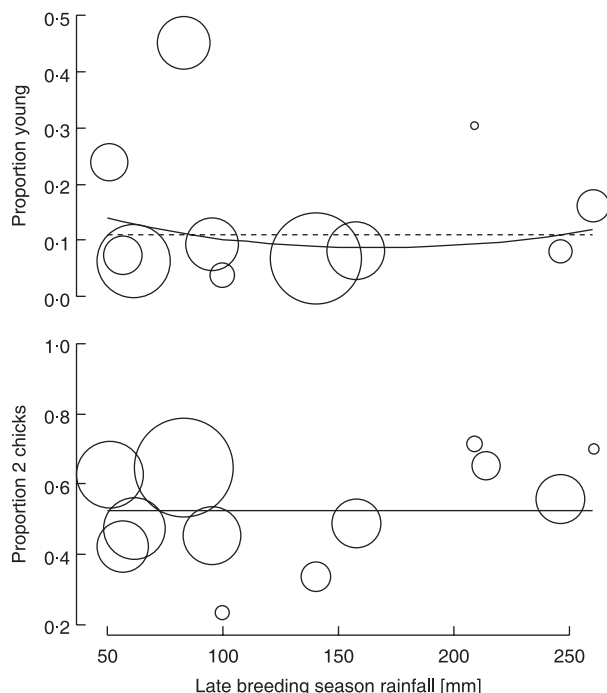


Fig. 5. Reproduction in blue cranes in relation to summer rainfall. See legend to Fig. 4 for details. The broken line in the upper panel shows the constant model, which was nearly as well supported as the quadratic one.

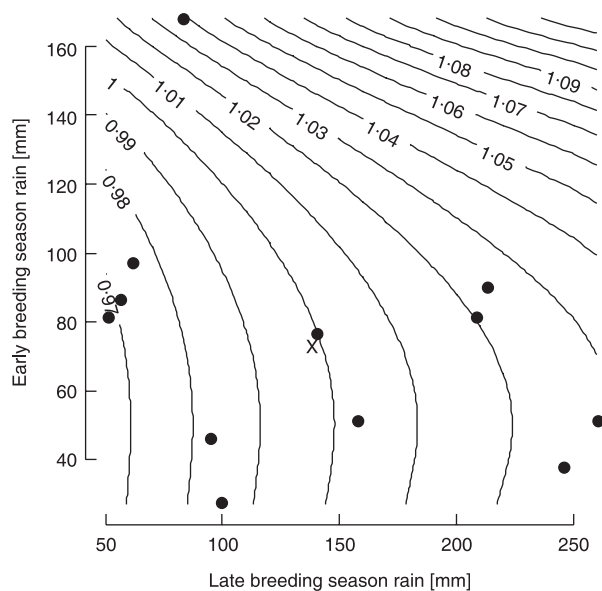


Fig. 6. Effect of early (y -axis) and late breeding season rainfall (x -axis) on the population growth rate λ . $\lambda > 1$ indicates a growing population and $\lambda < 1$ indicates a declining population. The contours show λ predicted by a matrix population model (eqns 1 and 2), based on the fitted relationships between rainfall and survival/reproduction (Figs 2–4). The graph is based on calculations of λ at all combinations of early and late breeding season rainfall, at 1 mm intervals. Dots show the observed rainfall for the 11 years of our study, and 'X' shows average rainfall over the study period.

POPULATION GROWTH

The asymptotic population growth rate (λ) obtained from the matrix population model (eqns 1 and 2) using the mean observed values for survival and reproduction from Model 1 (Table 1) was 0.994 (95% confidence interval: 0.878 to 1.030). Our result thus suggests that this population was stable, even though the confidence interval was wide. λ was most sensitive to variation in age class 3 survival (sensitivity: 0.930, CI: 0.900 to 0.949), less sensitive to variation in the number of young produced per adult (sensitivity: 0.302, CI: 0.189 to 0.407) and age class 2 survival (sensitivity: 0.101, CI: 0.081 to 0.127), and least sensitive to variation in age class 1 survival (sensitivity: 0.050, C: 0.040 to 0.063).

We then examined how late breeding season rainfall affected λ through its effect on survival (see Fig. 3), and how early breeding season rainfall affected λ through its effect on reproduction (see Fig. 4). The combined effect of early and late breeding season rainfall on λ is shown in Fig. 6. λ increased with rainfall in both seasons. However, λ increased at an accelerating rate with early breeding season rainfall (concave-up; increasingly steeper slope along the y -axis, Fig. 6), and at a decelerating rate with late breeding season rainfall (concave-down; decreasing slope along the x -axis).

The stochastic population growth rate λ_s for the scenario in which all fitness components varied with rainfall was nearly identical to the deterministic population growth rate λ (difference between λ_s and λ : -0.00005 , standard deviation for

the 100 runs with different yearly sequences: 0.00017). Stochasticity only in survival reduced the population growth slightly (-0.00026 , $sd = 0.00017$), whereas stochasticity only in reproduction increased the population growth rate (0.00146, $sd = 0.00019$) compared to the deterministic growth rate.

Discussion

We examined the effect of rainfall during different seasons on survival and reproduction of blue cranes living in the semi-arid eastern Nama Karoo region of South Africa. A wet early breeding season was followed by a high production of young, whereas rainfall during the late breeding season improved survival of blue cranes in all age classes. We need to gauge the relative importance of survival and reproduction on the population growth rate to predict the effect of changes in rainfall on blue crane populations. We used a simple matrix population model to do this. The model predicts population growth based on the observed relationships between rainfall and survival/reproduction. Using this approach, we examined the effects of three aspects of rainfall (and possible changes in each of them) on this population: (i) the total amount of rainfall; (ii) the seasonal pattern of rainfall; and/or (iii) the variability in rainfall. As a caveat we note that our study was based on 12 years of observations, which may not be enough to (repeatedly) observe infrequent extreme events. Such events can have a disproportionate impact on populations (Altwegg *et al.* 2006).

TOTAL RAINFALL

Our results showed that early and late breeding season rainfall positively covaried with blue crane population growth over the observed range, but the demographic mechanisms differed between the two seasons. Late breeding season rainfall improved blue crane survival (see Fig. 3). This is consistent with earlier studies showing that survival was positively related to rainfall in the arid overwintering areas of migrating birds (Cave 1983; Kanyamibwa *et al.* 1990). Our results further suggest that all age classes of blue cranes were affected by rainfall in similar ways, even though our sample sizes may have been too small to detect differences among the age classes. Earlier studies showed that different age classes generally differ in their susceptibility to environmental variation (ungulates, reviewed by Gaillard *et al.* 2000; reptiles: Altwegg *et al.* 2005; birds, e.g., Altwegg *et al.* 2006). The mechanistic link between rainfall and blue crane survival is probably through food abundance. The availability and abundance of the blue cranes' diet of bulbs, seeds, invertebrates and small vertebrates (Allan 2005) is largely dependent on the timing and amount of rainfall. An example is the brown locust *Locustana pardalina*, which during outbreaks (Todd *et al.* 2002) results in an abundant food source for blue cranes.

We found a positive relationship between reproduction in blue cranes and rainfall during the early but not late breeding season (see Fig. 4). Our results are consistent with earlier studies showing that many arid zone birds use rainfall as a

trigger for reproduction (Maclean 1970; Immelmann 1973) and that some species adjust their clutch sizes to the amount of rainfall received (Lloyd 1999), even though we do not know whether our results are caused by variation in clutch size or nestling mortality.

RAINFALL SEASONALITY

Early breeding season rainfall was related to reproduction and late breeding season rainfall was related to survival. Based on the matrix model, we predict that shifts towards more rainfall in summer and less rainfall in spring would increase survival at the expense of reproduction and not affect the overall population response markedly (see Fig. 6). The converse would be true for shifts from summer to spring rains. Nonbreeding season rainfall did not affect survival, and we do not expect it to affect breeding either because it is well outside the blue cranes' breeding season. We therefore expect a shift towards more rainfall during autumn and early winter at the expense of other seasons to have a mostly negative impact on blue crane populations.

RAINFALL VARIATION

Environmental variance generally lowers the population growth rate, which is a multiplicative process (Tuljapurkar 1982). However, in our case the relationship between early breeding season rainfall and population growth was concave-up, in which case variability can increase population growth. Both effects are manifestations of Jensen's inequality, a mathematical property of nonlinear relationships (Ruel & Ayres 1999; Drake 2005), and in our case they have opposite effects. Our stochastic simulations showed that these two effects were small and cancelled each other in the case of blue cranes affected by rainfall variability. The reason why the effects were small is that the population growth rate was most sensitive to age class 3 survival, which varied little. Overall, the stochastic growth rate was nearly identical to the deterministic one. Blue cranes appear to be relatively insensitive to inter-annual variation in rainfall over the observed range in rainfall variability. A small effect of environmental variability has been found in other long lived animals, such as red deer (Benton, Grant & Clutton-Brock 1995), but also in relatively short-lived barn owls (Altwegg, Schaub & Roulin 2007).

Climate change is expected to change the rainfall regime in many arid and semi-arid regions (Weltzin *et al.* 2003). Apart from the total annual rainfall, the seasonality of rainfall and the variance in the amount of rainfall may also change (Usman & Reason 2004; Tadross *et al.* 2005; New *et al.* 2006). In the region of our study, climate change scenarios predict slightly higher summer rainfall for 2050 (statistical downscaling of six general circulation models, M.A. Tadross, personal communication). Summer rainfall may also become more variable. During the rest of the year, the climate models either predict little change or disagree on the direction of change. Our results predict both positive and negative consequences for blue crane populations. On the one hand, increased

summer rainfall is predicted to improve survival. On the other hand, if the increased variability in rainfall leads to occasional dry years, long-term average survival may become lower than observed during our study. Given the uncertainty still associated with climatic predictions, it is not clear whether the net effect of climate change on blue crane populations will be positive or negative. Nevertheless, our study provides the basis for predicting population changes in blue cranes in response to a range of climate change scenarios, including potential changes in rainfall seasonality.

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References

- Allan, D.G. (1993) *Aspects of the Biology and Conservation Status of the Blue Crane Anthropoides Paradiseus, and the Ludwig's Neotis Ludwigii and Stanley's N. Denhami Stanleyi Bustards in Southern Africa*. University of Cape Town, Cape Town.
- Allan, D.G. (2005) Blue crane *Anthropoides paradiseus*. *Roberts-Birds of Southern Africa* (eds P.A.R. Hockey, W.R.J. Dean & P.G. Ryan), Vol. VII, pp. 309–311. The Trustees of the John Voelcker Book Fund, Cape Town.
- Altwegg, R., Roulin, A., Kestenholz, M. & Jenni, L. (2003) Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*. *Journal of Animal Ecology*, **72**, 391–399.
- Altwegg, R., Dummermuth, S., Anholt, B.R. & Flatt, T. (2005) Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. *Oikos*, **110**, 55–66.
- Altwegg, R., Roulin, A., Kestenholz, M. & Jenni, L. (2006) Demographic effects of extreme winter weather in the barn owl. *Oecologia*, **149**, 44–51.
- Altwegg, R., Schaub, M. & Roulin, A. (2007) Age-specific fitness components and their temporal variation in the barn owl. *American Naturalist*, **169**, 47–61.
- Anderson, M.D. & Taljaard, D. (2003). Eastern Karoo Precinct. *Big Birds on Farms: Mazda CAR Report 1993–2001* (eds D.J. Young, J.A. Harrison, R.A. Navarro, M.D. Anderson & B.D. Colahan), pp. 145–150. Avian Demography Unit, Cape Town.
- Benton, T.G., Grant, A. & Clutton-Brock, T.H. (1995) Does environmental stochasticity matter? Analysis of red deer life-histories on Rum. *Evolutionary Ecology*, **9**, 559–574.
- Brownie, C., Anderson, D.R., Burnham, K.P. & Robson, D.S. (1985) *Statistical Inference From Band Recovery Data – a Handbook*, 2nd edn. US Fish and Wildlife Service, Resource Publication 156, Washington, DC.
- Burnham, K.P. (1993) A theory for combined analysis of ring recovery and recapture data. *Marked Individuals in the Study of Bird Populations* (eds J.-D. Lebreton & P.M. North), pp. 199–213. Birkhäuser Verlag Basel, Switzerland.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. Springer, New York.
- Caswell, H. (2001) *Matrix Population Models*, 2nd edn. Sinauer, Sunderland, MA.
- Cave, A.J. (1983) Purple Heron survival and drought in tropical west Africa. *Ardea*, **71**, 217–224.
- Coulson, T., Catchpole, E.A., Albon, S.D., Morgan, B.J.T., Pemberton, J.M.,

- Clutton-Brock, T.H., Crawley, M.J. & Grenfell, B.T. (2001) Age, sex, density, winter weather, and population crashes in Soay sheep. *Science*, **292**, 1528–1531.
- Desmet, P.G. & Cowling, R.M. (1999) The climate of the Karoo – a functional approach. *The Karoo, Ecological Patterns and Processes* (eds W.R.J. Dean & S.J. Milton), pp. 3–16. Cambridge University Press, Cambridge.
- Drake, J.M. (2005) Population effects of increased climate variation. *Proceedings of the Royal Society B—Biological Sciences*, **272**, 1823–1827.
- Dugger, K.M., Faaborg, J., Arendt, W.J. & Hobson, K.A. (2004) Understanding survival and abundance of overwintering Warblers: Does rainfall matter? *Condor*, **106**, 744–760.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. (2000) Climate extremes: observations, modeling, and impacts. *Science*, **289**, 2068–2074.
- Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.
- Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Moller, A.P. & Weimerskirch, H. (2008) Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews*, **83**, 357–399.
- Immelmann, K. (1973) Role of the environment in reproduction as source of 'predictive' information. *Breeding Biology of Birds* (ed. D.S. Farner), pp. 121–147. National Academy of Sciences, Washington, DC.
- Kanyambwa, S., Schierer, A., Pradel, R. & Lebreton, J.D. (1990) Changes in adult annual survival rates in a western European population of the White Stork *Ciconia ciconia*. *Ibis*, **132**, 27–35.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.
- Lloyd, P. (1999) Rainfall as a breeding stimulus and clutch size determinant in South African arid-zone birds. *Ibis*, **141**, 637–643.
- Low, A.B. & Rebelo, A.G. (1996) *Vegetation of South Africa, Lesotho and Swaziland*. Department of Environmental Affairs & Tourism, Pretoria.
- Macleane, G.L. (1970) The breeding seasons of birds in the south-western Kalahari. *Ostrich*, **Suppl. 8**, 179–192.
- McCann, K. & Wilkins, H. (1995) *A Study of the Annual Biology and Movement Patterns of the Three Crane Species in the KwaZulu-Natal Midlands for the Purpose of Aiding the Selection of the Route for the Ariadne-Venus 400 kV Transmission Powerline*. Eskom & Endangered Wildlife Trust, KwaZulu, Natal, South Africa.
- McCann, K.I., Shaw, K., Anderson, M.D. & Morrison, K. (2001) Techniques for determining movement patterns of Blue and Wattle Cranes in South Africa—colour-ringing versus satellite telemetry. *Ostrich*, **15**, 104–108.
- Midgley, G.F., Chapman, R.A., Hewitson, B., Johnston, P., De Wit, M., Ziervogel, G., Mukheibir, P., von Niekerk, L., Tadross, M., Van Wilgen, B.W., Kgope, B., Morant, P.D., Theron, A., Scholes, R.J. & Forsyth, G.G. (2005) A status quo, vulnerability and adaptation assessment of the physical and socio-economic effects of climate change in the Western Cape, Rep. No. CSIR Report No. ENV-S-C 2005-073.
- Morris, W.F. & Doak, D.F. (2002) *Quantitative Conservation Biology*. Sinauer Associates Inc., Sunderland, MA.
- Morris, W.F., Pfister, C.A., Tuljapurkar, S., Haridas, C.V., Boggs, C.L., Boyce, M.S., Bruna, E.M., Church, D.R., Coulson, T., Doak, D.F., Forsyth, S., Gaillard, J.M., Horvitz, C.C., Kalisz, S., Kendall, B.E., Knight, T.M., Lee, C.T. & Menges, E.S. (2008) Longevity can buffer plant and animal populations against changing climatic variability. *Ecology*, **89**, 19–25.
- New, M., Hewitson, B., Stephenson, D.B., Tsiga, A., Kruger, A., Manhique, A., Gomez, B., Coelho, C.A.S., Masisi, D.N., Kululanga, E., Mbambalala, E., Adesina, F., Saleh, H., Kanyanga, J., Adosi, J., Bulane, L., Fortunata, L., Mdoka, M.L. & Lajoie, R. (2006) Evidence of trends in daily climate extremes over Southern and West Africa. *Journal of Geophysical Research—Atmospheres*, **111**, D(14).
- Noy-Meir, I. (1973) Desert ecosystems: environments and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Pfister, C.A. (1998) Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proceedings of the National Academy of Sciences*, **95**, 213–218.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*, 2.7.1 edn. R Foundation for Statistical Computing, Vienna, Austria.
- Ruel, J.J. & Ayres, M.P. (1999) Jensen's inequality predicts effects of environmental variation. *Trends in Ecology and Evolution*, **14**, 361–366.
- Sæther, B.-E., Tufto, J., Engen, S., Jerstad, K., Røstad, O.W. & Skåtán, J.E. (2000) Population dynamical consequences of climate change for a small temperate songbird. *Science*, **287**, 854–856.
- Sæther, B.E., Sutherland, W.J. & Engen, S. (2004) Climate influences on avian population dynamics. *Birds and Climate Change: Advances in Ecological Research*, **35**, pp. 185–209.
- Tadross, M.A., Hewitson, B.C. & Usman, M.T. (2005) The interannual variability of the onset of the maize growing season over South Africa and Zimbabwe. *Journal of Climate*, **18**, 3356–3372.
- Todd, M.C., Washington, R., Cheke, R.A. & Kniveton, D. (2002) Brown locust outbreaks and climate variability in southern Africa. *Journal of Applied Ecology*, **39**, 31–42.
- Tuljapurkar, S. (1982) Population dynamics in variable environments. III. Evolutionary dynamics of r selection. *Theoretical Population Biology*, **21**, 141–165.
- Tuljapurkar, S. & Haridas, C.V. (2006) Temporal autocorrelation and stochastic population growth. *Ecology Letters*, **9**, 324–334.
- Usman, M.T. & Reason, C.J.C. (2004) Dry spell frequencies and their variability over southern Africa. *Climate Research*, **26**, 199–211.
- Weltzin, J.F., Loik, M.E., Schwinning, S., Williams, D.G., Fay, P.A., Haddad, B.M., Harte, J., Huxman, T.E., Knapp, A.E., Lin, G., Pockman, W.T., Shaw, M.R., Small, E.E., Smith, M.D., Smith, S.D., Tissue, D.T. & Zak, J.C. (2003) Assessing the response of terrestrial ecosystems to potential changes in precipitation. *BioScience*, **53**, 941–952.
- White, G.C. & Burnham, K.P. (1999) Program MARK: Survival estimation from populations of marked animals. *Bird Study*, **46**, S120–139.
- Wilkinson, L.H. (1963) *Cranes of the World*. Winchester Press, New York.

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