

Climate change, variable colony sizes  
and temporal autocorrelation:  
consequences of living in changing  
environments

Ph.D. Thesis  
Monika Schwager

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Dept. of Plant Ecology and Nature Conservation  
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Institut für Biochemie und Biologie  
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Monika Schwager

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## Declaration

This thesis comprises three scientific studies, which cover different aspects of environmental change and population ecology. Chapter one is a modelling study which is entirely result of work that has been done by myself. Chapter two and three are a synthesis of field studies and modelling studies. In these chapters, most of the field data were kindly provided by Rita Covas, by the time of the study member of the Percy Fitzpatrick Institute, University of Cape Town. It is clearly outlined in these chapters which parts are result of work that has been done by myself, and which parts are based on data by Rita Covas.

All three chapters are written as independent papers to be submitted to international scientific journals in cooperation with co-authors. This approach results regrettably in a certain amount of repetition in model description and description of the species of investigation.

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# Summary

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Natural and human induced environmental changes affect populations at different time scales. If they occur in a spatial heterogeneous way, they cause spatial variation in abundance. In this thesis I addressed three topics, all related to the question, how environmental changes influence population dynamics.

In the first part, I analysed the effect of positive temporal autocorrelation in environmental noise on the extinction risk of a population, using a simple population model. The effect of autocorrelation depended on the magnitude of the effect of single catastrophic events of bad environmental conditions on a population. If a population was threatened by extinction only, when bad conditions occurred repeatedly, positive autocorrelation increased extinction risk. If a population could become extinct, even if bad conditions occurred only once, positive autocorrelation decreased extinction risk. These opposing effects could be explained by two features of an autocorrelated time series. On the one hand, positive autocorrelation increased the probability of series of bad environmental conditions, implying a negative effect on populations. On the other hand, aggregation of bad years also implied longer periods with relatively good conditions. Therefore, for a given time period, the overall probability of occurrence of at least one extremely bad year was reduced in autocorrelated noise. This can imply a positive effect on populations. The results could solve a contradiction in the literature, where opposing effects of autocorrelated noise were found in very similar population models.

In the second part, I compared two approaches, which are commonly used for predicting effects of climate change on future abundance and distribution of species: a "space for time approach", where predictions are based on the geographic pattern of current abundance in relation to climate, and a "population modelling approach" which is based on correlations between demographic parameters and the inter-annual variation of climate. In this case study, I compared the two approaches for predicting the effect of a shift in mean precipitation on a population of the sociable weaver *Philetairus socius*, a common colonially living passerine bird of semiarid savannahs of southern Africa. In the space for time approach, I compared abundance and population structure of the sociable weaver in two areas with highly different mean annual precipitation. The analysis showed no difference between the two populations. This result, as well as the wide distribution range of the species, would lead to the prediction of no sensitive response of the species to a slight shift in mean precipitation. In contrast, the population modelling approach, based on a correlation between reproductive success and rainfall, predicted a sensitive response in most model types. The inconsistency of predictions was confirmed in a cross-validation between the two approaches. I concluded that the inconsistency was caused, because the two approaches reflect different time scales. On a short time scale, the population may respond sensitively to rainfall. However, on a

long time scale, or in a regional comparison, the response may be compensated or buffered by a variety of mechanisms. These may include behavioural or life history adaptations, shifts in the interactions with other species, or differences in the physical environment. The study implies that understanding, how such mechanisms work, and at what time scale they would follow climate change, is a crucial precondition for predicting ecological consequences of climate change.

In the third part of the thesis, I tested why colony sizes of the sociable weaver are highly variable. The high variation of colony sizes is surprising, as in studies on coloniality it is often assumed that an optimal colony size exists, in which individual bird fitness is maximized. Following this assumption, the pattern of bird dispersal should keep colony sizes near an optimum. However, I showed by analysing data on reproductive success and survival that for the sociable weaver fitness in relation to colony size did not follow an optimum curve. Instead, positive and negative effects of living in large colonies overlaid each other in a way that fitness was generally close to one, and density dependence was low. I showed in a population model, which included an evolutionary optimisation process of dispersal that this specific shape of the fitness function could lead to a dispersal strategy, where the variation of colony sizes was maintained.



# General Introduction

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*It's hard to make predictions, especially about the future.*

*(Niels Bohr, or maybe someone else)*

*The key to prediction and understanding lies in the elucidation of mechanisms underlying observed patterns.*

*(Simon A. Levin 1992)*

Predicting, how natural systems are affected by changes in the environment – human induced changes as well as naturally occurring variation – is one of the ultimate tasks of ecological research. However, it is also one of the most difficult tasks, due to the contrast between the complexity of biological systems on the one hand, and the difficulty and high effort of empirical studies for gaining the necessary data basis and understanding on the other hand. A way of making a complex system understandable is to reduce and abstract it in simple models to an essence, where the dynamics and mechanisms are understandable, but the vital properties of the system remain. Since their introduction in ecological research, different kinds of simple models have been extensively used for understanding mechanism and processes behind the complex system dynamics, for explaining observed patterns as well as for risk assessment and population viability analysis in applied nature conservation.

Changes in the environment affect populations on very different temporal and spatial scales (Levin 1992). On a short temporal scale, random fluctuations of the abiotic or biotic environment cause random fluctuations of birth and death rates of populations (environmental noise). Though environmental noise occurs in any natural population, it may be a major threat for population survival, as it increases the risk that the population size hits zero just by chance. Further, a high variance of environmental noise diminishes the mean per capita growth rate of a population, as the effect of the annual per capita growth rate on population size is multiplicative, not additive. Especially for small populations of endangered species, understanding the role of environmental noise for extinction risk is therefore crucial for making successful conservation decisions (e.g. Burgman *et al.* 1993).

In theoretical population ecology, the effect of environmental noise on extinction risk has thus been a major topic of research for a long time. It has been shown that extinction risk increases with decreasing carrying capacity, per capita growth rate, initial population size, and with increasing variance of environmental noise (e.g. Leigh 1981, Wissel & Stöcker 1989, Lande 1993, Foley

1994, Vucetich *et al.* 2000, Drake & Lodge 2004). However, other attributes of environmental noise are less well understood. The question, how exactly environmental fluctuations translate into fluctuations of the vital rates (i.e. the biological filter between fluctuations of the environment and environmental noise), which frequency distribution of vital rates results, and how different frequency distributions affect extinction risk has only recently been addressed (Laakso *et al.* 2001, 2004).

A feature of environmental noise which has drawn the attention of theoretical ecologists since the 1990s is its temporal autocorrelation, or the colour of noise. Positive temporal autocorrelation means that the values of a time series of environmental noise are dependent on the previous values, and successive values tend to be similar. The similarity results in a predominance of long-term (low-frequency) fluctuations in the time series, compared to short-term fluctuations. In analogy to the spectrum of light, positively autocorrelated noise is therefore often called red noise. In contrast, white (uncorrelated) noise consists of an equal mix of fluctuations at all frequencies. The recent interest in coloured noise in theoretical ecology is caused by increasing evidence that many time series of natural fluctuations of the biotic and abiotic environment are in fact red shifted (e.g. Mandelbrot & Wallis 1969, Steele 1985, Pimm & Redfearn 1988, Inchausti & Halley 2002, Vasseur & Yodzis 2004). However, the question, how the colour of noise affects extinction risk, turned out to be more complex than initially thought. Despite an increasing amount of literature, it is still debated under which conditions positive or negative effects prevail (e.g. Ripa & Lundberg 1996, Johst & Wissel 1997, Petchey *et al.* 1997, Cuddington & Yodzis 1999).

The effect of environmental noise on extinction risk becomes even more complicated, if more detail and reality is included into model systems, i.e. age structured populations or spatially heterogeneous populations. Environmental fluctuations can affect the vital rates of different age or stage classes in different ways. Especially in long-lived vertebrates, reproduction and early juvenile survival are often more variable among years than adult survival. However, population dynamics depends strongly on which life stage is affected most by fluctuations, if reproduction or survival is affected, as well as on the generation time of species (e.g. Gaillard *et al.* 1998, Gaillard *et al.* 2000, Saether *et al.* 2000, Lande *et al.* 2003). Further, high environmental noise during early life stages may lead to time delays in the population's response to these fluctuations, especially in species with delayed maturity (e.g. Thompson & Ollason 2001).

In a spatially structured population, the effect of environmental noise depends crucially on its spatial autocorrelation, i.e. the similarity of the current environmental status in adjacent subpopulations, and on the dispersal ability of organisms. In general, spatial autocorrelation increases extinction risk, as it raises the chance of simultaneous extinction of several subpopulations (e.g. Palmqvist & Lundberg 1998, Johst *et al.* 2002, Johst & Drechsler 2003).

On a long time scale, directional trends in environmental conditions, as they are produced by anthropogenic global change, may cause shifts in population abundances, the extinction of

populations, and major disruptions of community structure. In this context, especially consequences of human induced climate change have concerned ecologists since the 1980s (Roberts 1988). Since then, a large body of literature has been established, on how species' life histories and distribution ranges have already altered under the recent anomalies of the climate (reviews in Hughes 2000, McCarty 2001, Walther *et al.* 2002, Crick 2004, meta-analysis in Parmesan and Yohe 2003, Root *et al.* 2003), as well as on predicting how future climate change may affect the distribution ranges, abundances and extinction risks of species (e.g. Iverson & Prasad 1998, Whittaker & Tribe 1998, Roy *et al.* 2001, Thomas *et al.* 2004).

Climate change may affect populations directly (e.g. physiologically), as well as indirectly via shifts in food availability (e.g. Ernest *et al.* 2000), changes in the structure of the environment (Brown *et al.* 1997), shifts in competitive or predator-prey relationships (e.g. Post *et al.* 1999, Lemoine & Böhning-Gaese 2003) or disruptions of the synchrony between interacting species (Harrington *et al.* 1999). However, predictions of the ultimate effect of future climate change on populations are difficult, due to the long time scale, at which the dynamics of a system has to be foreseen. The difficulty is even increased, as the effects of a changed climate may differ largely between different time scales. At a short time scale, more direct effects prevail, which may be well known from experiments, or from correlations between the naturally occurring short-term variation of climate and the response of a species. However, at longer time scales, climate change may lead to major changes of the biotic environment of a species, which can hardly be foreseen, and which make predictions based on short-term correlations questionable (Ives 1995, Rastetter 1996, Hughes 2000, Forchhammer & Post 2004). These effects may either buffer or amplify the sensitivity of a species (Ives & Gilchrist 1993), the ability of buffering depending on the time scale at which they occur in relation to the fast pace of climate change (Roberts 1988, Root & Schneider 1993, McCarty 2001). Moreover, species may become adapted to the changed climate, either phenotypic or genotypic (e.g. Rodríguez-Trelles & Rodríguez 1998, Przybylo *et al.* 2000). Again the question whether adaptation can buffer the effect of climate change depends strongly on the time scale at which it occurs.

The problem of foreseeing population changes on long time scales has often tried to be overcome by a "space for time approach". This approach has been adopted from the study of plant succession (Pickett 1989), and is based on the assumption that the currently occurring spatial pattern of abundance in relation to local climate is the result of a long-term response to local climatic conditions. It is further assumed that the same processes will result in the same pattern of abundance in relation to climate under climate change. Current variation in space is therefore seen as a template for predictions of future changes in time.

A space for time approach has frequently been used to create maps of future distribution ranges of a high number of species (climate envelope models, e.g. Iverson & Prasad 1998, Erasmus *et al.* 2002, Peterson *et al.* 2002, Hilbert *et al.* 2004, Thomas *et al.* 2004). These models are highly valuable as a first step for evaluating consequences of climate change on abundances of single

species and on species diversity. However, the approach has often been criticised, as its underlying assumptions can hardly be tested (e.g. Pickett 1989, Rastetter 1996). Further, it does mostly not consider the mechanisms behind the current pattern of abundance, specifically the dispersal ability of organisms and their interactions with other species (Davis *et al.* 1998a, b, Jiang & Morin 2004, see also Hodkinson 1999). It does therefore not differentiate the time scales, at which the processes which determine a species' abundance in relation to climate, would follow future climate change. A deeper understanding of the processes and mechanisms, which lead to current patterns of abundance, and knowledge of the time scales at which these processes occur is therefore needed to make more powerful predictions.

On the other hand, models which are oriented towards processes usually rely on data from time series or experiments which are no longer than several years. As a consequence, these models often cannot include processes which occur only on longer time scales. This problem has been pointed out by Rastetter (1996), who claimed that models and model validation based on short-term data or on a space for time approach alone are not appropriate for predicting effects of climate change. He proposed that only a validation between different models, which have a high degree of independence and which are based on different principles, can solve this dilemma.

In a spatial extent, temporal variation of the environment can cause distinct spatial patterns of abundance. Random fluctuation of environmental conditions may by chance lead to an increase in abundance in one location, whereas bad conditions at another site cause a decrease in local population size. E.g Ives & Klopfer (1997) have shown in a simple population model that temporal variation could explain a frequently observed pattern of bird abundance, with some persistent hot spots of high abundance, and many sites with low abundance. They concluded that a spatially heterogeneous pattern of abundance does not necessarily reflect long-term spatial heterogeneity of the environment, with "good sites" and "bad sites".

However, it has been shown in evolutionary models that spatially uncorrelated fluctuations of environmental quality favour high dispersal rates (e.g. Levin *et al.* 1984, McPeck & Holt 1992, Wiener & Tuljapurkar 1994). Dispersal may mitigate spatial variation, even if it occurs in a non-directional, density independent way, because it leads to a net flux from patches with high abundance to patches with low abundance. Further, mobile animals may have a choice to select a site, which is optimal to maximise their fitness, and they may escape from bad or from too crowded locations. These considerations have led to the theory of an "ideal free distribution" (Fretwell & Lucas 1970, Fretwell 1972), where directed dispersal goes on, until populations are distributed in a way that the fitness at each location equals one. In a spatially homogenous environment this would lead to an evenly distributed population.

However, populations are variable in space, and especially for colonially living birds it has often been questioned, why colony sizes are so variable even if no indications of spatial heterogeneity of habitat quality are known (Brown *et al.* 1990, Brown & Brown 2001).

## Outline of the thesis

In this thesis I use different population modelling approaches, to address three questions which fall in the context of the above given introduction.

1. How does temporal autocorrelation of environmental noise affect extinction risk? In the first chapter I address a contradiction in the literature, where Petchey *et al.* (1997) found an increased extinction risk under temporal autocorrelation, whereas Heino *et al.* (2000) found the opposite, though very similar models were used in both studies. Here, I show in a simple abstract population model, how slightly different model assumptions lead to opposing effects, and I explain under which ecological conditions which effect prevails.

2. Can we predict how a species will be affected by climate change? Do two approaches, which operate on different time scales, lead to the same predictions? In the second chapter, I cross-validate a space for time approach and a population modelling approach, to predict the effect of a shift in mean annual precipitation on the sociable weaver *Philetairus socius*, a colonially living passerine bird of semiarid southern Africa. In the space for time approach, I compare the abundance and population structure of the species in two areas with highly different mean annual precipitation. In the population modelling approach I simulate the population dynamics of the sociable weaver, based on a correlation between reproductive success and the short-term variation of rainfall. Then I cross-validate the two approaches by testing, whether the population model is able to predict the observed abundance of the species in the two regions.

3. How can the wide variation of colony sizes of the sociable weaver be explained? In the third chapter I test the hypothesis that the variation of colony sizes can be explained by the specific form of the density dependent fitness function, which does not favour a specific colony size. I first analyse data on reproductive success and survival in relation to colony size, to reveal an estimation of the fitness function in relation to colony size. Then I use a population model, which includes an evolutionary optimisation process of dispersal strategy, to test if the given form of the fitness function can lead to the observed variation of colony sizes, and if the variation is maintained by dispersal strategy.

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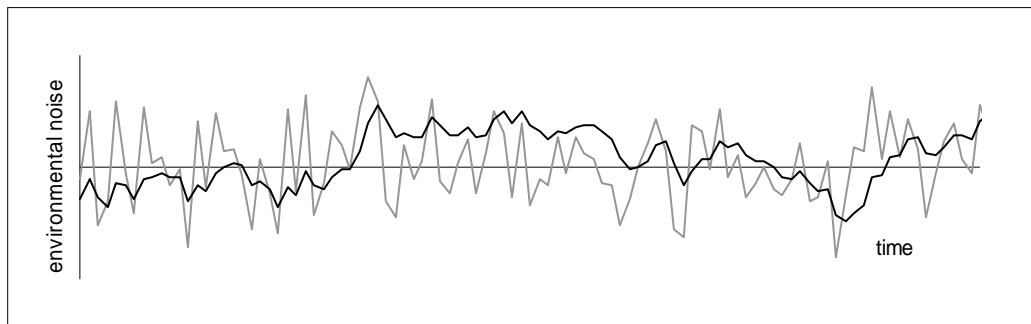


# Chapter 1

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## Population extinction under temporally autocorrelated environmental noise - the importance of single extreme events and series of unfavourable conditions

Recent studies have shown the importance of positive autocorrelation in environmental noise (red noise) for the risk of population extinction. However, it is still debated whether reddened noise increases or decreases extinction risk. For population models with undercompensatory dynamics, earlier studies revealed negative effects of red noise, whereas another study found positive effects. We show that these opposing results can be explained by two features of a red noise time series: On the one hand, positive autocorrelation increases the probability of series of bad environmental conditions, implying a negative effect on populations. On the other hand, aggregation of bad years also implies longer periods with relatively good conditions. Therefore, for a given time period, the overall probability of occurrence of at least one extremely bad year is reduced compared to white noise. This can imply a positive effect for populations. In simulations of extinction risk, we showed that whether positive or negative effects prevail depends on the vulnerability of a population to single extreme events of bad conditions, compared to a series of such conditions. Namely, populations are more prone to extinction after single extreme events if their dynamics is compensatory, and if environmental noise is likely to reach very low values. Our overall results provide a simple explanation for previous contradictory findings and are a crucial step towards a general understanding of the effect of noise colour on extinction risk.



Simulated time series of red and white environmental noise

## 1. Introduction

Natural environments are variable in space and time. Understanding, how environmental noise affects extinction risk is therefore a crucial task in population ecology, both from a theoretical point of view, as well as for conservation and management. One feature of environmental noise has been a focus of several recent studies in theoretical population ecology: the temporal autocorrelation, or colour of noise (e.g. Ripa & Lundberg 1996, Halley 1996, Petchey *et al.* 1997, Cuddington & Yodzis 1999, Inchausti & Halley 2003). Positive autocorrelation in environmental fluctuations, or red noise, means that successive values of environmental noise are dependent on each other and tend to be similar, leading to a predominance of long-term fluctuations in the environmental variation. In contrast, white noise means that the values of environmental noise are independent random numbers.

The increasing interest in red noise in theoretical population ecology is caused by strong evidence that many natural time series are red-shifted, e.g. time series of abiotic environmental variables (e.g. Mandelbrot & Wallis 1969, Steele 1985, Cuddington & Yodzis 1999, Vasseur & Yodzis 2004), or ecological time series (e.g. Pimm & Redfearn 1988, Arino & Pimm 1995, Inchausti & Halley 2002). Halley (1996) concluded that red noise is generally a better null-model for ecological time series. The importance of understanding the implications of noise colour for animal and plant populations is supported by several theoretical studies, which indicate an effect on population dynamics (e.g. Roughgarden 1975, Kaitala *et al.* 1997, Petchey 2000, Jiang & Shao 2003), source-sink dynamics (Gonzales & Holt 2002), coexistence (Caswell & Cohen 1995) and extinction risk (Mode & Jacobson 1987a, Mode & Jacobson 1987b, Foley 1994, Ripa & Lundberg 1996, Johst & Wissel 1997, Petchey *et al.* 1997, Heino 1998, Cuddington & Yodzis 1999, Halley & Kunin 1999, Morales 1999, Heino *et al.* 2000, Greenman & Benton 2003). The effect on extinction risk has been confirmed in a recent analysis of long-term population data for some

animal taxa. In this study, Inchausti & Halley (2003) showed that population persistence could be directly related to the "redness" in their population dynamics.

However, despite the increasing number of studies about coloured noise effects on extinction risk, their results are still ambiguous, whether reddened noise decreases or increases extinction risk. Intuitively, one should expect that positive autocorrelation increases extinction risk, since a population may be capable of surviving a single event of bad environmental conditions, but not a series of subsequent bad conditions (Petchey *et al.* 1997, Morales 1999, see also Lawton 1988). However, several theoretical studies have demonstrated that this intuitive case is not generally true. It could be shown that whether reddened noise has a positive or a negative effect depends on (i) the noise generating process and the darkness of noise (Cuddington & Yodzis 1999, Halley & Kunin 1999, Morales 1999), (ii) the variance of red noise (Heino *et al.* 2000), (iii) the difference between age structured or spatially structured populations and unstructured populations (Petchey *et al.* 1997, Heino 1998, Heino & Sabadell 2003), and (iv) the type of density regulation (Petchey *et al.* 1997, Cuddington & Yodzis 1999, Heino *et al.* 2000).

The latter case has been discussed in detail by Petchey *et al.* (1997, see also Ripa & Heino 1999), who concluded that for a population with overcompensatory density regulation, reddened noise decreases extinction risk, whereas for a population with undercompensatory dynamics reddened noise increases extinction risk. The result of Petchey *et al.* (1997) for overcompensatory dynamics was confirmed by other studies (Ripa & Lundberg 1996, Cuddington & Yodzis 1999, Heino *et al.* 2000). However, for undercompensatory density regulation, some studies confirmed the negative effect of reddened noise (Foley 1994, Johst & Wissel 1997, Cuddington & Yodzis 1999), whereas in a study of Heino *et al.* (2000) the opposite was found. In this study, we solve this contradiction, and explain in general why and under which conditions red noise can have either a negative or a positive effect, even if only undercompensatory to compensatory density regulation is regarded.

In their studies, Petchey *et al.* (1997) and Heino *et al.* (2000) used very similar population models, but they made slightly different assumptions about the frequency distribution of environmental noise. Heino *et al.* (2000) assumed a normal distribution of the carrying capacity, with a carrying capacity  $K \leq 0$  implying extinction. This model allowed for the occurrence of catastrophic extinctions, where the whole population is deleted within one time step, irrespective of previous population size or the type of density regulation. Petchey *et al.* (1997) did not allow such catastrophic events in their model, by restricting the carrying capacity to a lower limit of five. Even at the worst environmental conditions, five individuals could survive in their model, and extinction occurred only due to demographic noise. Here, we show why these model types lead to opposing patterns of a population's extinction risk under red noise. First, we analyse two features of a red noise time series that are crucial for a population's extinction risk. Then, we show that the response of a population's extinction risk to autocorrelated noise can be explained by these two features. We simulate extinction risk under autocorrelated noise for different model variations, and examine the conditions under which extinction typically occurs.

## 2. Methods

### a. Features of red noise time series

For the extinction risk of a population, whose dynamics is influenced by environmental fluctuations, mainly two features of environmental noise are crucial: the probability for the occurrence of extremely unfavourable conditions which threaten the population, and the duration of a series of such conditions. For showing how autocorrelation influences these features, we simulated time series of white and red noise and analysed them for (i) the probability for an extremely low value to occur at least once in a time series of a certain length and (ii) the probability for the occurrence of a series of at least  $n$  successive extremely low values in the time series.

Similar to the approach taken by Petchey *et al.* (1997) and Heino *et al.* (2000), we generated the red noise time series by a first order autoregressive process (AR1 process):

$$\Phi_{t+1} = \alpha \cdot \Phi_t + \beta \cdot \varepsilon_{t+1} \quad (1)$$

where  $\alpha$  is the degree of autocorrelation between two successive values ( $\alpha = 0$  reveals white noise,  $0 < \alpha < 1$  reveals red noise),  $\beta$  is a parameter that determines the variance of the time series, and  $\varepsilon$  is a random number drawn from a normal distribution with zero mean and unit variance. To adjust the asymptotic variance of the time series to the same value for all degrees of autocorrelation,  $\beta$  was set to

$$\beta = \sigma \cdot \sqrt{1 - \alpha^2} \quad (2)$$

where  $\sigma$  is the standard deviation of the time series. This method of adjusting the variance has been discussed by Heino *et al.* (2000) and Wichmann *et al.* (in press). However, as the scaling of variance is not the focus of this study, we stayed here with the most frequently used method of Eq. 2, in order to make our results comparable to other studies.

The noise process was started at its mean ( $\Phi_0 = 0$ ), but we omitted the first 1000 values from the analysis to make the results independent of the initial value. The variance of the time series was set to one, as this does not influence the results. As an extremely low value, we chose  $\Phi_t \leq 2.5 \cdot \sigma$ , but similar results were obtained for  $\Phi_t \leq 2 \cdot \sigma$  and for  $\Phi_t \leq 3 \cdot \sigma$ . Results are shown for a time scale of 500 time steps, but also here results were similar for shorter (100 steps) and longer (1000 steps) time scales. The degree of autocorrelation  $\alpha$  was varied between 0 and 0.99 in steps of 0.05. Simulations were done in 10000 replicates.

### b. Simulations of extinctions risk

We used a simple population model, introduced by Maynard Smith & Slatkin (1973), to simulate extinction risk of a population under white and red environmental noise. This model has been

proposed by Bellows (1981) to be able to describe a wide range of empirical data on density dependence. The population dynamics is given by the equation:

$$N_{t+1} = N_t \cdot \frac{\lambda}{1 + (\lambda - 1) \cdot (N_t / K_t)^\beta} \quad (3)$$

where  $N_t$  is the population size at time  $t$ ,  $\lambda$  is the maximum rate of increase,  $K_t$  is the carrying capacity and  $\beta$  is a parameter controlling the density dependence of the population between overcompensation ( $\beta > 1$ ) compensation ( $\beta = 1$ ) and undercompensation ( $\beta < 1$ ). This model is comparable to the generalized version of the Ricker model that was used in Petchey *et al.* (1997) and Heino *et al.* (2000). As we were able to reproduce the qualitative results of both studies, we concluded that the choice of the model does not influence the results shown here.

Demographic noise was included into the model by letting  $N_{t+1}$  be an integer, drawn from a Poisson distribution with the expected mean  $N_{t+1}$  of Eq. 3. Environmental noise was introduced as an additive effect on the mean carrying capacity, and three different assumptions were made about its frequency distribution:

*Model (1)* Comparable to the study of Heino *et al.* (2000), environmental noise was normally distributed, and a carrying capacity  $K \leq 0$  implied extinction:

$$K_t = K_{\text{mean}} + \Phi_t \quad (4)$$

$$N_{t+1} = 0 \quad \text{if} \quad (K_t \leq 0) \quad (5)$$

where  $K_{\text{mean}}$  is the mean carrying capacity and  $\Phi_t$  is the environmental noise given by an AR1 process (Eq. 1 and 2).

*Model (2)* Comparable to the study of Petchey *et al.* (1997), environmental noise was normally distributed (Eq. 4), but the carrying capacity was restricted to a lower limit, and catastrophic extinctions due to  $K \leq 0$  did not occur:

$$K_t = K_{\text{min}} \quad \text{if} \quad (K_t \leq 0) \quad \text{with} \quad K_{\text{min}} > 0 \quad (6)$$

*Model (3)* Environmental noise was lognormally distributed:

$$\ln(K_t) = \ln(K_{\text{mean}}) + \Phi_t \quad (7)$$

In this model, catastrophic extinction of  $K \leq 0$ , are excluded by the frequency distribution *per se*.

For all model variations, simulations of extinction risk were done in 10000 replicates and started at a population size of  $N_0 = K_{\text{mean}}$ . The parameters used in all simulations shown here were  $K_{\text{mean}} = 100$  and  $\lambda = 4.5$ . However, very similar results were revealed for  $\lambda = 1.5$ . To show the effect of density dependence, the parameter  $\beta$  was varied between  $\beta = 0.5$  (strong undercompensation),  $\beta = 0.75$  (moderate undercompensation) and  $\beta = 1$  (compensation). The standard deviation of the noise process (Eq. 1 and 2) was varied between  $\sigma = x \cdot K_{\text{mean}}$  and  $\sigma = x \cdot \ln(K_{\text{mean}})$  in model (1) and model (3), respectively, with  $x = 0.25; 0.3; 0.35; 0.4$ . In model (2) the standard deviation was set  $\sigma$

$= 0.4 \cdot K_{\text{mean}}$ , but  $K_{\text{min}}$  was varied between  $K_{\text{min}} = 0.1; 0.5; 1; 3; 5$ . The degree of autocorrelation  $\alpha$  was varied between 0 and 0.99 in steps of 0.05. Results are shown here for a time scale of 500 generations.

After the simulations, we examined the conditions under which the population became extinct. For model (1) we counted at which percentage of the simulations extinction occurred due to a carrying capacity  $K \leq 0$ , corresponding to a catastrophic extinction from any population size. For model (2) and (3) we examined the vulnerability of the population to extremely bad environmental conditions occurring once, compared to a series of such conditions: We started simulations at a high population size ( $N_0 = K_{\text{mean}}$ ), and at a low carrying capacity, where extinctions typically occurred ( $K_0 = K_{\text{low}}$ ). Then we simulated extinction risk for different degrees of autocorrelation  $\alpha$  in the following ten generations. If there was no autocorrelation ( $\alpha = 0$ ), these simulations showed the short-term effect of a single extreme event of bad conditions on a large population. If noise was reddened ( $\alpha > 0$ ), they showed the short-term effect of an extreme event that was likely to be followed by more, i.e. the effect of series of bad conditions.

### 3. Results

#### a. Features of red noise time series

The simulations revealed that the probability for the occurrence of at least one extremely low value in a time series of a given length decreased continuously as noise was reddened (Fig. 1a). This can be explained as in a red noise time series, the environment undergoes more long term fluctuations, but stays more constant at a short time scale compared to white noise. Therefore, on the average, it takes a longer time until an extremely low value occurs. This feature implies a positive effect on a population, as extremely bad conditions are generally less likely to occur.

On the other hand, if an extremely low value occurs once in a red noise time series, it is likely to be followed by more. Therefore, the probability of a series of low values increased in our simulations, as noise was reddened (Fig. 1b). This implies a negative effect of red noise on a population. However, there was a peak at high autocorrelation (about at  $\alpha = 0.85$  to  $\alpha = 0.95$ ) after which the probability of series decreased again as  $\alpha$  approached one. Only for very long series of nine or more successive extreme values we found the probability for bad series to increase continuously. The decrease at very high  $\alpha$  for shorter series can be explained by comparing Fig. 1a and b. At very high autocorrelation, the probability of the occurrence of an extremely low value was so small, that here also series of low values were very unlikely.



## b. Simulations of extinction risk

### *Model (1): normal distribution of environmental noise*

If a normal distribution was assumed for environmental noise and a carrying capacity  $K \leq 0$  implied extinction, we revealed an unambiguous result: extinction risk continuously decreased with increasing degree of autocorrelation. There was no substantial difference between compensatory and undercompensatory density dependence, and different variances of environmental noise had no effect on the qualitative results (Fig. 2a).

Fig. 2b shows that except for very high  $\alpha$ , nearly all extinctions occurred at a carrying capacity  $K \leq 0$ , corresponding to catastrophic extinctions. As catastrophic events were the main cause of extinction, extinction risk was mainly determined by the question whether a carrying capacity  $K \leq 0$  occurred in the time series of environmental noise. The decrease in extinction risk under reddened noise can therefore be explained by the time series analysis in the previous section, where it has been shown that the probability of at least one extremely low value (as  $K \leq 0$ ) is decreased in a red noise time series. A comparison of Fig. 2a and Fig. 1a shows actually that the curve of extinction risk has the same shape as the curve of the probability of at least one extremely low value in the time series.

### *Model (2): normal distribution of environmental noise, restricted to a lower limit of the carrying capacity*

If catastrophic events ( $K \leq 0$ ) were excluded by setting a lower limit  $K_{\min}$  to the fluctuations of the carrying capacity, the effect of autocorrelation on extinction risk depended on the degree of undercompensation, as well as on the value of  $K_{\min}$  (Fig. 3a). If dynamics was compensatory to moderately undercompensatory, and  $K_{\min}$  was low, reddened noise decreased extinction risk. If dynamics was strongly undercompensatory, or  $K_{\min}$  was moderately high, reddened noise increased extinction risk until high autocorrelation ( $\alpha = 0.8$  to  $\alpha = 0.95$ ), followed by a decrease as  $\alpha$  approached one. At a very high value of  $K_{\min} = 5$ , extinction risk increased continuously as noise was reddened.

The examination of the causes of extinction (Fig. 3b) showed that in all cases, where reddened noise increased extinction risk (highly undercompensatory dynamics or high values of  $K_{\min}$ ), a very low carrying capacity did not lead to a considerable extinction risk for a large population if it was likely to occur only once ( $\alpha = 0$ ). Short-term extinction risk was only high if the low carrying capacity was likely to be followed by more ( $\alpha > 0$ ). On the other hand, in cases where reddened noise decreased extinction risk (compensatory dynamics and low values of  $K_{\min}$ ), even the single occurrence of bad environmental conditions implied a considerable extinction risk. These results show that a population which was prone to extinction by single extreme events, had a decreased extinction risk under reddened noise, whereas a population which was threatened only by series of bad conditions, had an increased extinction risk. Similar to model (1), this result was further

supported by the similarity of the curves of extinction risk in Fig. 3a and the curves of the time series analysis in Fig. 1a and b.

The different vulnerabilities of a population to single extreme events under compensatory and undercompensatory density dependence can be explained by an examination of the recruitment function of the population model at low carrying capacities (the recruitment function describes the population size  $N_{t+1}$  in dependence on the previous population size  $N_t$ ; Fig. 3c). Under compensatory density regulation, the population size resulting from a low carrying capacity is quite independent of the previous population size. Bad environmental conditions can therefore result in a substantial extinction risk, even for a previously large population. Under highly undercompensatory dynamics, where the population tracks the changing carrying capacity only slowly, the population size resulting from extremely bad conditions strongly depends on the previous population size. A very small population size which is at a high risk of extinction will only be reached, if the previous population size was already low.

#### *Model (3): lognormal distribution of environmental noise*

Qualitatively similar results as in model (2) were revealed, if environmental noise was lognormally distributed (Fig. 4a). If dynamics was undercompensatory, reddened noise increased extinction risk until high autocorrelation, followed by a decrease, as  $\alpha$  approached one. If dynamics was compensatory the impact of autocorrelation depended on the variance of environmental noise. Reddened noise increased the extinction risk up to a high  $\alpha$  if the variance was low, but decreased extinction risk, if the variance was high. Here, a high variance of environmental noise had a similar effect as low values of  $K_{\min}$  in model (2), as both imply that the carrying capacity can reach very low values.

The examination of the vulnerability of the population to extremely bad environmental conditions gave also a similar picture as in model (2) (Fig. 4b). Under highly undercompensatory dynamics, an extremely low carrying capacity only led to a considerable extinction risk, if it was likely to be followed by more. In contrast, under compensatory dynamics and a high variance of environmental noise, the population was threatened by bad environmental conditions, even if they occurred only once.

Generally, the qualitatively similar results of model (2) and model (3) demonstrate that the differing effects of reddened noise do not depend on the type of frequency distribution (normal or lognormal), or on the way by which catastrophes of  $K \leq 0$  are excluded from the model.

## 4. Discussion

Our simulations on extinction risk revealed two opposite patterns of how reddened noise affects a population's extinction risk: a continuous decrease of extinction risk with increasing autocorrelation and an increase of extinction risk until high autocorrelation of about  $\alpha = 0.8$  to 0.95, followed by a decrease as  $\alpha$  approaches one. These opposite patterns could be explained by

two features of red noise time series: First, the probability that an extremely low value of environmental conditions occurs at least once in a time series of a certain length is decreased as noise is reddened. This implies a positive effect on a population, as bad conditions are generally less likely to occur, and explains the first pattern. Second, the probability that series of bad values occur is increased under reddened noise until high autocorrelation, followed by a decrease as  $\alpha$  approaches one. This implies a negative effect of reddened noise (at least until high autocorrelation) and explains the second pattern.

From our results, we conclude that the question, which of the two patterns prevails, depends on what is the main cause of extinction: series of poor environmental conditions or single events of bad conditions. If a population has a high potential to survive bad conditions occurring once, and only series of such conditions bear a considerable extinction risk, the second pattern prevails. On the other hand, if single events of bad conditions bear a high extinction risk for a large population, the lower risk of the occurrence of such conditions in red noise can outweigh the negative effect of more likely series, and the first pattern prevails. We found that generally a population is more prone to extinction after single events of bad conditions (i) the more compensatory density regulation is and (ii) the worse the environment is likely to get (i.e. the lower  $K_{\min}$  is in model (2) and the higher the variance of environmental noise is in model (3)). However, there are no clear thresholds but continuous changes.

Given these explanations we can solve the contradiction in previous studies, where Petchey *et al.* (1997) found an increase of extinction risk as noise is reddened whereas Heino *et al.* (2000) found the opposite. Heino *et al.* (2000) used a model with a normal distribution of environmental noise and a carrying capacity  $K \leq 0$  implying extinction. We showed (in concordance with Heino *et al.* 2000) that in this model, catastrophes at which the population inevitably becomes extinct from any population size are the main cause of extinction. Therefore, reddened noise has a positive effect on the population because these catastrophes are less likely to occur. The occurrence of catastrophes can be a realistic model assumption, but care should be taken, if much of the behaviour of the model can be explained by them, and if other features of the model-system are masked by the simple question whether or whether not a catastrophe occurs. In many studies catastrophes were treated separately from the "common" environmental stochasticity and their relative importance for extinction risk was assessed (e.g. Lande 1993). We suggest that treating catastrophes separately would be interesting also in studies on the effect of coloured environmental noise, as it could give a better insight into more subtle model behaviour.

Petchey *et al.* (1997) used a model where the carrying capacity cannot fall below five individuals, and extinction can occur only because of demographic stochasticity. In this model, single events of even the worst environmental conditions do not bear a substantial extinction risk for a large population, as long as they occur only once. Here, clearly series of unfavourable conditions determine extinction risk and reddened noise increases extinction risk. However, we showed that the continuous increase of extinction risk that was found by Petchey *et al.* (1997) occurs only for a

very persistent population, whereas in most of our simulations, we found that the increase of extinction risk is followed by a decrease at very high autocorrelation.

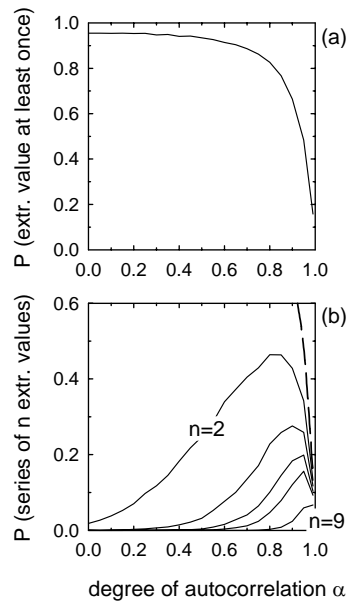
In other studies, different assumptions were made on how environmental noise is included into the model. However, they still confirm our general findings. For example Foley (1994) included environmental noise by assuming a lognormal distribution of the growth rate. Johst & Wissel (1997) assumed the birth rate to be uniformly distributed and restricted to values larger or equal to zero, whereas the death rate was constant. In both models, sudden catastrophic extinctions did not occur and consequently both studies revealed a decreased persistence time as noise was reddened.

The results of this study were obtained using a first order autoregressive process as noise model, and the question remains if they can be transferred to other red noise models. Halley (1996) suggested that pink  $1/f$  noise is a better null-model for environmental noise, as in  $1/f$  noise the variance of a time series increases with no limit as the length of the time series increases, whereas in an AR1-process the variance approaches a finite value. The question, how pink  $1/f$  noise affects extinction risk was addressed in some recent studies. They indicate that our conclusions also hold for pink  $1/f$  noise, but further research is required for an affirmation: Cuddington & Yodzis (1999) used the same model as Petchey *et al.* (1997), and on concordance with Petchey *et al.* (1997) they revealed an increased extinction risk for undercompensatory dynamics under red noise. It would be interesting if also here differing results were achieved if the model population was more prone to extinction by single extreme events. In contrast, Halley & Kunin (1999) assumed the population size to be directly influenced by the noise process. In this model, sudden extinction could occur from any population size and consequently the result was a decreased extinction risk under pink noise as long as the variance of noise was not too small. Morales (1999) found an increased extinction risk under pink noise for a random walk model, but a decreased extinction risk for the generalized Ricker model. Similar to our case, he concluded that the opposing results were caused by different conditions of extinction, i.e. extinction from low population sizes compared to extinction from large population sizes.

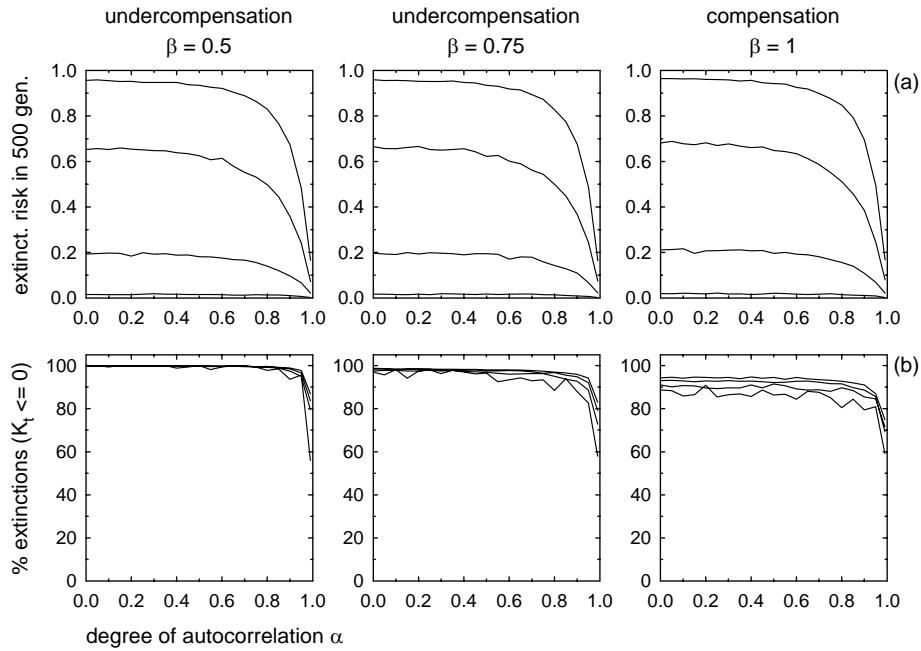
A common drawback of all studies on the effect of red noise on extinction risk is that results must be seen in the context of the scaling of the variance (Heino *et al.* 2000). Since in red noise time series, the variance increases with time, the question raises, at which time scale the variance should be adjusted to the variance of white noise. This problem has been discussed by Heino *et al.* (2000) and Wichmann *et al.* (in press), who showed that different approaches can lead to very different results. In this study, we adjusted the red noise variance to the variance of white noise at infinite time scale, but as in all similar studies, our results strongly depend on this assumption. However, there is no straightforward answer, which time scale is best for adjusting the variance.

In general, we showed that no unambiguous statement can be made on the question if reddened noise increases or decreases extinction risk. Contrary to the conclusion of Petchey *et al.* (1997), this holds true even if we focus only on undercompensatory to compensatory density regulation. However, we gave an explanation, why opposite effects of temporal autocorrelation occur and we

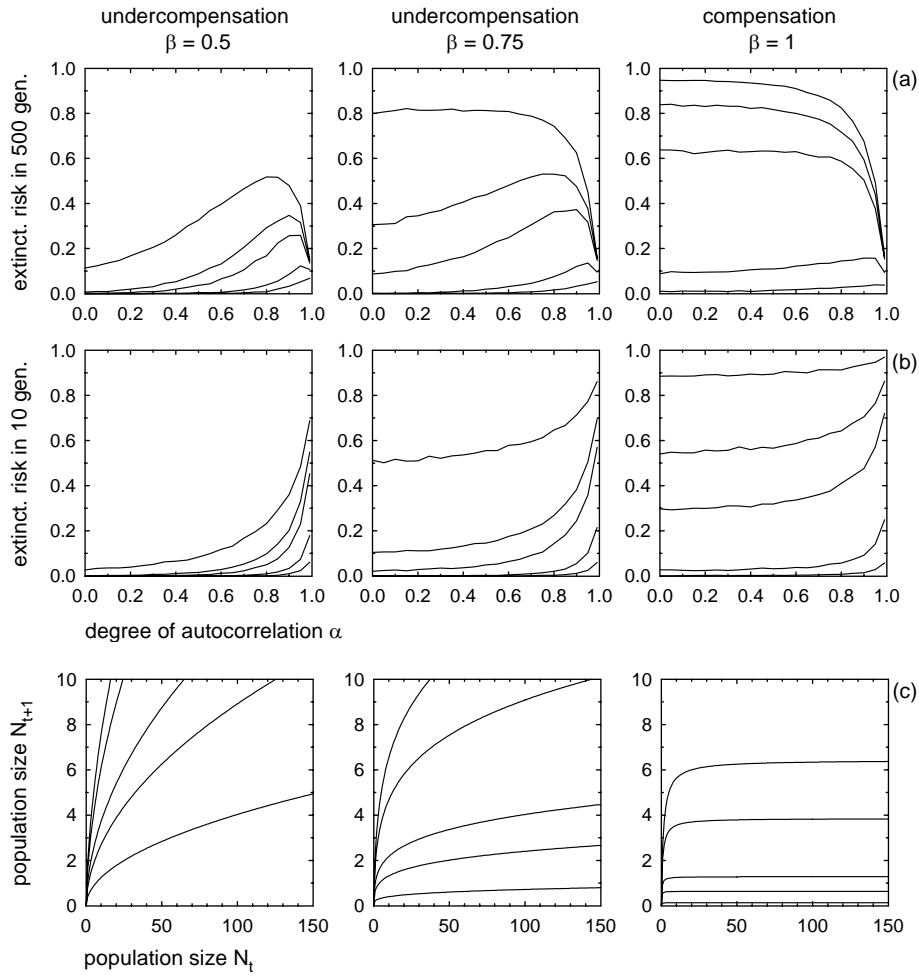
showed that the effect of red noise on population extinction is mainly determined by the question how endangered a population is by the occurrence of single extreme events of bad environmental conditions. This could give a general rule of thumb to decide whether red noise increases or decreases the extinction risk of a population.



*Figure 1:* (a) Probability for the occurrence of at least one extremely low value ( $\Phi_t \leq 2.5 \cdot \sigma$ ) in a time series of 500 steps, as a function of temporal autocorrelation  $\alpha$ . (b) Probability for the occurrence of a series of at least  $n = 2; 3; 4; 5; 9$  successive extremely low values ( $\Phi_t \leq 2.5 \cdot \sigma$ ) in a time series of 500 steps, as a function of temporal autocorrelation  $\alpha$ . The dashed line is given as a reference and shows the curve of (a). Both figures: time series form an AR1 process (Eq. 1 and 2);  $\sigma = 1$ ; mean of 10000 replicates.

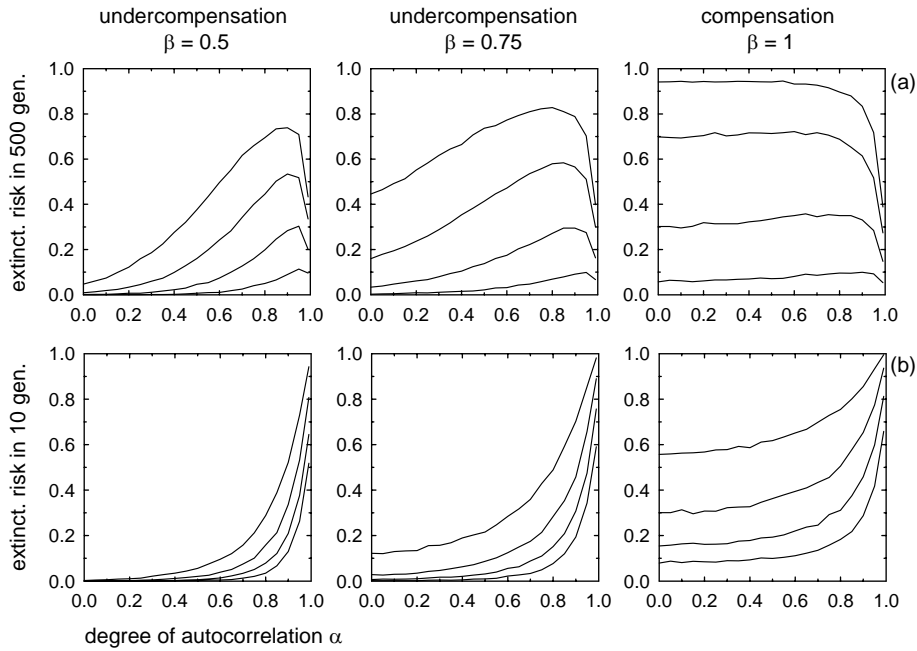


*Figure 2:* (a) Extinction risk in 500 generations as a function of temporal autocorrelation  $\alpha$ , using a normal distribution of the carrying capacity that is not restricted to a lower limit (model 1). The lines correspond to different values for the standard deviation of the noise process (Eq. 1 and 2)  $\sigma = x \cdot K_{\text{mean}}$  with  $x = 0.25; 0.3; 0.35; 0.4$  from bottom to top. (b) Percentage of extinctions in (a) that occurred at a carrying capacity  $K_t \leq 0$ . Lines as in (a). In both figures, the left panel corresponds to strong undercompensation ( $\beta = 0.5$ ), the middle panel to moderate undercompensation ( $\beta = 0.75$ ) and the right panel to compensation ( $\beta = 1$ ). See model description for further details.



*Figure 3:* (a) Extinction risk in 500 generations as a function of temporal autocorrelation  $\alpha$ , using a normal distribution of the carrying capacity that is restricted to a lower limit  $K_{\min}$  (model 2). The lines correspond to different values for  $K_{\min} = 0.1; 0.5; 1; 3; 5$  from top to bottom. The standard deviation of the noise process (Eq. 1 and 2) was  $\sigma = 0.4 \cdot K_{\text{mean}}$ . (b) Extinction risk within 10 generations after the occurrence of an extremely low carrying capacity  $K_{\text{low}}$ , starting at a high population size of  $N_0 = K_{\text{mean}}$ . The lines correspond to different values for  $K_{\min}$  and  $K_{\text{low}}$  with  $K_{\min} = K_{\text{low}} = 0.1; 0.5; 1; 3; 5$  from top to bottom. (c) Recruitment functions of the population model at extremely low carrying capacities  $K_{\text{low}} = 0.1; 0.5; 1; 3; 5$  from bottom to top. In all figures, the left panel corresponds to strong undercompensation ( $\beta = 0.5$ ), the middle panel to moderate undercompensation ( $\beta = 0.75$ ) and the right panel to compensation ( $\beta = 1$ ). See model description for further details.





*Figure 4:* (a) Extinction risk in 500 generations as a function of temporal autocorrelation  $\alpha$ , using a lognormal distribution of the carrying capacity (model 3). The lines correspond to different values for the standard deviation of the noise process (Eq. 1 and 2)  $\sigma = x \cdot \ln(K_{\text{mean}})$  with  $x = 0.25; 0.3; 0.35; 0.4$  from bottom to top. (b) Extinction risk within 10 generations after the occurrence of an extremely low carrying capacity  $K_{\text{low}}$ , starting at a high population size of  $N_0 = K_{\text{mean}}$ . The lines correspond to different values for the standard deviation of the noise process  $x = 0.25; 0.3; 0.35; 0.4$ , and corresponding values of  $K_{\text{low}} = 2; 1.5; 1; 0.5$  from bottom to top. In both figures, the left panel corresponds to strong undercompensation ( $\beta = 0.5$ ), the middle panel to moderate undercompensation ( $\beta = 0.75$ ) and the right panel to compensation ( $\beta = 1$ ). See model description for further details.

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In the first chapter of the thesis I addressed the question, how temporally autocorrelated fluctuations of the environment affect the extinction risk of populations. I showed that this question depends (amongst other) on the vulnerability of a population to single catastrophic events of bad environmental conditions, compared to series of bad conditions. In this part of the thesis, the mean and variance of environmental fluctuations were kept constant over the entire study. Only a certain feature of environmental noise, its temporal autocorrelation, was varied.

In the next chapter I will analyse, how a long term trend in the mean of environmental variation, as it may occur under climate change, may affect the abundance of a specific species, the sociable weaver *Philetairus socius*. I will compare and cross-validate two approaches, which are widely used for making predictions on the future abundance and distribution of species under climate change.

# Chapter 2

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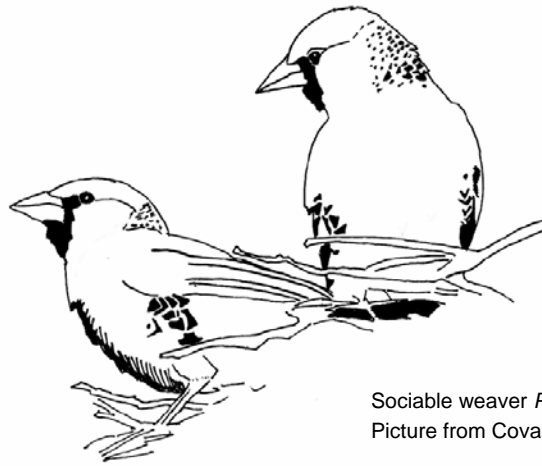
## Predicting effects of climate change on a passerine bird in southern Africa - a cross-validation of two approaches on different time scales

The response of populations to environmental changes depends on the time scale at which these changes occur. However, studies, which aim to predict effects of climate change on populations, comprise mostly two approaches, which operate either on very long or on very short time scales: In a "space for time approach" predictions are based on the geographical pattern of current abundance in relation to climate, which may reflect the long-term response of systems to a certain climate. In a "population modelling approach" predictions are based on the short-term response of demographic parameters or abundances to naturally occurring climate fluctuations.

In this study we show in a cross-validation that the two approaches may lead to different predictions about a species' sensitivity to climate change. We compared the approaches for predicting the sensitivity of the sociable weaver *Philetairus socius*, a common passerine bird of semiarid southern Africa, to a shift in mean precipitation caused by climate change. In the "space for time approach", we compared population density and structure in two regions with different mean precipitation. The analysis showed no difference between the two populations. This result, as well as the wide distribution range of the species, would imply no sensitive response of the species to climate change. In contrast, the "population modelling approach", based on a correlation between reproductive success and rainfall, predicted a sensitive response in most model types. Further, in the cross-validation, the population model could not predict the observed abundances in both regions. We conclude that on a regional scale, long-term mechanisms exist, which buffer or compensate the consequences of climatic variation. The results imply that understanding the difference between long-term and short-term processes in a species' response to climatic variation is a crucial precondition for predicting ecological consequences of climate change.

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In this chapter, the data on colony sizes in the region of Kimberley, which were used in the regression between mean colony size and number of nestchambers in a colony (Fig. 2), have been provided by Rita Covas.



Sociable weaver *Philetairus socius*  
Picture from Covas (2002)

## 1. Introduction

Predicting, how climate change will affect the abundance, distribution and composition of species is a major challenge in current ecological research. There is increasing evidence that the anomalous climate of the 20th century has already affected a broad range of organisms across the major taxonomic groups (reviews in Hughes 2000, McCarty 2001, Walther *et al.* 2002, Crick 2004, meta-analysis in Parmesan & Yohe 2003, Root *et al.* 2003), and further severe impacts on species and ecosystems might be expected under the fast pace of climate change (Roberts 1988, Hughes 2000, McCarty 2001, Hannah *et al.* 2002, Thomas *et al.* 2004). However, predictions on future consequences of climate change are difficult, due to the complexity of biological systems, the rarity of long-term data sets, the high effort of conducting experiments, and the difficulty of validating models (Root & Schneider 1993, Ives 1995, Rastetter 1996, Hughes 2000, Walther *et al.* 2002).

Current research comprises mainly two approaches on predicting effects of a changed climate on species' abundance and distribution:

In the first approach, here called "population modelling approach", abundances or demographic parameters are related to the naturally occurring inter-annual variation of certain climatic variables. Based on these data, population models are developed, which project population dynamics into the future under scenarios of climate change (e.g. Whittaker & Tribe 1998, Saeter *et al.* 2000, Roy *et al.* 2001, Clark *et al.* 2003, Wichmann *et al.* 2003).

In the second approach, a "space for time approach", abundances or distributions are correlated with climatic variables across a certain geographical range. From these data, climatic niches of species (climate envelopes) are delineated, which define a species' range according to its requirements to climate. On this basis, predictions are developed on the future geographic distribution of species under scenarios of climate change (e.g. Iverson & Prasad 1998, Erasmus *et al.* 2002, Peterson *et al.* 2002, Hilbert *et al.* 2004, Thomas *et al.* 2004). In this approach, current spatial variation of abundance in relation to climate is seen equivalent to the temporal variation of abundance under future climatic changes, i.e. space is substituted for time (Pickett 1989).

However, the two approaches reflect a species' response to climatic conditions on very different time scales (Rastetter 1996). The population modelling approach extrapolates knowledge on the responses to short-term climatic variation into the future, but may not consider processes, which act on longer time scales, and which are not visible in relatively short time series of population dynamics and processes. On the other hand, the space for time approach, based on the geographic variation of abundance, may reflect the long-term adaptation of a species or system to a certain climate. But being mostly observational, the approach does often not consider the mechanisms and processes behind the responses of a species. It does therefore not differentiate the time scales at which processes would follow a directional trend in climatic conditions like future climate change. However, the question of scale at which a biological system is regarded may be crucial, and different responses may be expected on different time scales (Levin 1992).

In this study we show in a cross-validation of the two approaches that they may lead to different predictions on a species' sensitivity to climate change, and that they may not be compatible. Our study species is the sociable weaver *Philetairus socius*, a colonially living passerine bird of arid and semiarid savannahs of southern Africa. In arid and semiarid systems, the main climate variable determining biological processes is the low and usually highly variable and unpredictable rainfall (Noy-Meir 1973, Weltzin *et al.* 2003). Rain determines primary production and thereby food availability of most animal species at different trophic levels. Consequently, rain has been identified as a determinant of reproduction and/ or abundance of many species, including reptiles (e.g. Dickman *et al.* 1999), mammals (e.g. Ernest *et al.* 2000, Lima *et al.* 2001) and birds (e.g. Hustler & Howells 1990, Lloyd 1999, Morrison & Bolger 2002), and ranging from primary consumers to top predators. Shifts in precipitation regimes, as they are predicted by global climate models may therefore have severe effects in these systems. These effects may cascade through the food web and affect the spatial and temporal dynamics of consumers at all trophic levels (Weltzin *et al.* 2003).

For the sociable weaver, several studies have shown a strong relationship between rainfall and several components of reproductive success, i.e. (i) the length of the breeding season, (ii) the number of breeding attempts within a breeding season, (iii) clutch size, (iv) nestling weight, and (v) the probability of brood success (Maclean 1973, Marsden 1999, Covas 2002). In general, the sociable weaver's breeding strategy is highly opportunistic, with a high breeding investment in good rain years, but skipping breeding at all in years of exceptionally low rainfall (Maclean 1973, Covas 2002). All summarizes to a strong correlation between rainfall and reproductive rate, and indicates a high sensitivity of population dynamics to precipitation regime. However, the sensitive response of population processes is contradicted by the wide distribution of the species, which ranges from semiarid areas with 600 mm mean annual precipitation up to arid areas with as low as 80 mm mean annual precipitation (Maclean 1973, Mendelsohn & Anderson 1997). The distribution range would rather suggest that this species is hardly affected by precipitation regime.

Given this contrast, we compare and cross-validate here the two above described approaches for predicting the sensitivity of the sociable weaver to a shift in mean annual precipitation under climate change. In the first part of the study, we compare in a space for time approach population density and population structure of the sociable weaver in two regions with highly different mean annual precipitation. In the population modelling approach, we develop a spatial-explicit simulation model of the species, which is based on the current knowledge that reproductive success is correlated with the monthly or yearly variation in rainfall (see above, Maclean 1973, Marsden 1999, Covas 2002). Using this model, we simulate the population dynamics under a realistic scenario of climate change (IPCC 2001). Finally, we cross-validate the two approaches by testing, whether the population model is able to predict realistic population densities in the two respective areas under the current precipitation regimes.

## 2. Study species

The sociable weaver is a colonial passerine bird, endemic to semiarid and arid savannahs of southern Africa. The distribution range covers most parts of Namibia and the north-western part of South Africa, ranging from 80 to 600 mm mean annual precipitation (Maclean 1973, Mendelsohn & Anderson 1997). Sociable weavers build large apartment block like communal nests of grass and twigs with multiple separate chambers, which are occupied over the whole year. Colony size is highly variable, with a maximum size of 500 birds (Maclean 1973). Nests are mainly built on large *Acacia erioloba* trees, but also other tree species (*Boscia albitrunca*, *Aloe dichotoma*, and other *Acacia* species), or human made structures like telephone poles are frequently used (Maclean 1973, Mendelsohn & Anderson 1997). Sociable weavers feed on insects and grass seeds, insects making up about 80% of food (Maclean 1973, Ferguson 1988). Reproduction is closely related to rainfall, as rain is the main determinant of food availability (see above). In some areas, breeding is highly opportunistic, occurring at any time of the year triggered by rainfall and food availability. In other areas, the breeding season is more discrete and confined to the (wet) summer season (Maclean 1973, Mendelsohn & Anderson 1997, Covas 2002). Nest predation by snakes (mainly cape cobra *Naja nivea* and boomslang *Dispholidus typus*) is a main cause of reproductive failure, leading to a mean loss of 75% of broods in our study area (Maclean 1973, Marsden 1999, Covas 2002). In contrast to reproductive success, the yearly survival rate seems to be not influenced by rainfall (Brown *et al.* 2003).

## 3. Space for time approach: comparison of populations

### a. Study areas

Population density and population structure of the sociable weaver were compared in two areas, which differ in mean annual precipitation by a factor of more than two. The first population was surveyed at Benfontein Game Farm, near Kimberley, South Africa (*ca.* 28°53' S, 24°49' E, further



referred to as "Kimberley"). The site is located at the south-eastern edge of the distribution range of the sociable weaver, with an annual precipitation of  $400 \pm 101$  mm (Mean  $\pm$  SD) (Zucchini *et al.* 1992). It consists of an open *Acacia erioloba* savannah, dominated by *Stipagrostis* grass. The sociable weaver population at this site is well known, as it has been surveyed in a capture mark recapture study since 1993 (Covas 2002, Brown *et al.* 2003). The abundance of sociable weaver colonies at this site is high compared to surrounding areas, and nests are almost exclusively built on large *A. erioloba* trees.

The second population was surveyed on three farms between Askham and Twee Rivieren, in the north-western corner of South Africa (*ca.* 26°40' S, 20°36' E, further referred to as "Askham"). The sites are situated in the core of the distribution area of the sociable weaver, with an annual precipitation of  $176 \pm 72$  mm (Mean  $\pm$  SD) (Zucchini *et al.* 1992). In this area, tree density is much lower than in Kimberley. The abundance of sociable weaver colonies may therefore mainly be limited by the abundance of suitable nesting trees, and the three farms of the survey were chosen to cover different tree densities. The dominant tree species are *Boscia albitrunca* and *A. erioloba*. Sociable weaver nests are built on both tree species, but nests on *A. erioloba* are significantly larger than nests on *B. albitrunca* (M. Schwager, unpublished data).

Despite the difference in mean annual precipitation, the seasonal pattern of precipitation is very similar in the two areas (Fig. 1). Both experience highly variable and unpredictable summer rainfall, and a dry winter season.

## b. Methods

The study sites were surveyed by foot and all occupied sociable weaver nests were counted. The surveyed area covered 17.6 km<sup>2</sup> in Kimberley, and 33.3 km<sup>2</sup> in Askham. The occupation of a nest was indicated either by the presence of birds, or by fresh faeces below the nest. In 21 colonies in Kimberley and in 42 colonies in Askham, the number of individual nestchambers in the communal nest was recorded as a measure of colony size. Marsden (1999) reported a strong correlation between the number of nestchambers in a colony and colony size. To confirm this correlation, we calculated a regression between colony size and the number of nestchambers in a colony for the study area of Kimberley, using mean colony sizes from an 8 year capture mark recapture study in this area (Covas 2002, Brown *et al.* 2003, R. Covas, unpublished data). This regression was used to estimate real colony sizes and abundances in the two study areas.

As a measure of population structure, mean and standard deviation of the number of nestchambers per colony were calculated, and compared between the two regions by an unpaired T-test, and a Levine test for homogeneity of variances, respectively. As a measure of population density, density of nestchambers was estimated as the average number of nestchambers per colony times the density of colonies.

### c. Results

The number of nestchambers in a colony correlated strongly with mean colony size over 8 years according to the equation: number of nestchambers =  $0.753 (\pm 0.064) \cdot \text{mean colony size} + 4.08 (\pm 3.55)$  (SE) ( $p < 0.001$ , adj.  $R^2 = 0.91$ , Fig. 2).

The density of nestchambers hardly differed between the two areas (Table 1). The density of about 50 nestchambers per km<sup>2</sup> in both areas corresponds to a population density of about 60 birds per km<sup>2</sup>, according to the regression of Fig. 2. Also population structure (mean and standard deviation of nestchambers per colony) was very similar in the two areas (Table 1) and did not differ significantly (mean:  $T = 0.55$ ,  $p = 0.59$ ; variance:  $F = 0.35$ ,  $p = 0.56$ ). The mean nest size of about 35 chambers corresponds to a mean colony size of about 40 birds, according to the regression in Fig. 2.

## 4. Population modelling approach and cross-validation

The population dynamics of the sociable weaver was simulated in a spatial-explicit model, in which reproductive success was correlated with rain. As the exact shape of the relationship between rain and reproductive success is not known, we tested a high number of possibilities for this relationship (Table 2), i.e. (i) different functions: a linear function, a saturation function and saturation function with a lower threshold (Fig. 3), (ii) different temporal resolutions: yearly time-steps and monthly time-steps, and (iii) a model where reproductive success was related to current yearly/ monthly rainfall, compared to a model, where reproductive success was related to current *and* previous yearly/ monthly rainfall.

As many parameters of the model have a high uncertainty, reasonable parameter values were derived in a parameter fitting procedure by comparing the population density and structure which emerged from the model with the realistic pattern in the field. This method of "pattern oriented modelling" is a widely used approach for the calibration and validation of models (Grimm *et al.* 1996, Wiegand *et al.* 2003). In this procedure, the model was repeatedly run under a random variation of all unknown parameters within certain limits, and parameter combinations, which generated realistic populations, were selected.

Parameter fitting was done for the high rainfall regime of Kimberley and for the low rainfall regime of Askham, separately (Table 2). By doing this, we revealed a realistic set of model types and parameterisations for the Kimberley population, and a set for the Askham population, which covered a wide range of the possible parameter space.

Both model sets, Askham and Kimberley, were used to predict the range of possible responses of the sociable weaver population to a decrease in mean annual precipitation, as predicted by climate models (IPCC 2001). Finally, in the cross-validation of the population modelling and the space for time approach, we tested whether the models of the Kimberley rainfall regime were able to predict a realistic population density under the Askham rainfall regime, and vice versa.

### a. Model description

The model consisted of a 10 by 20 km<sup>2</sup> landscape with 20000 randomly scattered trees, on each of which a sociable weaver colony could be built. At this tree density, the availability of trees did not limit the population. Birds within each colony differed only by their age. Age classes were defined as juveniles (< 1 year), subadults (1 and 2 years) and adults (≥ 3 years), following the results of Covas (2002), who showed that 95% of birds did not breed below the age of 3 years. The main processes in the model, breeding, survival and dispersal, are described below.

#### (i) Breeding

The reproductive success (the number of fledglings per adult in colony *i* and year *t*) in each colony was simulated according to a widely used function of density dependence (Maynard Smith & Slatkin 1973, Bellows 1981):

$$B_{it} = B'_{it} / (1 + (1/A_B) \cdot NA_{localit}) \quad (1)$$

where  $B'_{it}$  is the maximum reproductive success without density dependence,  $A_B$  is a parameter describing the strength of density dependence and  $NA_{localit}$  is the local density of adult birds. Local density of adult birds included the birds of colony *i*, as well as birds from neighbouring colonies within a radius  $R_B$ , weighted by their distance:

$$NA_{localit} = NA_{it} + \sum_{j=1}^{NC_{Rit}} NA_{jt} \cdot w(d_{ij}) \quad \text{with} \quad w(d_{ij}) = 1 - (d_{ij}/R_B)^{\frac{1}{3}} \quad (2)$$

where  $NC_{Rit}$  is the number of colonies within a radius  $R_B$ ,  $NA_{it}$  is the number of adult birds in colony *i* at time *t*, and  $w$  is a weighting function in dependence of the distance  $d_{ij}$ . A negative density dependence of sociable weaver's reproductive success as described by Eq. (1) has been shown at our study site in Kimberley (chapter 3 of this thesis). The influence of neighbouring colonies (Eq. 2) adds a (necessary) form of global density regulation to the model, and is justified under the assumption that a depression of reproductive success in large colonies occurs mainly due to food depletion.

The effect of rainfall on reproductive success was included by letting maximum reproductive success in a given year ( $B'_t$ ) be a function of rainfall, as described below. In addition, local environmental noise was added by drawing  $B'_{it}$  for each colony from a normal distribution with a constant coefficient of variation  $CV_B$  and the expectation  $B'_t$ . Demographic noise was included by drawing the number of fledglings in each colony from a Poisson distribution with the expectation  $B_{it} \cdot NA_{it}$ .

#### (ii) Effect of rainfall

For the relationship between rainfall and reproductive success, three functions were compared: A linear function (Eq. 3), a saturation function (Eq. 4) and a saturation function with a threshold, below which reproduction was not possible (Eq. 5) (Fig. 3).

$$f(\text{Rain}) = a \cdot \text{Rain} \quad (3)$$

$$f(\text{Rain}) = B'_{\max} \cdot \text{Rain} / (k + \text{Rain}) \quad (4)$$

$$f(\text{Rain}) = \begin{cases} 0 & \text{if } \text{Rain} \leq R_{\min} \\ B'_{\max} \cdot (\text{Rain} - R_{\min}) / (k + (\text{Rain} - R_{\min})) & \text{if } \text{Rain} > R_{\min} \end{cases} \quad (5)$$

In the models with Eq. 4 and 5, rain entered the model either in a yearly resolution (Eq. 6) or in a monthly resolution (Eq. 7).

$$B'_t = f(\text{Rain}_t) \quad (6)$$

$$B'_t = \sum_{m=1}^{m=12} f(\text{Rain}_{tm}) \quad (7)$$

where  $\text{Rain}_t$  is the total rain in year  $t$  and  $\text{Rain}_{tm}$  is the rain in year  $t$  and month  $m$ . In the model with a linear relationship between rainfall and breeding success (Eq. 3), different temporal resolutions were not compared, as they do mathematically not change the model.

Further, reproductive success was either related to current rain (as above Eq. 6 or 7), or related to a weighted sum of current and previous rain (Eq. 8 or 9).

$$B'_t = f(\text{Rain}_t + 0.5 \cdot \text{Rain}_{t-1}) \quad (8)$$

$$B'_t = \sum_{m=1}^{m=12} f(\text{Rain}_{tm} + 0.5 \cdot \text{Rain}_{tm-1}) \quad (9)$$

Yearly or monthly rain was simulated by a stochastic rain model of South Africa, which is based on a statistical analysis of South African rain records of the past century (Zucchini *et al.* 1992). Using this model, realistic time series of annual or monthly rainfall were produced for the two regions, Kimberley and Askham. For simulations of climate change scenarios, these time series were modified accordingly (see below).

### (iii) Survival

Brown *et al.* (2003) gave evidence for an increased survival rate in large colonies, compared to medium-sized and small ones. According to their results, we assumed a sigmoid threshold function of survival rate in relation to colony size:

$$S_{it} = S_{\min} + (S_{\max} - S_{\min}) / (1 + e^{(A_s - N_{it})b_s}) \quad (10)$$

where  $S_{\min}$  is the survival rate in small colonies,  $S_{\max}$  is the survival rate in large colonies,  $A_s$  is the threshold colony size, above which survival rate raises,  $b_s$  is a parameter, determining the sharpness of the threshold, and  $N_{it}$  is the current colony size, including birds of all age classes. Further, local environmental noise was included by drawing the current survival rate in each colony from a beta distribution with the parameters  $\alpha = S_{it} \cdot (1/\text{Var}_s - 1)$  and  $\beta = (1 - S_{it}) \cdot (1/\text{Var}_s - 1)$ , where  $\text{Var}_s$  is a parameter scaling the variance of the distribution. Demographic noise was added

by drawing the number of surviving birds for each age class from a binomial distribution with  $p = S_{it}$ .

*(iv) Dispersal*

Two different processes were assumed for dispersal: dispersal and subsequent formation of new colonies, and dispersal, if colony size fell below a minimum threshold. For new colonisation, the emigration probability of a bird was simulated as a density dependent threshold function:

$$P_e = \begin{cases} D_P & \text{if } N \leq D_{\text{Thres}} / (1 - D_P) \\ (N - D_{\text{Thres}}) / N & \text{if } N > D_{\text{Thres}} / (1 - D_P) \end{cases} \quad (11)$$

where  $D_P$  is the emigration probability at low colony sizes, and  $D_{\text{Thres}}$  is the threshold colony size, above which the emigration probability raises quickly. During the colonisation process, emigrants were selected randomly according to their emigration probability. As the sociable weaver is obligatory colonial and new colonies are known to be found by a group of birds (White *et al.* 1975, M. Schwager, personal observation), we assumed that new colonisation was only possible if the number of emigrants exceeded a minimum group size  $N_{\text{minCol}}$ . If the minimum group size was exceeded, birds were distributed randomly into groups of the size  $N_{\text{minCol}}$  and emigrated. The emigrant groups selected randomly a tree within a radius of 2 km and established a new colony. If there was no unoccupied tree in the respective radius, the group moved 2 km into a random direction and searched for a tree within the same radius around their current position. Moving and searching for a tree was repeated until an unoccupied tree was found. The dispersal radius of 2 km was chosen as data on intercolony dispersal showed a preference of immigrating into a colony within a radius of 2 km of the home colony (R. Covas, unpublished data). No mortality was assumed during the colonisation process.

The obligatory coloniality of the sociable weaver was also accounted for by a minimum threshold of colony size  $N_{\text{min}}$ , below which all birds dispersed into randomly chosen colonies within the radius of 2 km. If there was no colony reachable within this radius, the dispersing birds died.

*(v) Simulations and parameter fitting*

In each model run, the main processes described above were repeated yearly in the following order: (i) dispersal and establishment of new colonies, (ii) breeding, (iii) mortality, and (iv) dispersal from small colonies. Model runs were initiated with 400 randomly distributed colonies of 40 adult birds. Simulations were run for 500 years and population parameters (mean population density, mean colony size, and mean coefficient of variation) were measured in the last 100 years of each model run. A time scale of 500 years was appropriate, as test runs showed that a stationary distribution of population size and population structure was mostly reached after about 100 years.

In the parameter-fitting procedure, each model type in Table 2 was repeatedly run under a random variation of all parameters, which had a high uncertainty (Table 3). Parameter combinations, which produced a realistic population size and structure, were selected for further simulations. A

realistic population size and structure was defined as having a mean population density between 20 and 100 birds per km<sup>2</sup>, a mean colony size between 30 and 60 birds, and a mean coefficient of variation of colony size larger than 0.5 (Covas 2002, Brown *et al.* 2003, M. Schwager, unpublished data). These ranges were chosen to be rather broad than narrow, as we wanted to test a wide range of the parameter space.

The parameter fitting procedure was done for the Askham rainfall regime and the Kimberley rainfall regime separately, by using time series of annual and monthly rainfall of the respective areas. The procedure was repeated, until 100 possible parameter combinations were available for each region and each model type of Table 2.

*(vi) Prediction of abundance under climate change*

Under scenarios of intermediate global warming, most climate models predict significant decreases in rainfall during the growing season in southern Africa by 5 to 15% (IPCC 2001). According to this scenario, we simulated the sociable weaver population under a 10% decrease in rainfall, by reducing each value in the random rainfall time series by 10%. Simulations were done with models of both regions, Kimberley and Askham, and for each model type and parameterisation. Simulations were done in 50 replicates, and the average reduction of population density was calculated for each parameterisation.

*(vii) Cross-validation*

In the cross-validation, all models of the Kimberley area were extrapolated to the rainfall regime of Askham, and vice versa. For both areas, mean annual precipitation in the model was systematically varied between 100 and 450 mm in steps of 20 mm, by changing each value of the random rainfall series accordingly. The resulting population density was recorded and compared to the population density revealed in the field study.

## b. Results

*(i) Prediction of abundance under climate change*

Under all model types, population density was decreased under the scenario of climate change. However, the sensitivity of the population depended strongly on the model type. In models with a linear relationship between rainfall and breeding success, the population responded extremely sensitive to the climate change scenario. The 10% decrease in mean annual precipitation led to a decrease in population density between 40 and 90%, or even extinction, in most models (Fig. 4, left). Inclusion of an effect of the previous year/ month slightly diminished the sensitivity of the Askham models, but had no effect in the Kimberley models.

In models with a saturation function between rainfall and breeding success, the sensitivity was greatly reduced, but still most of the parameterisations predicted a decrease in population density between 20 and 60% (Fig. 4, middle). Differences in the temporal resolution of the model, or

inclusion of an effect of rainfall in the previous month/ year had no major influence on the sensitivity, but monthly resolution slightly increased sensitivity.

In models with a saturation function with a lower threshold as a relationship between rainfall and breeding success, sensitivity was dependent on the temporal resolution, as well as on the inclusion of an effect of previous rainfall (Fig. 4, right). Monthly resolution greatly increased the sensitivity of the population, as at this time scale, rainfall was more often close to the threshold below which breeding was not possible. Including an effect of previous rainfall decreased the sensitivity, as it damped the effect of years/ month with extremely low rainfall.

#### *(ii) Cross-validation*

None of the models, which were fitted under the Kimberley rainfall regime, could predict a realistic population density under the Askham rainfall regime (Fig. 5). Under a linear relationship between rainfall and breeding success, all models of the Kimberley area predicted extinction of the population in Askham (Fig. 5, left). Under a saturation function between rainfall and breeding success, some parameterizations resulted in a small abundance under the Askham rainfall regime, but the observed population density of about 60 birds per km<sup>2</sup> was never reached (Fig. 5, middle and right). Further, nearly all models led to the extinction of the population below 100 mm mean annual precipitation, though sociable weavers are reported to occur in arid areas up to 80 mm mean annual precipitation (Maclean 1973, Mendelsohn & Anderson 1997).

Vice versa, all models which were fitted under the Askham rainfall regime, led to an unrealistically high population density in Kimberley (Fig. 6). Under a linear relationship between rainfall and breeding success, all models predicted a population density of more than 200 birds per km<sup>2</sup> in Kimberley (Fig. 6, left). In the other model types, predicted population densities under the Kimberley rainfall regime were lower under some parameterizations, but as before, the observed population density of about 60 birds per km<sup>2</sup> was never reached (Fig. 6, middle and right).

The results indicate a substantial difference between the models of the two respective areas. This difference is also shown in Fig. 7, where the relationship between breeding success and rainfall is compared between the Askham and the Kimberley models. The ranges of the functions overlap, but reproductive success was generally higher in the Askham models than in the Kimberley models.

## 5. Discussion

The response of populations to environmental changes depends strongly on the time scale at which these changes occur (Levin 1992). On a short time scale, direct effects like physiological constraints or direct influences on resources may prevail the response, whereas on longer time scales, indirect effects like shifts in the interactions between species, or evolutionary adaptations may mitigate or amplify the short-term response (Ives 1995, Forchhammer & Post 2004). The questions how species will be affected by climate change depends therefore on how quickly they

can respond to change (Roberts 1988, Root & Schneider 1993, McCarty 2001). However, studies, which aim to predict effects of climate change on populations are usually only based on either the short-term response of populations to naturally occurring fluctuations of the climate (here called the "population modelling approach"), or on the long-term response, given by a species' geographic distribution in relation to climate ("space for time approach").

In this study, we tested whether these two approaches lead to different predictions on a species' sensitivity to climate change, and if a cross-validation of the two approaches corroborates the predictions made by them. We used the sociable weaver and its sensitivity to a predicted decrease in mean annual precipitation as an example. In the "space for time approach" we compared population density and structure of the sociable weaver in two areas which differ largely in mean annual precipitation. The comparison showed no difference between the two populations. This result, as well as the wide distribution of the species ranging from 80 to 600 mm mean annual precipitation (Maclean 1973, Mendelsohn & Anderson 1997), would lead to the prediction that the species does not respond sensitively to a slight shift in mean annual precipitation of 5 to 15%, as it is predicted by most climate models (IPCC 2001). In contrast the "population modelling approach", based on a strong correlation between reproductive success and the short-term variation of rainfall, predicted a sensitive response in most of the tested model types. The contrast between the two approaches was stressed in the cross-validation, where population models of the high-rainfall Kimberley area were not able to predict a realistic population in the low-rainfall Askham area and vice versa.

We argue that these results were caused, as the two approaches reflect processes which act on different time scales. On a short time scale, the response of breeding success to annual rainfall causes strong population changes. But in a regional comparison, or at longer time scales, buffering or compensating mechanisms may balance the consequences of different mean precipitation in the two regions. However, if predictions how a species responds to climate change should be made, it would be essential to know how these mechanisms work, at which time scale they operate, and how fast (or if at all) they would follow the fast rate of future climate change.

Besides our study, we are aware of only two studies, which compared and validated predictions on the effect of climate change, using both approaches (Whittaker & Tribe 1996 *versus* 1998, Knapp *et al.* 2002). In contrast to our study, in both cases the cross-validation was successful and provided strong confidence into the predictions on the effect of climate change. However in many cases, mainly where indirect effects like interactions between species prevail over direct physiological effects, this may not be the case. Especially in arid and semiarid regions, the contrast between a sensitive short-term response to variation in precipitation on the one hand, and a broad distribution range on the other hand, as it has been shown here for the sociable weaver, may be a common pattern for many animal species (Skinner & Smithers 1990, Maclean 1993).



### Space for time approach

Population density in Kimberley and Askham did not differ, despite a difference in mean annual precipitation by a factor of more than two between the two areas. Population density was estimated about 60 birds per km<sup>2</sup> in both areas. This figure may be only a rough estimation, due to the small size of the surveyed areas compared to the high spatial variation in the abundance of sociable weaver colonies. However, in the (high rainfall) Kimberley region, colony abundance at our study site was much higher than in the surrounding areas, indicating rather an overestimation of population density in this area. In the (low rainfall) Askham region, the surveyed area covered sites with different tree densities and may therefore represent a more realistic picture of the overall population density in this region. On a larger scale, average population density might therefore even be higher in Askham than in Kimberley. Further, our estimates lay within the range of other estimates of sociable weaver abundance. Maclean (1973) estimated 80 birds per km<sup>2</sup> in the dry Nossob river bed, which is close to our study sites in Askham, but within which tree density is much higher. In an area in Namibia with 354 mm mean annual precipitation, population density was estimated 45 birds per km<sup>2</sup> from data on colony size and colony density of Marsden (1999).

Besides population density, also population structure given by the mean and coefficient of variation of colony sizes was very similar in the two areas. This may be surprising, as it has often been observed that nests in the north-western part of South Africa are larger than in Kimberley (M.D. Anderson, personal communication). However, the size of sociable weaver nests depends strongly of the size and species of the nesting tree (M. Schwager, unpublished data). The relatively low mean colony size in Askham of this study was caused mainly, as in Askham most of the recorded nests were situated on small *B. albitrunca* trees, whereas in Kimberley nearly all surveyed nests were on larger *A. erioloba* trees. If only nests on *A. erioloba* were considered, nests in Askham were in fact larger than in Kimberley ( $66.4 \pm 17.8$  versus  $37.1 \pm 6.9$ ; Mean  $\pm$  SE nestchambers per colony). Also this trend indicates rather a bias towards a higher population density in Askham than in Kimberley.

In summary, despite the strong effect of yearly rainfall on breeding success, the similarity between the two populations indicates a high insensitivity of sociable weaver abundance to mean annual precipitation, at least in the core of the distribution range. This is further supported by the distribution map (Mendelsohn & Anderson 1997), which shows (within certain boundaries) no strong association of reporting rates with mean annual precipitation. In general, the occurrence and abundance of sociable weavers may be more determined by vegetation structure than by climatic conditions. Mendelsohn & Anderson (1997) reported a strong association of the occurrence of sociable weaver colonies with the typical open savannah structure of the southern Kalahari vegetation, where reporting rates are more than three times greater than in any other vegetation type.

### Population modelling approach

The population modelling approach predicted a reduction in population density or even extinction under a decrease of mean annual precipitation by 10%. However the strength of the decrease depended strongly on the model type and on the parameterisation of the model. The difference between model types was most distinct between a linear function and a saturation function as a relationship between rainfall and breeding success. Temporal resolution and including an effect of rainfall in the previous month/ year, had only a pronounced effect on sensitivity, if a lower threshold of rainfall was assumed, below which breeding was not possible.

The difference between the various model types stresses the importance of the shape of the relationship between climate and demographic parameters for making predictions about a species' response to climate change. Also Laakso *et al.* (2001, 2004) emphasized in a broader context the crucial role of how exactly environmental fluctuations translate into demographic processes (i.e. the "biological filter" between environmental variation and biological processes) for population variability and extinction risk. However, it is often difficult to draw the exact shape of this relationship from field data, even if long-term time series are available. This is due to the complexity of non-linear responses and the frequent need to extrapolate the relationship to non-observed values. In many studies, a simple function (e.g. a linear function or an exponential function) has therefore been assumed *a priori* (e.g. Roy *et al.* 2001, Clark *et al.* 2003, Wichmann *et al.* 2003). Here, we intended to overcome this uncertainty by testing a high number of different relationships. Despite the high variation in sensitivity under these model types, all models predicted a decrease in population density under the tested scenario of climate change, and most models predicted a severe reduction.

### Comparison of the approaches: cross-validation

The cross-validation of the population modelling approach and the space for time approach showed clearly the inconsistency of the two approaches: Though all tested population models could predict realistic populations in either Kimberley or Askham, none of the tested models could predict a realistic population density in both areas. Parameterizations of the model, which lead to a realistic population under the Kimberley rainfall regime predicted extinction or a very low population size in Askham, and parameterisations of Askham predicted a unrealistically high population size in Kimberley. This was so, though we tested a high number of possible relationships between rainfall and reproductive success, as well as a high number of parameter combinations. Further, none of the models could predict the distribution range of the sociable weaver, covering areas from 80 to 600 mm mean annual precipitation.

We conclude that the similar population densities in Askham and Kimberley can only be explained, if the two populations differ in at least one of the essential demographic parameters, either in the relationship between rainfall and breeding success, or in the survival rate. This conclusion is supported as models of the Askham area had mostly a higher reproductive rate in

relation to rainfall than models of the Kimberley area. Such a geographic difference in the effect of climate on population dynamical processes has been found for several plant and animal species (Post & Stenseth 1999, Sanz 2002, Saether *et al.* 2003, Visser *et al.* 2003).

Aside from our case study of the sociable weaver, this interpretation of our results is straightforward. If less rain means a lower reproductive rate, areas with less rain (all other being similar) should have a lower population size. The same population size can only be reached, if other mechanisms exist, which balance the disadvantages of a lower mean annual precipitation, i.e. which increase reproductive success or survival rate. Such compensating mechanisms may either work as buffering mechanisms (*sensu* Jeltsch *et al.* 2000), or be independent of the difference in mean annual precipitation. Possible explanations cover behavioural or life history adaptations (genotypic or phenotypic) (e.g. Wichmann *et al.* in press), differences in the interactions with other species, either on the same or on different trophic levels (Ives & Gilchrist 1993), or differences in the physical environment.

In the case of the sociable weaver, the most likely explanation may be shifts in the interactions with other species. Populations of different species follow changes in the climate in different ways, with inevitable consequences for competitive and predator-prey interactions, and their feedbacks to local abundance (e.g. Ives & Gilchrist 1993, Ives 1995, Post *et al.* 1999, Fox & Morin 2001, Jiang & Kulczycki 2004). This topic has often been emphasized (Harrington *et al.* 1999, McCarty 2001, Walther *et al.* 2002, Forchhammer & Post 2004), however, we are far from an understanding of its implications for predicting the response of species to climate change. For the sociable weaver, differences in food availability in relation to rainfall, either caused by interspecific competition or by a different response of insect abundance to rainfall, as well as differences in the predation rate by snakes may be a likely explanation for a higher breeding success in Askham than in Kimberley.

Further, the two populations are known to differ in their flexibility of the beginning of the breeding season. Whereas sociable weavers in the Askham region start breeding only after the first considerable rains of the season (Maclean 1973), the population in Kimberley starts breeding in September, independently of the first rains (Covas 2002). The higher flexibility of the Askham population might be an adaptation to the higher unpredictability of rain in this area, in order to avoid investment in breeding attempts which are at a high risk of failure due to food shortage. A lower number of breeding attempts might in turn lead to a higher survival rate in Askham, as the number of breeding attempts of passerine birds is often negatively correlated with their survival rate (Dobson 1990). Also McCleery *et al.* (1998) reported a higher survival rate of Australian passerines in semi-arid areas than in more mesic areas, and suggested that this was caused by a shorter breeding season and consequently lower number of breeding attempts in the low rainfall areas. Finally, differences in the mean minimum winter temperature might be responsible for a higher survival rate of the sociable weaver in Askham (6.4 in Askham vs. 5.4°C in Kimberley,

South African weather service), as Covas (2002) showed a dependency of the survival rate on the mean minimum winter temperature.

#### Implications for model validation in ecological climate change research

Rastetter (1996) pointed out the crucial role for climate change research of the time scale at which models are developed, the time scale at which models are validated, and the time scale at which predictions can be made. He argued that models which were developed and validated on a short time scale (years or decades) did not proof their validity at the scale at which climate change may occur, i.e. decades or centuries. The same argument holds for space for time substitutions, which may reflect time scales of thousands of years (Rastetter 1996). However, there is no straightforward solution to this dilemma, as model development as well as model validation at the intermediate time scale appropriate for climate change is mostly not possible.

We propose that the cross-validation of short-term population models and the space for time approach may be a helpful step out of this dilemma. If the cross-validation is successful, as in the studies of Whittaker & Tribe (1996, 1998) and Knapp *et al.* (2002), it will provide strong confidence in the predictions to be valid also on an intermediate time scale. If it is not successful, as in our study, it will highlight the contrasts between long-term and short-term processes, and draw us to important mechanisms and processes where gaps of knowledge exist, on which future research should focus.

Table 1: Comparison of sociable weaver populations in the regions of Askham and Kimberley

	<b>Annual rain Mean <math>\pm</math> SD [mm]</b>	<b>Nestchambers per colony Mean <math>\pm</math> SE</b>	<b>Nestchambers per colony SD</b>	<b>Density of colonies [km<sup>-2</sup>]</b>	<b>Density of nestchambers <sup>1)</sup> [km<sup>-2</sup>]</b>
<b>Askham</b>	176 $\pm$ 72 <sup>2)</sup>	32.0 $\pm$ 5.1	33.1	1.45	46.24
<b>Kimberley</b>	400 $\pm$ 101 <sup>2)</sup>	36.7 $\pm$ 6.6	30.3	1.42	52.14

<sup>1)</sup> Calculated as average nestchambers per colony times density of colonies.

<sup>2)</sup> Zucchini *et al.* (1992)

Table 2: Overview of model types

<b>Relationship between rainfall and reproductive success</b>	<b>Temporal resolution</b>	<b>Time scale of effect</b>	<b>Rainfall regime of parameter fitting</b>
Linear	Yearly	Only current rainfall affects repr. success	Askham (low rainfall)
Saturation	Monthly	Current and previous rainfall affect repr. success	Kimberly (high rainfall)
Saturation with lower threshold			

*Table 3:* Ranges of model parameters. Parameter estimations are based on literature data (Maclean 1973, White *et al.* 1975, Covas 2002, Brown *et al.* 2003), and on an 8 year survey of the sociable weaver population in Kimberley (R. Covas, unpublished data). See model description for a detailed description of parameters.

	<b>Parameter</b>	<b>Estimated range</b>
<b>Reproduction in relation to rainfall</b>	a	0.002 - 0.04
	B' <sub>max</sub>	3 - 10 / 0.5 - 2 <sup>1)</sup>
	k	50 - 250 / 10 - 50 <sup>1)</sup>
	R <sub>min</sub>	25 - 50 / 5 - 25 <sup>1)</sup>
<b>Reproduction, other parameters</b>	A <sub>B</sub>	1 - 25
	R <sub>B</sub>	200 - 1000 m
	CV <sub>B</sub>	0.1 - 0.7
<b>Survival</b>	S <sub>min</sub>	0.55 - 0.75
	S <sub>max</sub>	0.65 - 0.9
	A <sub>S</sub>	60 - 120
	b <sub>S</sub>	0.05 - 1
	Var <sub>S</sub>	0 - 0.15
<b>Dispersal</b>	D <sub>P</sub>	0 - 0.2
	D <sub>Thres</sub>	200 - 400
	N <sub>min</sub>	3 - 8
	N <sub>minCol</sub>	10 - 30

<sup>1)</sup> First range: model with annual resolution; second range: model with monthly resolution

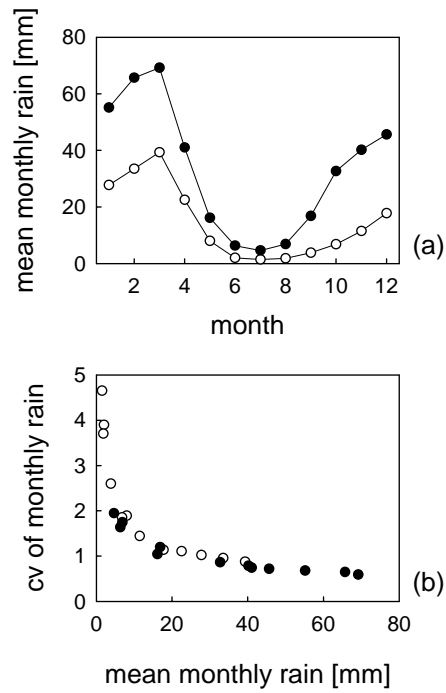


Figure 1: (a) Mean monthly rain and (b) coefficient of variation of rain in relation to mean in Kimberley (black circles) and Askham (white circles) (after Zuchini *et al.* 1992).

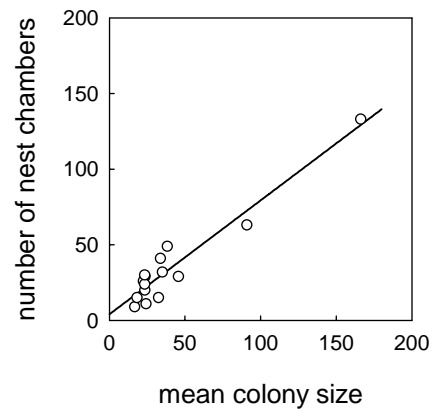


Figure 2: Number of nest chambers in a colony, in relation to colony size (mean over 8 years, Kimberley). Regression: adj.  $R^2 = 0.91$ ;  $p < 0.001$ ; slope =  $0.753 \pm 0.064$  (SE); intercept =  $4.08 \pm 3.55$  (SE).

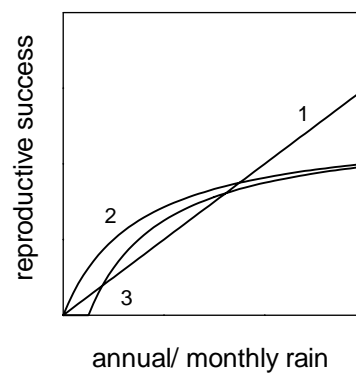
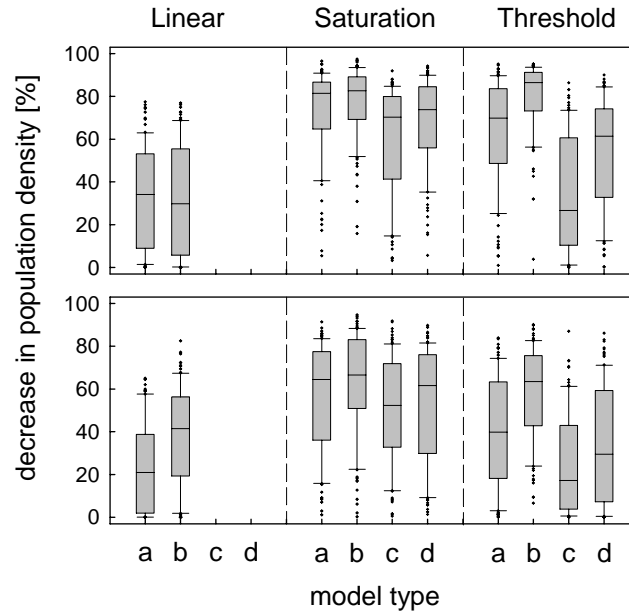
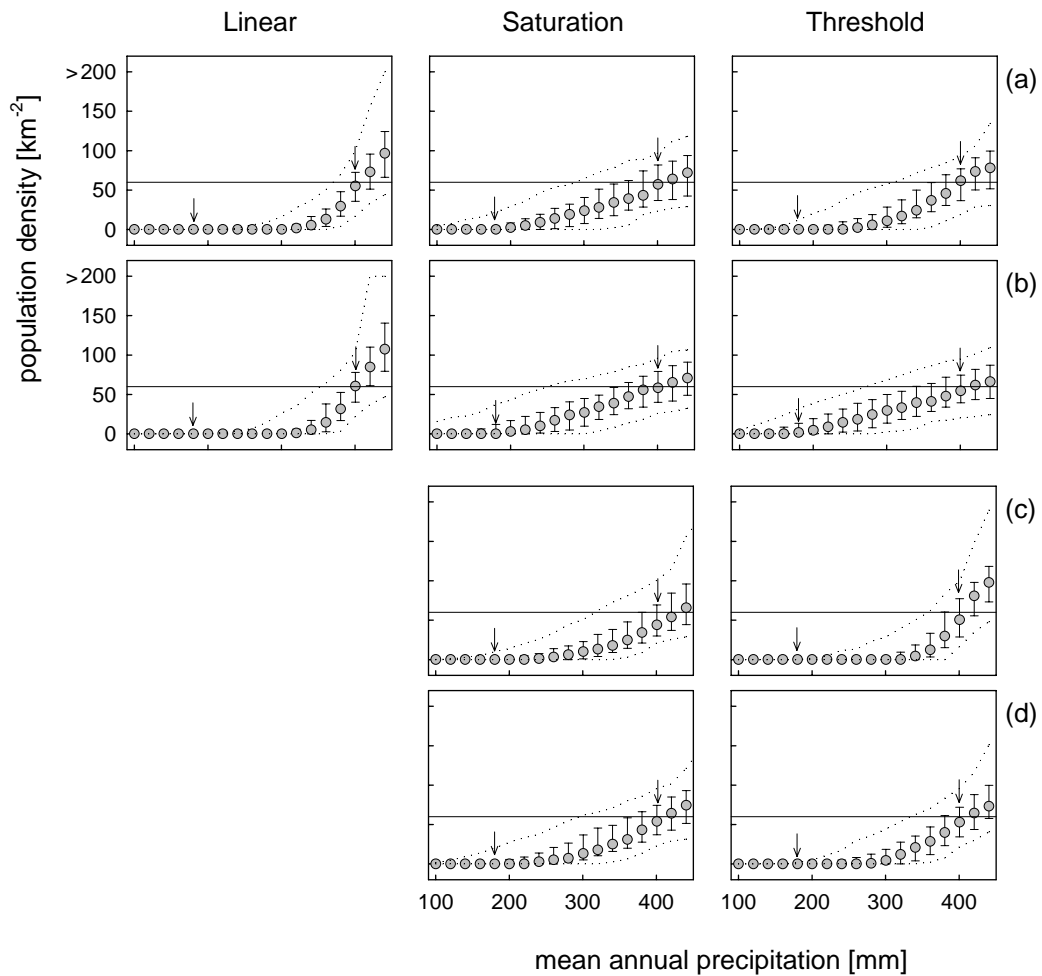


Figure 3: Relationship between reproductive success and annual/ monthly rain in different model types: (1) linear function; (2) saturation function; (3) saturation function with a lower threshold.

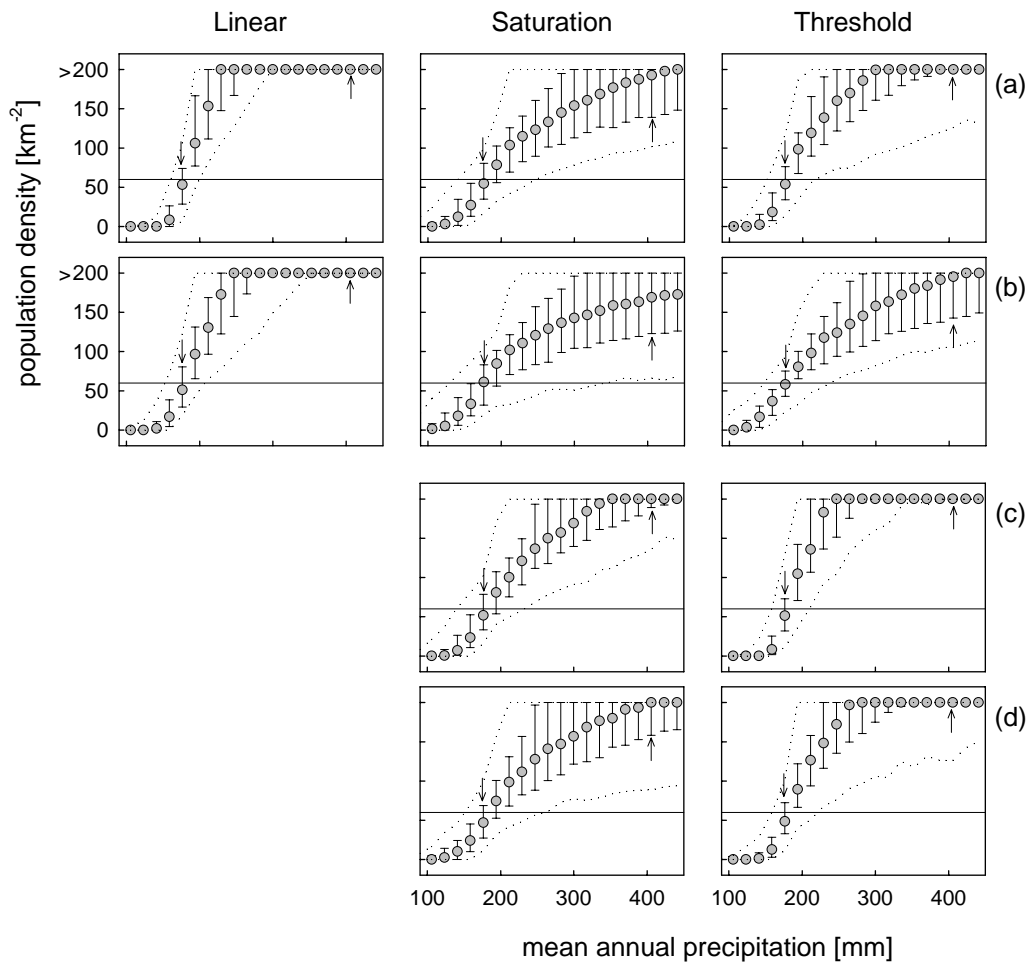




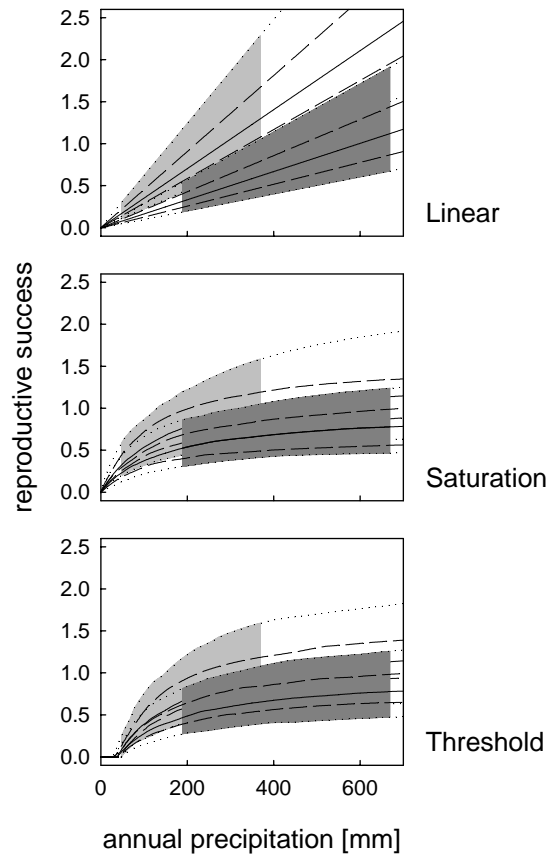
*Figure 4:* Decrease of population density, resulting from a decrease in mean annual precipitation by 10% in different model types. Top: models fitted under the Kimberley rainfall regime (400 mm mean annual precipitation); bottom: models fitted under the Askham rainfall regime (176 mm mean annual precipitation). Panels refer to different functions for the relationship between rainfall and reproductive success (Fig. 3, Table 2). Labels on the x-axis refer to further model types as in Table 2: (a) yearly resolution/ effect of current rainfall only; (b) yearly resolution/ effect of current and previous rainfall; (c) monthly resolution/ effect of current rainfall only; (d) monthly resolution/ effect of current and previous rainfall.



*Figure 5:* Population density in relation to mean annual precipitation, extrapolated from models of Kimberley (400 mm mean annual precipitation). Circles and errorbars show median, 0.25 and 0.75 quantiles, dotted lines show 0.05 and 0.95 quantiles. Solid lines show population density according to the field survey. Arrows indicate the mean annual precipitation in Askham and Kimberley, respectively. Columns refer to different functions for the relationship between rainfall and reproductive success (Fig. 3, Table 2). Rows refer to further model types as in Table 2: (a) yearly resolution/ effect of current rainfall only; (b) yearly resolution/ effect of current and previous rainfall; (c) monthly resolution/ effect of current rainfall only; (d) monthly resolution/ effect of current and previous rainfall.



*Figure 6:* Population density in relation to mean annual precipitation, extrapolated from models of Askham (176 mm mean annual precipitation). Circles and errorbars show median, 0.25 and 0.75 quantiles, dotted lines show 0.05 and 0.95 quantiles. Solid lines show population density according to the field survey. Arrows indicate the mean annual precipitation in Askham and Kimberley, respectively. Columns refer to different functions for the relationship between rainfall and reproductive success (Fig. 3, Table 2). Rows refer to further model types as in Table 2: (a) yearly resolution/ effect of current rainfall only; (b) yearly resolution/ effect of current and previous rainfall; (c) monthly resolution/ effect of current rainfall only; (d) monthly resolution/ effect of current and previous rainfall.



*Figure 7:* Reproductive success in a colony of 40 birds in relation to annual precipitation, in models fitted to the Askham (light grey) and Kimberley (dark grey) rainfall regime, respectively. Lines show 0.05, 0.25, 0.5, 0.75 and 0.95 quantiles of all fitted models; grey areas show the typical range of annual rainfall in the respective area. Rows refer to different functions for the relationship between rainfall and reproductive success (Fig. 3, Table 2). Results are displayed for the model with yearly resolution and effect of current rainfall only.

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In the second chapter I analysed the consequences of a shift in mean precipitation, as it might occur under climate change, for the sociable weaver *Philetairus socius*. I showed that making predictions about the response of a species to climate change is difficult, as the commonly used approaches operate on time scales which are either too long or too short compared to the time scale of climate change. I proposed that a cross-validation of approaches on different time scales may be an important step towards identifying gaps of knowledge, on which future research should focus.

In the next chapter I will analyse a spatial pattern of abundance. I will address the question, why the colony sizes of the sociable weaver are so variable, and why this spatial variation is not mitigated by a dispersal mechanism which selects for an optimal colony size.



# Chapter 3

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## Colony size variation explained by density dependent fitness - a model test for the sociable weaver *Philetairus socius*

Most colonially living bird species display a wide variation of colony sizes and several theories have been developed as an explanation for the occurrence of this variation. However, theories do not consider the specific form of the fitness function in relation to colony size of a species. We show here in a combined field and modelling study for the sociable weaver *Philetairus socius*, a colonial passerine of southern Africa, that the variation of colony sizes may be explained by the form of density dependence of reproductive success and survival, and by a dispersal strategy which may have evolved as a consequence of this density dependence. In the field study, we examine a real pattern of colony size distribution, estimate models for density dependence of reproductive success and survival rate, and derive an estimation of the per capita growth rate as a measure of fitness in relation to colony size. The per capita growth rate does neither follow an optimum function, nor a continuous decrease or increase with increasing colony size. Instead it is highest in small colonies, decreases at medium-sized colonies, but increases again slightly in large colonies. In the second part of the study, we simulate the population dynamics of the sociable weaver in a spatial explicit model, which is based on the results of the field study, and which includes an evolutionary optimisation process of dispersal strategy. A comparison of the resulting colony size distribution to the distribution in the field shows that the model can entirely explain the pattern of colony size distribution, even if no further assumptions are made, which would constrain the dispersal strategy towards the maintenance of the variation of colony sizes.

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In this chapter, the data of part 3 (field study) have been provided by Rita Covas. Data analysis and the modelling study are result of my own work.



Sociable weaver nest in the southern Kalahari  
Picture by F. Jeltsch

## 1. Introduction

Colony size is highly variable in many colonial bird species, ranging typically from less than ten to a few hundred or thousand birds (Brown *et al.* 1990). This naturally occurring high variation has often been used in studies on costs and benefits of living in colonies, within the general theory on the evolution and maintenance of coloniality (Siegel-Causey & Kharitonov 1990, Brown & Brown 1996, Danchin & Wagner 1997, Brown & Brown 2001). However, while the consequences of living in colonies of different sizes are well understood, the reason why such a high variation of colony sizes occurs is still unknown for many species.

The high variation in colony sizes is puzzling, as in most species several components of fitness such as breeding success, success in food acquisition, predation risk or infestation with parasites vary systematically with colony size (e.g. Hoogland & Sherman 1976, Møller 1987, Shields & Crook 1987, Wiklund & Andersson 1994, Brown & Brown 1996). The individual fitness of colony members may often be determined by a trade off between costs and benefits associated with particular colony sizes (Hoogland & Sherman 1976, Møller 1987, Wiklund & Andersson 1994, Brown & Brown 1996, Brunton 1999). Consequently, the existence of an optimal colony size, being at low, medium or large colony size, has often been proposed (e.g. Brown *et al.* 1990). However, if some colony sizes provide a higher fitness than others, birds should follow a dispersal strategy, which keeps colony sizes close to the optimum, and they should disperse from too small and too large colonies. Following these considerations, Brown *et al.* (1990) stated in a review on the choice of colony size in birds that "any general theory for the evolution of coloniality, if such a theory is possible, must account for colony size variation and for the choices individuals make that lead to this variation".

There are currently four hypotheses being discussed as a reason for the high variation of colony sizes (Brown *et al.* 1990, Brown & Brown 2001): (i) colony sizes may reflect the spatial

heterogeneity of habitat quality (e.g. Gibbs *et al.* 1987, Brown & Rannala 1995, Gibbs & Kinkel 1997, Griffin & Thomas 2000, Ambrosini *et al.* 2002, Brown *et al.* 2002). (ii) The variation of colony sizes may be a result of intercolony competition for food (e.g. Furness & Birkhead 1984, Ainley *et al.* 1995, Zemel & Lubin 1995, Griffin & Thomas 2000, Forero *et al.* 2002, Ainley *et al.* 2004). (iii) Birds may vary individually in their choice of optimal colony size (Pulliam & Caraco 1984, Brown & Brown 2000, Møller 2002, Brown *et al.* 2003). (iv) Achieving an optimal colony size may be constrained by the behaviour of individuals of seeking and joining a group (Fretwell & Lucas 1970, Sibley 1983, Pulliam & Caraco 1984, Giraldeau & Gillis 1985, Higashi & Yamamura 1993, Rannala & Brown 1994).

All hypotheses have a potential to explain the wide variation of colony sizes and have support in field data for some species. However, though all are based on the assumption that fitness varies between different colony sizes, they do not consider the specific shape of the fitness function in relation to colony size. Theoretical studies on group living species mostly assume that fitness in relation to colony size follows a unimodal function (e.g. Sibly 1983, Pulliam & Caraco 1984, Giraldeau & Gillis 1985, Higashi & Yamamura 1993, Rannala & Brown 1994, Avilés 1999, Avilés *et al.* 2002). Although there is only limited empirical evidence for an optimum function of fitness (Brown & Brown 2001), it is an intuitively appealing assumption under the consideration of different costs and benefits of coloniality. As an alternative to a unimodal function, a continuous decrease or increase of fitness in relation to colony size has been proposed for species where living in large colonies is dominated by either costs or benefits (Brown *et al.* 1990). However, the interaction between positive and negative effects of colony size may also result in a different shape of the fitness function, and this shape may be crucial for explaining the choice of birds to stay in colonies of different sizes, given that the function has not only one, but several maxima, or that density dependence is generally low (Brown & Brown 2001, Brown *et al.* 2003).

In this paper, we show in a combined field and modelling study for the sociable weaver *Philetairus socius*, a colonial passerine of southern Africa, that the variation of colony sizes may be explained by a fitness function, which differs from a unimodal or a continuous function. In the first part of our study, we show the frequency distribution of colony sizes of the sociable weaver, and estimate a model of the per capita growth rate in relation to colony size, as a measure of fitness. Brown *et al.* (2003) gave evidence that the survival rate of the sociable weaver is slightly higher in large colonies, compared to medium and small ones. We accomplish this study by data on density dependence of reproductive success and combine both, survival and reproductive success, to calculate the per capita growth rate in a given colony size.

In the second part, we develop an individual based spatial-explicit simulation model for the sociable weaver, which is based on the density dependence of reproductive success and survival observed in the field, and which includes an evolutionary optimisation process of the dispersal strategy. Using this model, we test the following hypothesis: (i) The form of density dependence of reproductive success and survival generates the observed colony size distribution, and allows

the evolution of a dispersal strategy which maintains the occurrence of different colony sizes. (ii) The variation of colony sizes is only maintained, if birds are constrained in their dispersal strategy from leaving unfavourable colony sizes. We consider two types of constraints for dispersal: First, switching between different colony sizes during intercolony dispersal may be bound to fitness costs, because of physiological or behavioural adaptations to a specific colony size. This would lead to an individual preference for a specific colony size, a mechanism which has been proposed as an explanation for the variation in colony sizes (see above; Brown & Brown 2000, Møller 2002, Brown *et al.* 2003). An individual preference for a specific colony size has been shown for the sociable weaver by Brown *et al.* (2003) and may be a reason for the variation of colony sizes in this species. Second, the formation of new colonies may be bound to fitness costs. Fitness costs of new colonisation have not been stated yet as a possible explanation for the variation of colony sizes. However, they may prevent birds from escaping from unfavourably large colonies by the foundation of new small ones. For the sociable weaver, it is not known whether the establishment of new colonies is associated with fitness costs, as new colonisation has rarely been observed. However, it could be a process, which is at high risk of failure, as it means exploring a new unknown nest site, as well as a considerable effort of constructing a new nest.

## 2. Study species

The sociable weaver is a colonial passerine bird, endemic to semiarid and arid savannahs of southern Africa. It builds large apartment block like communal nests of grass and twigs, with multiple separate chambers that are occupied over the whole year. Nests are mainly built on large *Acacia erioloba* trees, but also on other tree species or human made structures (Maclean 1973, Mendelsohn & Anderson 1997). Maclean (1973) reported highly variable colony sizes, ranging from 2 to 500 birds. However, colonies of only two birds seem to be a short-term exception (Maclean 1973). We therefore assume that the sociable weaver is obligatory colonial, which is further supported by the observation that new colonies are usually found by a group of birds (White *et al.* 1975, M. Schwager, personal observation). The obligatory coloniality may be caused by the high effort of constructing and maintaining the complex nest, which provides protection from predators and thermal benefits in winter and summer (White *et al.* 1975, Maclean 1973, Bartholomew *et al.* 1976). Dispersal between colonies is low and birds remain quite faithful to the same colony site from year to year (Brown *et al.* 2003). Sociable weavers feed predominantly on insects, but also on grass seeds (Maclean 1973, Ferguson 1988). Reproduction (length of breeding season, clutch size, fledgling success) is closely related to rainfall, as rain is the main determinant of food availability (Maclean 1973, Marsden 1999, Covas 2002). Nest predation by snakes (mainly cape cobra *Naja nivea* and boomslang *Dispholidus typus*) is a main cause of reproductive failure, leading to a mean loss of 75% of broods in our study area (Maclean 1973, Marsden 1999, Covas 2002).

### 3. Field study: Colony size distribution and density dependence of reproductive success, survival and per capita growth rate

#### a. Methods

The study was located in an open *Acacia erioloba* savannah at Benfontein Game Farm, 6 km southeast of Kimberley, South Africa (ca. 28°53' S, 24°49' E). At this site, the abundance of sociable weaver colonies was high, with about 25 colonies within the study area of approximately 3.5 x 5.5 km<sup>2</sup>. The area is semi-arid, experiencing low and unpredictable rainfall (Mean ± SD = 421 ± 139 mm per year, South African Weather Service, unpublished data), which falls mainly in the summer month.

The frequency distribution of colony sizes was calculated from data of an 8 year capture mark recapture study between August 1993 and November 2000 (Covas 2002, Brown *et al.* 2003), where 20 colonies were repeatedly captured with mist nets, and the number of birds was determined. Data were available for 6 to 18 colonies per year.

Reproductive success was determined in the years 1999 and 2000, by repeatedly checking the individual nestchambers of a colony for the occurrence of eggs and chicks with a dentist mirror. The number of chicks present 17 days after hatching was assumed to be the number of young fledged from that nest. Reproductive success was defined as the number of fledged young in a colony, divided by the size of the colony.

A model for density dependence of reproductive success was estimated by adjusting the following equation to the data by non-linear regression:

$$B = B' / (1 + (1/A) \cdot N) \quad (1)$$

where B' is the reproductive success without density dependence, A is a parameter defining the strength of density dependence, and N is the colony size. Eq. (1) is a simplified form of a widely used model for density dependence (Maynard Smith & Slatkin 1973), which has been proposed by Bellows (1981) to be able to describe a wide range of data on density dependence. As data on reproductive success in the same colony in two successive years were dependent on each other and could not enter the regression analysis as independent data points, data were pooled for one colony by doing the regression analysis with the means of colony size and reproductive success over the two years.

For survival rate, we used the results of Brown *et al.* (2003), who found a strong indication for a higher survival rate in large colonies (> 60 birds), compared to small (0 to 30 birds) and medium-sized (30 to 60 birds) ones, but no difference between small and medium-sized colonies. Mean survival rate was 0.660 ± 0.023 (SE) in small and medium colonies and 0.751 ± 0.040 (SE) in large colonies. According to these results, a model for survival rate was estimated as:

$$S = \begin{cases} S_{\min} & \text{if } N \leq N' \\ S_{\max} & \text{if } N > N' \end{cases} \quad (2)$$

with  $S_{\min} = 0.660$ ,  $S_{\max} = 0.751$  and  $N' = 60$ .

A model for the per capita growth rate was estimated, by combining the models on reproductive success and survival rate:

$$R = S \cdot (B + 1) \quad (3)$$

where  $S$  is the survival rate given by Eq. 2 and  $B$  is the reproductive success given by Eq. 1. The model was compared to the growth rates of colonies in our study area, which were calculated as

$$R = N_{t+1} / N_t \quad (4)$$

for all colonies for which colony size was available in two successive years.

## b. Results

The frequency distribution of colony sizes was characterized by a right skewed distribution with a clear peak at medium-sized colonies of 20 to 40 birds, and a long tale of the distribution at large colonies, reaching up to more than 200 birds (Fig. 1a). Within a year, mean colony size was  $41.1 \pm 4.1$  (SE) and the coefficient of variation was  $0.86 \pm 0.07$  (SE).

Reproductive success decreased significantly with increasing colony size ( $p < 0.05$ ) (Fig. 1b). The negative density dependence was overlaid by a high variation, as indicated by a low  $R^2$  (adj.  $R^2 = 0.22$ ). The regression coefficients were  $B' = 4.2 \pm 13.6$  (SE) and  $A = 2.9 \pm 10.8$  (SE).

The per capita growth rate was highest in very small colonies, declined at medium-sized colonies, but increased again slightly in large colonies (Fig. 1d). Due to the slight increase in large colonies, density dependence of the growth rate was generally low in medium and large colonies. A comparison of the estimated growth rate to the field data generally supports the model (Fig. 1d). However, as for reproductive success, the model is overlaid by a very high variation.

## 4. Simulation model: Explaining the pattern of colony size distribution

The population dynamics of the sociable weaver was simulated in a spatial-explicit model, which included the density dependence of reproductive success and survival rate, shown in the previous section. In this model, different components of the dispersal strategy of individual birds (the probability to emigrate and found a new colony, the probability to disperse between colonies, and the choice of immigration colony) were optimised in an evolution process of random mutations and selection.

As many parameters of the model have a high uncertainty, reasonable parameter values were derived in a parameter fitting procedure by comparing the distribution of colony sizes which emerged from the model with the pattern of colony size distribution in the field. This method of



"pattern oriented modelling" is a widely used approach for the parameterisation and validation of models (Grimm *et al.* 1996, Wiegand *et al.* 2003).

In this procedure, the model was repeatedly run under a random variation of all unknown parameters within certain limits, and parameter combinations, where the model was able to produce the pattern in the field, were selected. We chose two different criteria for the fit between the model population and field data. In a narrow one, the model should be able to explicitly reproduce the frequency distribution of colony sizes, observed in the field study. In a more general one, the model should be able to produce a low mean and a high variation of colony sizes. The model was generally assumed to explain the observed pattern of colony sizes, if at least one parameter combination was found, where the model fitted the field data according to the first criterion.

The hypotheses stated in the introduction were tested by comparing (i) a model without any constraints on dispersal (ii) a model with a slight mortality during switching colony size and (iii) models with different survival rates during colonisation. As the analysis in part one indicated only a slight effect of colony size on survival rate, we tested also the relevance of the increase in survival in large colonies for the maintenance of the pattern of colony size distribution. This was done by comparing the main model with a model, where the survival rate was independent of colony size. A summary of these model types is given in Table 1.

Besides constraints on the dispersal strategy, our model necessarily included other processes which may have enhanced the variation of colony sizes. First, our model included a certain degree of intercolony competition. This was necessary as a means of global density regulation, as it prevents the model population from growing without boundaries. Assuming intercolony competition is justified if the depression of breeding success in large colonies occurs mainly due to food depletion. Second, temporal variation of reproductive success and survival may lead to a higher variation of colony sizes. To test whether these processes were relevant for the variation of colony sizes, we compared the parameters, which determine these processes, in fitting and non-fitting models. We would assume a major influence of these processes only, if the respective parameter values were considerably higher in fitting models.

#### a. Model Description

The model consisted of a 10 by 20 km<sup>2</sup> landscape with 20000 randomly scattered trees, on each of which a colony could be built. At this tree density, the availability of trees did not limit the population. Birds within each colony differed individually by their age and by their dispersal strategy. Age classes were defined as juveniles (< 1 year), subadults (1 year and 2 years) and adults (≥ 3 years), following the results of Covas (2002), who showed that 95% of birds did not breed below the age of 3 years. The dispersal strategy of an individual bird was defined by four different parameters of intercolony dispersal and colonisation (see below). The main processes in the model were breeding, survival and dispersal. All processes were kept as simple as possible, but

implemented detailed enough to reveal a realistic picture of the spatial population dynamics of the sociable weaver.

(i) *Breeding*

The reproductive success in each colony was given by the density dependent equation:

$$B_{it} = B'_{it} / (1 + (1/A_B) \cdot NA_{localit}) \quad (5)$$

where  $B_{it}$  is the number of fledglings per adult in colony  $i$  and year  $t$ ,  $B'_{it}$  is the reproductive success without density dependence,  $A_B$  is a parameter describing the strength of density dependence and  $NA_{localit}$  is the local density of adult birds. The equation accounts for local density dependence of reproductive success, as revealed in the previous section. In addition to this, an influence of neighbour colonies on local reproductive success was assumed by letting local density of adult birds be the sum of all neighbouring colonies within a radius  $R_B$ , weighted by their distance:

$$NA_{localit} = NA_{it} + \sum_{j=1}^{NC_{Rit}} NA_{jt} \cdot w(d_{ij}) \quad \text{with} \quad w(d_{ij}) = 1 - (d_{ij}/R_B)^{\frac{1}{3}} \quad (6)$$

where  $NC_{Rit}$  is the number of colonies within the radius  $R_B$ ,  $NA_{it}$  is the number of adult birds in colony  $i$ , and  $w$  is a weighting function in dependence of the distance  $d_{ij}$ . The strength of intercolony competition is determined by the radius  $R_B$ , within which an effect of neighbouring colonies occurs.

As reproductive success of the sociable weaver follows closely the amount of rainfall (Maclean 1973, Marsden 1999, Covas 2002), a dependence on rainfall was added by letting  $B'$  in year  $t$  be a linear function of yearly rain:

$$B'_t = B'_{Rain} \cdot Rain_t \quad (7)$$

where rainfall  $Rain_t$  was randomly drawn from a time series of yearly rainfall in Kimberley from 1960 until 2000 (South African Weather Service, unpublished data). In addition to environmental noise caused by rainfall, local environmental noise was added by drawing  $B'_{it}$  for each colony from a normal distribution with expectation  $B'_t$  and a constant coefficient of variation  $CV_B$ . Assuming a high coefficient of variation accounts for the strong local variation of reproductive success, indicated by our data in part one. Demographic noise was included by drawing the number of fledglings of each adult bird from a Poisson distribution with the expectation  $B_{it}$ .

(ii) *Survival*

In our main model (model 1, Table 1), the survival rate in colony  $i$  at time  $t$  increased with increasing colony size as a sigmoid threshold function.

$$S_{it} = S_{min} + (S_{max} - S_{min}) / (1 + e^{(A_S - N_{it})b_S}) \quad (8)$$

where  $S_{\min}$  is the survival rate in small colonies,  $S_{\max}$  is the survival rate in large colonies,  $A_S$  is the threshold colony size, above which survival rate raises,  $b_S$  is a parameter, determining the sharpness of the threshold, and  $N_{it}$  is the current colony size, including birds of all age classes. The equation accounts for the density dependence of the survival rate, as shown in the previous section.

In model (2) the survival rate was constant:

$$S_{it} = S \quad (9)$$

Local environmental noise was included by drawing the current survival rate in each colony from a beta distribution with the parameters  $\alpha = S_{it} \cdot (1/\text{Var}_S - 1)$  and  $\beta = (1 - S_{it}) \cdot (1/\text{Var}_S - 1)$ , where  $\text{Var}_S$  is a parameter scaling the variance of the distribution. Demographic noise was added by drawing the number of surviving birds for each age class and dispersal type from a binomial distribution with  $p = S_{it}$ .

### (iii) Dispersal

Three different processes were assumed for dispersal: intercolony dispersal, dispersal and subsequent formation of new colonies and dispersal, if colony size fell below a minimum threshold. The third form of dispersal is based on the assumption that the sociable weaver is obligatory colonial. Obligatory coloniality was also accounted for in the process of new colonisation, by assuming that a minimum number of birds was needed for establishing a new colony.

*Intercolony dispersal:* Each individual bird was assigned two parameters, describing its dispersal strategy for intercolony dispersal: A constant emigration probability ( $\text{DIC}_P$ ) and a parameter ( $\text{DIC}_{\text{Choice}}$ ), describing its choice for immigration colony.  $\text{DIC}_{\text{Choice}}$  could either be a preference for colonies of the same size class ( $\text{DIC}_{\text{Choice}} = 1$ ), or random selection of immigration colony ( $\text{DIC}_{\text{Choice}} = 0$ ). If  $\text{DIC}_{\text{Choice}}$  was 1, birds had a ten times higher probability to immigrate into a colony of the same size class than to immigrate into a random colony. Size classes were defined as in Brown *et al.* (2003) as small (< 30 birds), medium (30 to 60 birds) and large (> 60 birds).

As data on intercolony dispersal showed that 93% of dispersing birds immigrated into colonies within a radius of 2 km (R. Covas, unpublished data), intercolony dispersal was restricted to this radius in the model. If there was no other colony within this radius, birds did not disperse.

The survival probability during immigration into a colony of the same size class was always one. Survival probability while immigrating into a colony of a different size class was either 1 or 0.9, as indicated in Table 1.

*Colonisation:* Each bird had an individual emigration probability, which followed a threshold function with increasing colony size:

$$P_e = \begin{cases} \text{DNC}_P & \text{if } N \leq \text{DNC}_{\text{Thres}} / (1 - \text{DNC}_P) \\ (N - \text{DNC}_{\text{Thres}}) / N & \text{if } N > \text{DNC}_{\text{Thres}} / (1 - \text{DNC}_P) \end{cases} \quad (10)$$

The function is described by two parameters:  $DNC_p$ , the emigration probability at low colony sizes, and  $DNC_{Thres}$ , the threshold colony size, above which the emigration probability raises quickly. The two parameters were assigned to individual birds, and defined their dispersal strategy for colonisation.

During the colonisation process, emigrants were selected randomly according to their emigration probability. If the number of emigrating birds in one colony exceeded the minimum group size  $N_{min_{Col}}$ , which was necessary for establishing a new colony, birds were distributed randomly into groups of the size  $N_{min_{Col}}$  and emigrated. The emigrant groups selected randomly a tree within a radius of 2 km and established a new colony. If there was no unoccupied tree in the respective radius, the group moved 2 km into a random direction and searched for a tree within the same radius around their current position. Moving and searching for a tree was repeated until an unoccupied tree was found.

New colonisation was either successful, or failed and the involved birds died. The probability of success was defined by the survival probability of colonisation, and varied in different models, as shown in Table 1.

*Dispersal at low colony size:* A minimum threshold of colony size was defined by the parameter  $N_{min}$ . If colony size fell below this threshold, all birds immigrated randomly into colonies within the radius of 2 km. If there was no colony reachable within this radius, the emigrating birds died.

The main processes described above were repeated yearly in the following order: (i) intercolony dispersal, (ii) dispersal and establishment of new colonies, (iii) breeding, (iv) survival, and (v) dispersal from small colonies.

#### *(iv) Evolution of dispersal strategy*

The four parameters, which describe the dispersal strategy of an individual bird,  $DIC_p$ ,  $DIC_{Choice}$ ,  $DNC_p$  and  $DNC_{Thres}$  were inherited from a (nonsexual) parent, but random mutations occurred in each parameter at a rate of  $10^{-4}$ . If a mutation occurred, the respective parameter was randomly determined within the following ranges:  $DIC_p$  [0, 0.5];  $DIC_{Choice}$  0 or 1;  $DNC_p$  [0, 0.5]; and  $DNC_{Thres}$  [ $N_{min_{Col}}$ , 400].

#### *(v) Simulation runs*

For each model in Table 1, 1000 replicates were done with a random variation of all relevant, but unknown parameters (Table 2). If available, parameter ranges were selected according to confidence limits from field data, in other cases, ranges had to be estimated. However, though some ranges are based on estimates, our results show that parameters were selected in a reasonable range. Of all random parameter combinations, only those were considered, where the model population did not become extinct, and where an unrealistically high population density of 300 birds  $km^{-2}$  was not exceeded. After each run, the colony size distribution in the model was compared to field data as described below.

In each run, the model was initiated with 400 randomly distributed colonies of 20 adult birds. The initial dispersal strategy was  $DIC_p = 0.1$ ;  $DIC_{Choice} = 1$ ;  $DNC_p = 0$  and  $DNC_{Thres} = N_{minCol}$ . However, several test runs showed that the resulting dispersal strategy was independent of initial conditions. The model was run for 10000 years, which was appropriate, as in test runs a steady state of dispersal strategies was reached after about 5000 years.

*(vi) Comparison to field data*

For the first criterion, the frequency distribution of colony sizes in the field was described by the means and the standard deviations of its percentiles over the sampling period. For both, means and standard deviations, 95% confidence intervals were produced by a bootstrap algorithm according to the following procedure: For each bootstrap sample, a permutation of the years, for which colony sizes were available, was drawn (7 years), and for each year a permutation of the colonies (9 to 18 colonies, depending on year). In each sample, the percentiles were determined in every year, and mean and standard deviation of percentiles were calculated over the 7 years. Confidence limits for means and standard deviations of percentiles were obtained as the 0.025 and 0.0975 percentiles of 10000 bootstrap samples, and are shown in Fig. 2.

A similar procedure was used to determine the means and standard deviations of percentiles in the model. In the last 500 years of a model run, each year 15 colonies were randomly selected, the percentiles were determined, and mean and standard deviation were calculated for each percentile over the 500 year sampling period. A model run was assumed to fit the data, if means as well as standard deviations of all percentiles were within the confidence limits of the field data.

The wider criterion two, low mean and high variation of colony sizes, was assumed to be met, if mean colony size in the last 500 years of the model run was between 30 and 60 birds, and if the mean coefficient of variation of colony size within a year was higher than 0.5 in the respective time period.

*(vii) Data analysis*

For each model, the percentage of parameter combinations, where the model fitted the field data according to the two criteria, was determined. Additionally, the mean per capita growth rate as a function of colony size was calculated for each parameter combination.

In a further analysis, the means of the parameters, which define the dispersal strategy, were calculated in the last 500 years of each model run, and compared between fitting and non-fitting models, according to criterion one. The comparison was done by a multifactorial ANOVA with the model  $Fit + Fit*NC_{Surv} + Fit*IC_{Surv}$ , where  $NC_{Surv}$  is the survival probability of colonisation and entered the model as a covariate, and  $IC_{Surv}$  is the survival probability of switching colony size and entered the model as a fixed factor. As the sample size was highly unbalanced between fitting and non-fitting models, the analysis was done with random subsamples of size 10 for each factor combination, where more than 10 model runs were available. Some of the analysed variables were log or arcsin-transformed (Table 3) to meet homogeneity of variances and normal distribution of

data. In some cases, the precondition of homogeneity of variances was still violated, however an examination of residual plots showed no specific pattern, and let us assume, that the ANOVA was justified. An exception was the mean of the dispersal parameter  $DIC_{\text{Choice}}$ . Here, the analysis was only done for model (1) without costs of switching colony size. In addition to F-values, partial  $\eta^2$  were calculated, which is a measure of the proportion of the total variance that is explained by a specific factor (e.g. Zar 1999).

The parameters, which define the degree of intercolony competition ( $R_B$ ) and the temporal variation of reproductive success and survival ( $CV_B$  and  $Var_S$ ) were compared in an ANOVA analysis as described above for the dispersal strategies. The ANOVA model was  $\text{Fit} + \text{Fit} * \text{NC}_{\text{Surv}} + \text{Fit} * \text{IC}_{\text{Surv}}$ , where both  $\text{IC}_{\text{Surv}}$  and  $\text{NC}_{\text{Surv}}$  entered the model as a fixed factor, as we do not necessarily assume a monotonic relationship here. All statistical analysis was done with SPSS 12.0.

## b. Results

### (i) Fit of model to field data

In our main model (model 1, Table 1), parameter combinations, where the model fitted the field data according to criterion one, were found for all tested model types, with and without constraints on dispersal strategy (Fig. 3a). Still, the percentage of fitting parameter combinations was higher, if new colonisation was bound to a considerable mortality. Including a mortality of switching colony size in the model had no major effect on the results. In contrast, model (2) could explain the colony size pattern according to criterion one only, if both, a considerable mortality during colonisation and mortality of switching colony size were assumed (Fig. 3b).

In general, the percentage of parameter combinations, where the model fitted the data according to criterion one, was low (less than 2.5%). This shows that only very specific parameter combinations could explain the precise pattern of colony size distribution in the field. However, Fig. 3e to h show that the fitting models were no random outliers, but were well within the distribution of mean and variation of colony sizes that emerged from the different parameter combinations. Further, the more general pattern of criterion two, a low mean and high variation of colony size, was met by a high percentage of parameter combinations (up to 30%, Fig. 3c and d). Here, few fitting parameter combinations were also found in model (2) without assuming any fitness costs of dispersal.

Fig. 4 shows the function of the mean per capita growth rate in relation to colony size in fitting models (criterion one) versus all models. In model (1), the growth rate in fitting models was highest in small colonies, equalled one at a colony size of about 40 birds, and switched between slightly under and slightly over one in larger colonies (Fig. 4a to f). In model (2), the fitting models were those, where the growth rate in large colonies was highest (Fig. 4g). However, as here the survival rate did not increase in large colonies, the mean growth rate was clearly below one in large colonies in all models. In general, the curves of fitting models covered only a small

section of all models, showing again that only specific parameter combinations can produce the precise pattern of colony size distribution according to criterion one.

*(ii) Dispersal strategies*

In all models, a polymorphism of several dispersal strategies evolved. Fig. 5 shows the means of the four parameters which defined the dispersal strategy in the different model types, and in fitting versus non-fitting models according to criterion one.

As expected, the probability of new colonisation increased with increasing survival during new colonisation, indicated by an increasing  $DNC_P$  and a decreasing  $DNC_{Thres}$  (Fig. 5a to d). However, under high survival rates during colonisation, the range of colonisation probabilities was clearly wider in model (1) than in model (2). Colonisation probability was much lower in fitting than in non-fitting models, if survival during colonisation was high (Fig. 5a to d). The difference, depending on survival during colonisation, was significant (Table 3), and indicates that a low colonisation rate was necessary to explain the pattern of colony sizes.

The probability of intercolony dispersal  $DIC_P$  decreased with increasing survival during colonisation, i.e. a higher rate of intercolony dispersal evolved, if birds were prevented from new colonisation by a high mortality (Fig. 5e and f). In model (1),  $DIC_P$  in fitting models was slightly lower than in non-fitting ones, and the difference was larger if costs of colonisation were low, or if no costs of switching colony size were assumed. In model (2), fitting models had a higher  $DIC_P$ , but the difference was not significant (Table 3).

The preference for an immigration colony of the same size class,  $DIC_{Choice}$ , could either be selected against or selected for in model (1), even if no costs of switching colony size were assumed (Fig. 5g, left). Fitting models had a higher mean  $DIC_{Choice}$ , if colonisation was not associated with high costs. The interaction between model fit and survival probability of colonisation was significant (Table 3). The difference indicates that the evolution of a preference for a specific colony size was important for maintaining the pattern of colony size distribution, at least if costs of new colonisation were low. In model (2),  $DIC_{Choice}$  was selected against, as long as survival during colonisation was low (Fig. 5h, left). At high survival rates during colonisation, colony sizes in model (2) stayed so small, that a preference for a certain colony size had no consequences, and was not selected against. As expected, in both models, a mean  $DIC_{Choice}$  close to one evolved, if slight costs of switching colony size were assumed (Fig. 5g and h, right).

*(iii) Temporal variation and intercolony competition in fitting versus non-fitting models*

In model (1), there was hardly any difference between the parameters, which define temporal variation and intercolony competition in fitting and non-fitting models (Fig. 6a, c and e). The degree of intercolony competition  $R_B$  was slightly higher in fitting models, but the trend was not significant. The variation of reproductive success  $CV_B$  was significantly higher in fitting models, but a low partial  $\eta^2$  indicates the low relevance of this difference (Table 4). In contrast, in model (2), the fitting models could clearly be assigned to a high variation of reproductive success and

survival as well as to a high degree of intercolony competition (Fig. 6b, d and f). The difference was significant for all three parameters (Table 4).

## 5. Discussion

Our simulation model showed that the distribution of colony sizes of the sociable weaver could entirely be explained by the form of density dependence of reproductive success and survival, and by a dispersal mechanism which evolved as a consequence of this form of density dependence. Additional assumptions, i.e. fitness costs of switching colony size, and costs of new colonisation, were no necessary preconditions for explaining the pattern. Even without them, realistic parameterisations of the model could be found, at which the model reproduced the colony size distribution in the field. The number of parameter combinations, where the model fitted exactly the field data, was low. However, this was caused as we used a very narrow criterion of fit between model results and field data. We chose this criterion, as our goal was to show that not only the high variation in colony sizes, but also the exact shape of the frequency distribution of colony sizes in a given area can be explained by the model. Loosening the criterion to a more general one (low mean and a high coefficient of variation) showed that the model was able to produce a high variation of colony sizes under a large number of parameter combinations.

Other mechanisms, which could have enhanced the variation of colony sizes in our model, were intercolony competition and temporal variation of reproductive success and survival. However, a comparison of the parameters defining these processes indicated that they did not play a strong role in producing the variation of colony sizes in our main model.

The modelling study was based on a field study, where we analysed the frequency distribution of colony sizes, and estimated models of reproductive success, survival rate and the per capita growth rate in relation to colony size. This is to our knowledge the first study, where both main components of fitness, reproduction and survival, are related to colony size, and an integrative measure of fitness, the per capita growth rate, is calculated in relation to colony size.

### Colony size distribution and density dependence of reproductive success, survival and per capita growth rate

The variation of colony sizes in our study area was characterised by a right skewed distribution with a high abundance of medium-sized colonies and a long tail of the distribution at large colonies. A similar shape of colony size distribution was observed for the sociable weaver in a habitat similar to our study area in Namibia (Marsden 1999), and in a more open savannah in the southern Kalahari (M. Schwager, unpublished data). This suggests that it is a general pattern for this species. A right skewed distribution with a long tail has also been described for the bank swallow and for the Magellanic penguin (Hoogland & Sherman 1976, Tella *et al.* 2001). However, as only few studies give explicitly the form of the frequency distribution of colony sizes, we cannot state whether this pattern can be generalized for colonially living birds.



Density dependence of demographic parameters of the sociable weaver was characterised by a decrease of reproductive success with increasing colony size, and by an increase of survival rate in large colonies (Brown *et al.* 2003). The negative density dependence of reproductive success may be caused by a combination of food depletion around large colonies and by a lower susceptibility of small colonies to nest predators. Marsden (1999) showed that fledgling weight of the sociable weaver decreased with increasing colony size in a study in Namibia, and that very small colonies had a lower frequency of nest predation by snakes than large ones. Nest predation might also be a cause for the high variation in the data on reproductive success. In our study area, some colonies were repeatedly predated by snakes and nearly all nestchambers were depleted, whereas other colonies had hardly any losses (R. Covas, unpublished data). The higher survival rate in large colonies was probably caused by a better thermoregulation in winter, and by a lower predation pressure on adult birds, as discussed by Brown *et al.* (2003).

The per capita growth rate did not follow an optimum curve, nor a continuous increase or decrease, as proposed by most theoretical studies on coloniality (Sibly 1983, Pulliam & Caraco 1984, Giraldeau & Gillis 1985, Higashi & Yamamura 1993, Rannala & Brown 1994, Avilés 1999, Avilés *et al.* 2002). Instead it was highest in very small colonies, decreased at medium-sized colonies, and increased again slightly in large colonies. The increase of survival rate in large colonies was low compared to the density dependence of reproductive success, and the function of the per capita growth rate resembles mostly a continuous decrease. However, the slight increase in survival can result in a considerably longer lifespan (Brown *et al.* 2003). Especially in variable environments like semiarid areas, where reproductive success is unpredictable from year to year due to the high variation in rainfall, this could mean an important fitness gain.

Our estimation of fitness in relation to colony size may be limited, as we used a very simple measure of fitness, i.e. the per capita growth rate, and calculated the per capita growth rate in a very straightforward way. We did not account for the age structure of the population, for the role of social behaviour, e.g. helping at the nest, nor for temporal variation in reproductive success and survival due to unpredictable rainfall (Covas 2002, Covas *et al.* 2004). Our estimation of fitness may therefore be by far incomplete. However, including more detail into the estimation of fitness may make the relationship between fitness and colony size even more complex and draw it further apart from a simple optimum or monotonous function.

#### Explaining the pattern of colony size distribution

The form of density dependence of reproductive success and survival could explain the pattern of colony size distribution of the sociable weaver for two reasons: First, the given form of density dependence generated a dynamics of reproduction and mortality, where the observed pattern of colony sizes emerged. A high mean growth rate in small colonies and a growth rate of one in medium-sized colonies led to a peak of the colony size distribution at medium colony size. In

larger colonies, a growth rate close to one led to the occasional growth of colonies to a large size, at which they stayed quite persistently.

Second, at the given form of density dependence, a dispersal strategy could evolve, at which the high variation of colony sizes was maintained. Despite the higher growth rate in very small colonies, the rare but persistent occurrence of large colonies was not prevented by emigration from these colonies in high numbers. A comparison of dispersal strategies in fitting and non-fitting models showed that for maintaining the variation, both, a low colonisation rate and an individual preference for a specific colony size were important. However, both could evolve in our model, even if no additional assumptions on costs of new colonisation or costs of switching colony size were made.

A comparison of our main model with a model, where the survival rate was independent of colony size showed that the decision of birds to stay in large colonies was caused by the slightly higher survival rate. In the model with constant survival rate, the colony size distribution could only be reproduced under considerable fitness costs of new colonisation and costs of switching colony size. Both constrained birds from emigrating from too large colonies. From the difference between the two models, we conclude that the increased survival rate in large colonies could balance the advantage of a higher reproductive success in small colonies. However, this balance may hold only, as long as colonies are not too small. In our model, colonies could hardly reach a very small size, as we assumed that the sociable weaver is obligatory colonial and a minimum group size is needed to maintain a colony as well as to establish new colonies. This assumption is justified, as the construction and maintenance of the large and complex nests, sociable weavers live in, may only be possible by a group of birds. The benefits, which the nest provides, protection from predators and thermal benefits in winter (White *et al.* 1975, Bartholomew *et al.* 1976, Maclean 1973), may be the main cause why sociable weavers live in colonies in general, and prevent birds from breeding in single pairs.

Many studies have shown that living in large colonies influences different components of fitness in different ways, and trade offs between costs and benefits may exist in many colonial species (Hoogland & Sherman 1976, Møller 1987, Wiklund & Andersson 1994, Brown & Brown 1996, Brunton 1999). However, as shown here, the interaction between different costs and benefits does not necessarily mean that there exists one particular colony size which is optimal and which is preferred in the choice of colony sizes. This view is also supported by a review of Brown & Brown (2001), who have shown that out of 64 studies, 25 found no significant effect of colony size on reproductive success, indicating either an exact balance between costs and benefits or a more subtle and complex relationship, which could not be detected in the data. From our results we conclude that such a relationship alone can be a cause of the high variation in colony sizes.

The main goal of this study was to evaluate the role of density dependence of reproduction and survival for explaining the high variation of colony size. However, besides this, other factors could

be identified, which were not a prerequisite for reproducing the pattern of colony size distribution, but which could enhance the high variation of colony sizes of the sociable weaver.

Fitness costs of new colonisation clearly enhanced the variation of colony sizes in our model, as they raised the number of parameter combinations, where the model fitted the field data. This was caused as a high mortality during colonisation forced the birds to stay in large colonies, even in cases where small colonies were more favourable. Unfortunately, new colonisation has rarely been described for colonial bird species (Oro & Ruxton 2001), and the costs that may be bound to this process are hard to quantify. However, the rare occurrence might be an indication that the formation of new colonies is often associated with fitness costs. Also the theories of conspecific attraction and of settlement decisions based on conspecific reproductive success predict that breeding at a site where other birds breed is less risky than exploring a new site, even if the density at the occupied site is very high (Shields *et al.* 1988, Forbes & Kaiser 1994, Danchin & Wagner 1997). We suggest therefore that fitness costs of colonisation might add to the variation of colony sizes and especially to the occurrence of very large colonies in many species.

Individual differences in the choice of colony size were a precondition for reproducing the pattern of colony size distribution in our model, as long as new colonisation was not associated with a high mortality. For the sociable weaver, an individual preference for specific colony sizes has been shown (Brown *et al.* 2003), and surely adds to the variation of colony sizes in this species. However, our model suggested that this behaviour can evolve, even if switching colony sizes is not associated with fitness costs.

High temporal variation of reproductive success and survival has rarely been mentioned in the discussion about reasons for variable colony sizes. However, in any population, temporal fluctuations of demographic parameters may lead to a spatial heterogeneity of abundance, if they occur in a spatially uncorrelated way. This effect has been demonstrated for non-colonial birds by Ives & Klopfer (1997), who showed that a typical pattern of bird abundance, where most patches have a low abundance but a few hotspots with a high abundance occur (Brown *et al.* 1995), could entirely be explained by low density dependence and high temporal variation of the per capita growth rate, without making further assumptions like spatial heterogeneity. Further, high temporal variation could be a reason for a less strict choice of colony size, as it makes future reproductive success and survival highly unpredictable. In our model, strong temporal variation was only a prerequisite for the variation of colony sizes of the sociable weaver if the survival rate was assumed to be constant. However, we assume that in the natural population, fluctuations of reproductive success, which arise due to the random occurrence of nest predation by snakes, strongly increase the variation of colony sizes.

Intercolony competition has been proposed as a cause of variation of colony sizes, if food depletion around a colony is caused not only by the size of the colony itself, but also by the abundance of individuals from other colonies within the feeding range. As a result, the variation in colony sizes may be determined by the number of competitors from neighbouring colonies.

Intercolony competition has been identified as a reason for variation of colony sizes for some bird species (e.g. Furness & Birkhead 1984, Griffin & Thomas 2000, Tella *et al.* 2001, Forero *et al.* 2002, Ainley *et al.* 2003, Ainley *et al.* 2004), whereas other studies did not find a strong relationship between local colony size and the abundance and size of neighbouring colonies (Ainley *et al.* 1995, Brown & Brown 2002). For the sociable weaver, we assume that intercolony competition for food occurs, as the species is not territorial and feeding ranges of different colonies overlap (R. Covas, personal observation). However, a detailed analysis of the spatial pattern of colony sizes would be needed to evaluate its influence on colony size variation.

An important point of our study was that reproducing a high variation of colony sizes did not depend on any form of spatial heterogeneity of the habitat. Differences in habitat quality are often a first guess for the explanation of spatially heterogeneous animal populations. However, though many explanations for colony size variation, other than habitat heterogeneity, exist, this is to our knowledge the first study, where a variable pattern of colony sizes could entirely be explained without assuming habitat heterogeneity. We assume that for the sociable weaver, habitat heterogeneity is unlikely to be a strong predictor of colony size, at least in our study area. The habitat of our study area is mostly a quite uniform savannah with no indication that sites with large colonies differ from other colony sites.

Finally, our study showed that the approach of "pattern oriented modelling", where we compared the results of a species specific simulation model with a pattern of colony size distribution in the field, is a helpful tool for evaluating different hypothesis on the explanation of the variation of colony sizes. This approach has been a useful strategy for identifying the underlying processes that lead to specific spatial or temporal patterns in many fields of ecology (e.g. Grimm *et al.* 1996, Jeltsch *et al.* 1997, Jeltsch *et al.* 1998, Jeltsch *et al.* 1999, Wiegand *et al.* 2003). We propose that this approach may be used more widely, to evaluate the role of existing explanation hypotheses for the high variation of colony sizes, and to identify gaps, where the variation can not yet entirely be explained.

Table 1: Overview of model types

	Survival rate	Costs of switching colony size	Costs of new colonisation
<b>Model (1)</b>	increases in large colonies	no costs survival = 0.9	survival = 0.2; 0.4; 0.6; 0.8; 1 survival = 0.2; 0.4; 0.6; 0.8; 1
<b>Model (2)</b>	independent of colony size	no costs survival = 0.9	survival = 0.2; 0.4; 0.6; 0.8; 1 survival = 0.2; 0.4; 0.6; 0.8; 1

Table 2: Ranges of variation of model parameters. See model description for a detailed description of parameters.

	Parameter	Estimated range	Source of estimation
<b>Reproduction</b>	$A_B$	1 - 25	this study
	$B'_{\text{Rain}}$	0.002 - 0.02	this study
	$R_B$	200 - 1000 m	$< 2 \cdot$ feeding radius, Maclean (1973)
	$CV_B$	0.1 - 0.7	this study
<b>Survival</b>	$S_{\text{min}}$	0.55 - 0.75	Brown <i>et al.</i> (2003)
	$S_{\text{max}}$	0.65 - 0.9	Brown <i>et al.</i> (2003)
	$A_S$	60 - 120	Brown <i>et al.</i> (2003)
	$b_S$	0.05 - 1	none
	$S$	0.6 - 0.7	Brown <i>et al.</i> (2003)
	$\text{Var}_S$	0 - 0.15	none
<b>Minimum colony size</b>	$N_{\text{min}}$	3 - 8	this study
	$N_{\text{minCol}}$	10 - 30	White <i>et al.</i> (1973)

Table 3: Dispersal strategies in fitting versus non-fitting models according to criterion one: results of ANOVA analysis. See model description for a detailed description of parameters.

Parameter	Factors	Model (1)			Model (2)		
		F	p	Part. Eta <sup>2</sup>	F	p	Part. Eta <sup>2</sup>
<b>DNC<sub>P</sub></b> <sup>1)</sup>	Fit	<0.1	0.86	<0.01	0.5	0.48	0.02
	Fit * NC <sub>Surv</sub>	24.0	<b>&lt;0.01</b>	0.21	4.4	<b>0.02</b>	0.23
	Fit * IC <sub>Surv</sub>	1.1	0.35	0.01	4) <sup>4)</sup>		
<b>DNC<sub>Thres</sub></b>	Fit	14.4	<b>&lt;0.01</b>	0.07	0.5	0.50	0.02
	Fit * NC <sub>Surv</sub>	16.3	<b>&lt;0.01</b>	0.15	0.3	0.78	0.02
	Fit * IC <sub>Surv</sub>	0.9	0.42	<0.01	4) <sup>4)</sup>		
<b>DIC<sub>P</sub></b>	Fit	1.5	0.23	0.01	3.0	0.09	0.09
	Fit * NC <sub>Surv</sub>	25.4	<b>&lt;0.01</b>	0.22	2.5	0.10	0.15
	Fit * IC <sub>Surv</sub>	18.0	<b>&lt;0.01</b>	0.17	4) <sup>4)</sup>		
<b>DIC<sub>Choice</sub></b> <sup>2,3)</sup>	Fit	<0.1	0.89	<0.01			
	Fit * NC <sub>Surv</sub>	5.0	<b>&lt;0.01</b>	0.10			

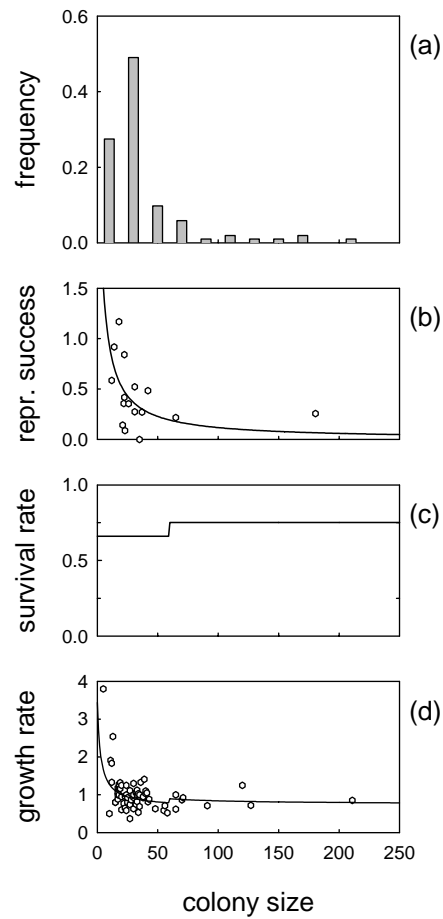
<sup>1)</sup> Variable was log transformed  $x' = \ln(x)$ . <sup>2)</sup> Variable was arcsin transformed  $x' = \arcsin(\sqrt{x})$ .

<sup>3)</sup> Due to the high difference in variances, the analysis was only done in model (1) without costs of switching colony size. <sup>4)</sup> The analysis was only done in the models with costs of switching colony size, as in the other models no fitting parameter combinations were found. Bold letters indicate significant differences at  $\alpha = 0.05$ .

*Table 4:* Parameters, defining the degree of intercolony competition ( $R_B$ ), and the temporal variation of reproductive success ( $CV_B$ ) and survival ( $Var_S$ ) in fitting versus non-fitting models according to criterion one: results of ANOVA analysis. See model description for a detailed description of parameters.

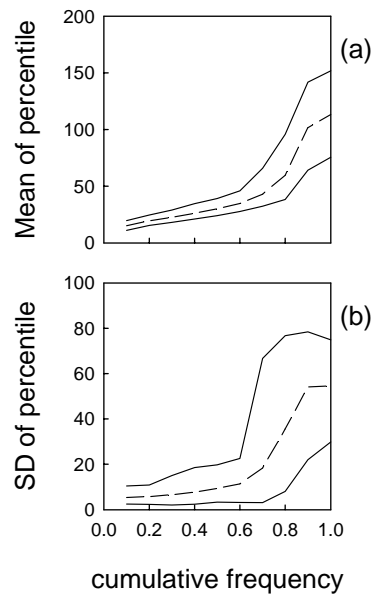
Parameter	Factors	Model (1)			Model (2)		
		F	p	Part. Eta <sup>2</sup>	F	p	Part. Eta <sup>2</sup>
$R_B$ <sup>1)</sup>	Fit	0.9	0.33	<0.01	9.5	<b>&lt;0.01</b>	0.25
	Fit * $NC_{Surv}$	1.1	0.36	0.05	0.1	0.86	0.01
	Fit * $IC_{Surv}$	0.5	0.59	<0.01	<sup>2)</sup>		
$CV_B$	Fit	7.8	<b>0.01</b>	0.04	7.1	<b>0.01</b>	0.20
	Fit * $NC_{Surv}$	1.3	0.22	0.06	0.7	0.48	0.05
	Fit * $IC_{Surv}$	0.1	0.88	<0.01	<sup>2)</sup>		
$Var_S$	Fit	0.1	0.82	<0.01	28.2	<b>&lt;0.01</b>	0.49
	Fit * $NC_{Surv}$	1.4	0.22	0.06	4.0	0.03	0.22
	Fit * $IC_{Surv}$	1.0	0.38	0.01	<sup>2)</sup>		

<sup>1)</sup> Variable was arcsin transformed  $x' = \arcsin(\sqrt{x})$ . <sup>2)</sup> The analysis was only done in the models with costs of switching colony size, as in the other models no fitting parameter combinations were found. Bold letters indicate significant differences at  $\alpha = 0.05$ .

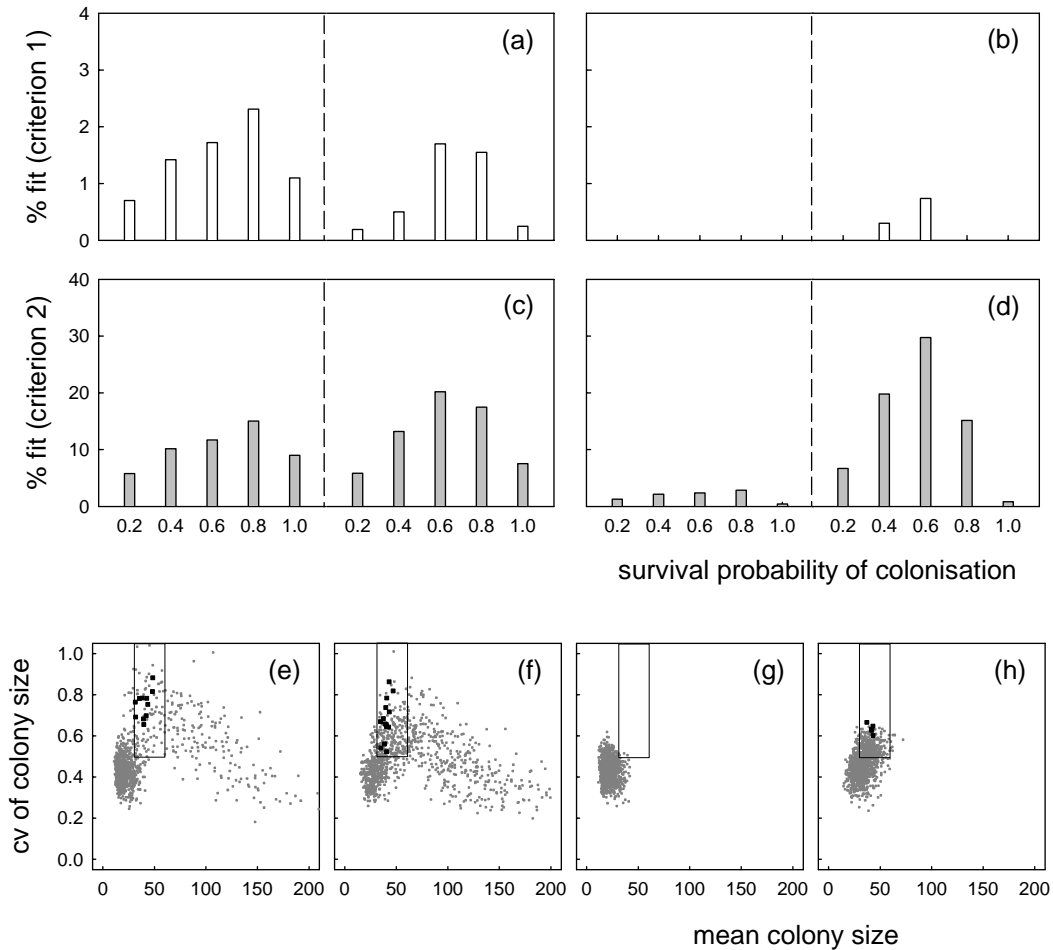


*Figure 1:* (a) Frequency distribution of colony sizes (data from 8 years, 6 to 18 colonies per year). (b) Reproductive success in dependence of colony size (regression model and data from two years, pooled for each colony). (c) Survival rate in dependence of colony size (model according to Brown *et al.* 2003). (d) Per capita growth rate in dependence of colony size (model calculated from the models in (b) and (c), and data from 7 years, 5 to 14 colonies per year).

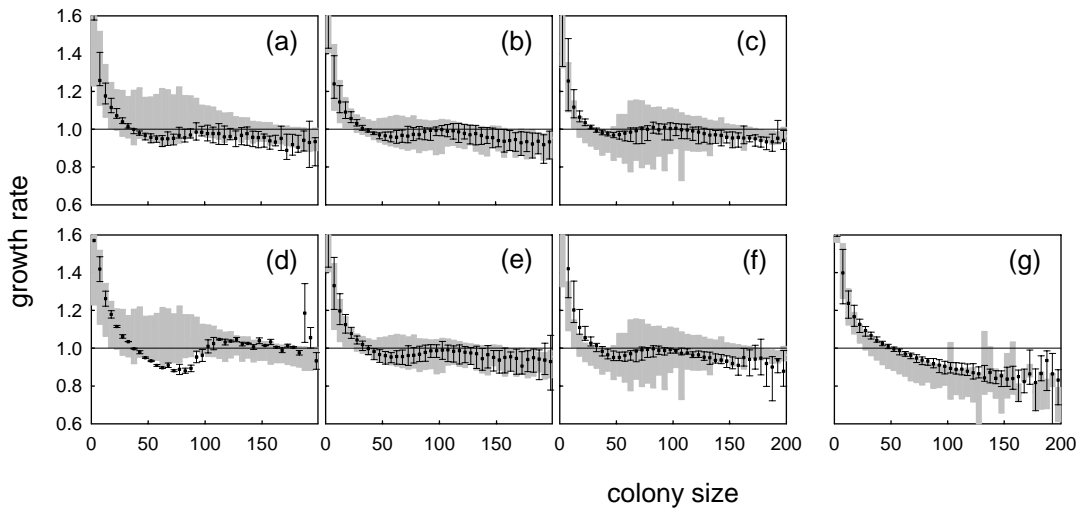




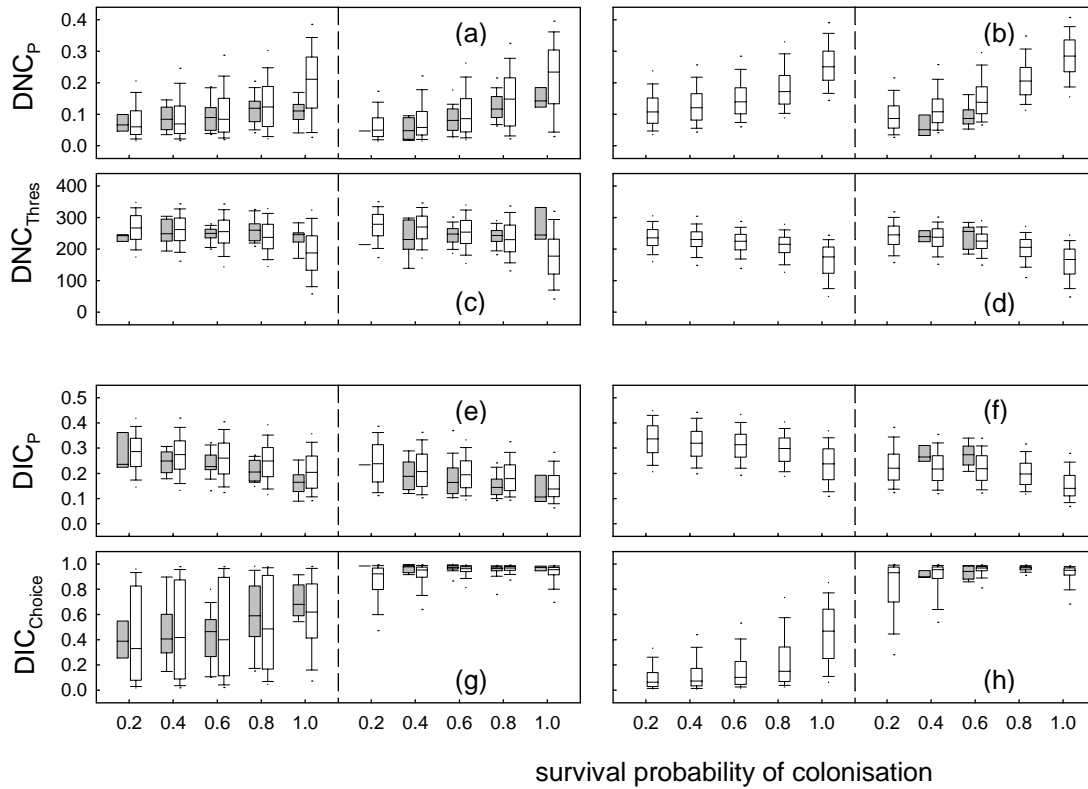
*Figure 2:* 95% confidence intervals for mean (a) and standard deviation (b) of percentiles of colony sizes frequency distribution in the field, used as a criterion for fit in the simulation model. Confidence limits were calculated by a bootstrap algorithm from 7 year data on colony sizes with 9 to 19 colonies per year.



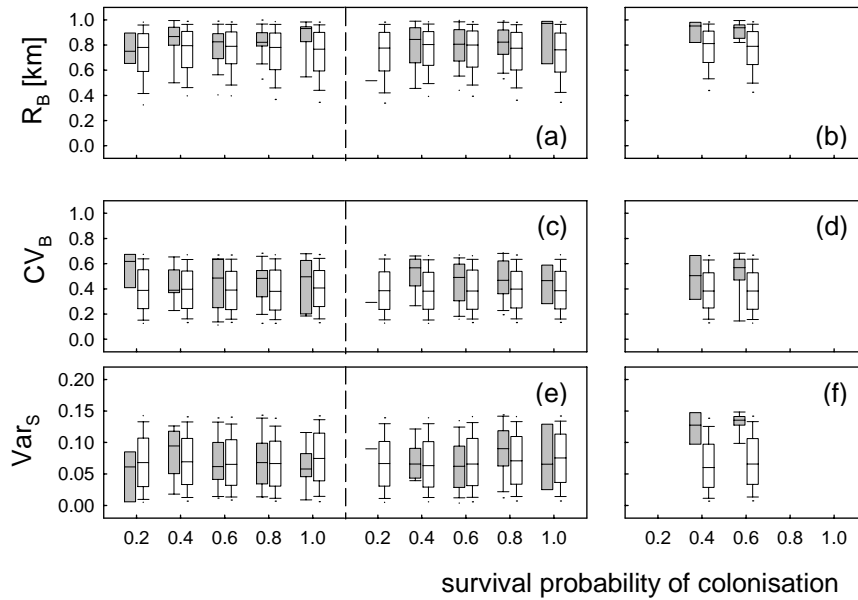
*Figure 3:* (a to d) Percentage of parameter combinations, where the model fitted the field data on frequency distribution of colony sizes according to criterion one (a, b) and criterion two (c, d). Models as in Table 1: model (1) (a, c) and model (2) (b, d), without (left) and with (right) fitness costs of switching colony size. X-axis shows different probabilities of success of the establishment of new colonies. (e to h) CV and mean of colony sizes in fitting models acc. to criterion one (black points) vs. all models (grey points). Frames display mean and CV according to criterion two. (e) Model (1) without any costs of dispersal. (f) Model (1) with cost of switching colony size and colonisation survival = 0.6. (g) Model (2) without any costs of dispersal. (h) Model (2) with cost of switching colony size and colonisation survival = 0.6.



*Figure 4:* Mean per capita growth rate in dependence of colony size in fitting models acc. to criterion one, and in all models. Black symbols give the median, 0.1 and 0.9 percentiles of mean growth rate in fitting models. Grey areas give the 0.1 and 0.9 percentiles of mean growth rate in all models. Models as in Table 1: Top: model (1) without fitness costs of switching colony size, colonisation survival = 0.2 (a), 0.6 (b), 1 (c). Bottom left: model (1) with costs of switching colony size, colonisation survival = 0.2 (d), 0.6 (e), 1 (f). Bottom right: model (2) with costs of switching colony size, colonisation survival = 0.6 (g).



*Figure 5:* Dispersal strategies that evolved in the different models. Boxes show means of the respective parameters in models, where the model fitted the field data according to criterion one (grey boxes), and in non-fitting models (white boxes). See model description for a detailed definition of parameters. Models as in Table 1: (a, c, e, g) model (1) and (b, d, f, h) model (2), without (left) and with (right) fitness costs of switching colony size. X-axis shows different probabilities of success of the establishment of new colonies.



*Figure 6:* Model parameters of strength of intercolony competition (a, b) temporal variation of reproductive success (c, d) and temporal variation of survival (e, f) in fitting versus non-fitting models acc. to criterion one. See model description for a detailed definition of parameters. Grey boxes show parameters in fitting models, white boxes show parameters in non-fitting models. Models as in Table 1: (a, c, e) model (1) and (b, d, f) model (2) without (left) and with (right) fitness costs of switching colony size. X-axis shows different probabilities of success of the establishment of new colonies.

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# General Discussion

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Natural populations are highly variable in space and time. This variation is driven by the internal dynamics of density dependent reproduction and survival, by interactions with other species, and by changes in the abiotic and biotic environment. Natural variation of the environment, as well as human induced changes, affect the temporal dynamics of populations at different time scales. If they occur in a spatial heterogeneous way, they cause spatial variation in abundance. In this thesis I addressed three topics, all related to the question, how environmental changes influence population dynamics.

In the first chapter, I addressed a topic of how randomly occurring fluctuations of the environment (environmental noise) affect extinction risk. I showed in an abstract modelling study that positive temporal autocorrelation of environmental noise (red noise) can have a positive as well as a negative effect on the extinction risk of populations. Specifically, populations, which were prone to extinction by extremely bad environmental conditions which occurred only once, had a decreased extinction risk under reddened noise. In contrast, populations, which were threatened only if bad conditions occurred consecutively, had a higher extinction risk under reddened noise. The results helped solving an apparent contradiction in the literature, and improved the general understanding on the effect of autocorrelated noise on extinction risk.

The study showed, as many others, that unfortunately the effect of red noise on extinction risk is not straightforward. Instead, it depends on how vulnerable a population is to environmental fluctuations (this study), on the form of density dependence (undercompensation *versus* overcompensation) (e.g. Petchey *et al.* 1997), on the structure of noise itself (e.g. Cuddington & Yodzis 1999), on the method of variance scaling (Heino *et al.* 2000), and probably much more. It might be further complicated, if more detail is included in the models, i.e. age structure and spatial structure (e.g. Petchey *et al.* 1997, Heino & Sabadell 2003). However, elucidating these differences and the mechanism which cause them is important, as they could give general rules of thumb under which conditions which effects prevail.

Despite their differences, all studies on the effect of red noise showed a strong impact on extinction risk. These results, together with the evidence that natural time series are often red shifted (Halley 1996), show the high relevance of this issue in conservation ecology. They should encourage modellers to include autocorrelated noise also in models of risk assessment in applied nature conservation. So far, there are only few approaches of including autocorrelation in environmental noise into applied or species specific population models (e.g. Foley 1994).

In the second chapter I analysed how a long-term unidirectional trend of mean environmental conditions, caused by climate change, could affect a population. I cross-validated two approaches for predicting the potential effect of future shifts in mean precipitation on the abundance of the

sociable weaver, a colonial passerine bird of semi-arid southern Africa. In a space for time approach, I compared populations of the sociable weaver in two regions with very different mean annual precipitation. The results showed no difference between the two populations, which would lead to the prediction of no sensitive response of the species to a shift in mean annual precipitation. In contrast, a population modelling approach, based on a correlation between breeding success and rainfall, showed a sensitive response in most model types. The inconsistency of the two approaches was confirmed in a cross-validation, as the population model could not predict the observed abundances of the species in the two regions. I concluded, that the difference between the two approaches was caused, because they operate on different time scales. On a long time scale, or in a regional comparison, the sensitive response to mean annual precipitation shown by the population model may be compensated or buffered by a variety of mechanisms. These may include behavioural adaptations, differences in the physical environment or interactions with other species. Predictions, how the sociable weaver population will respond to climate change would need a thorough investigation of these mechanisms, and an evaluation, at which time scale they would follow future climate change.

Climate change may be one of the most severe threats for natural populations, ranging closely after global habitat loss in this respect (Thomas *et al.* 2004). Several studies have stressed the necessity to include its consequences in developing conservation strategies (Roberts 1988, McCarty 2001, Hannah *et al.* 2002). This needs reliable predictions on how species and ecosystems will respond to climate change, and which species or systems are the most sensitive ones. However, as shown in this study, making predictions is notoriously difficult under the complexity of ecological systems. In this sense, this study might be discouraging at first sight, as it showed the limitations of the commonly used approaches, and in the specific case of the sociable weaver, unequivocal predictions could not be made. However, the study showed clearly, where gaps of knowledge exist, on which future research should focus. It will hopefully encourage other studies, to compare and cross-validate approaches working on different time scales, and to elucidate the mechanisms and processes behind different predictions.

In the third chapter of the thesis, I gave an explanation for a pattern of high spatial variation in colony sizes of the sociable weaver. I showed in a population model, which included an evolutionary optimisation of dispersal strategy, that this pattern could be caused by the specific form of the fitness function in relation to colony size. Positive and negative effects of colony size on reproduction and survival balanced each other in a way that no specific colony size was preferred over another. In consequence, a dispersal strategy could evolve under which the variation of colony sizes was maintained.

As stated by Brown *et al.* (1990), understanding the way, by which birds chose their breeding colony is a key to understanding the evolution and maintenance of coloniality. Today, several hypothesis on the choice of breeding colony, as well as on the evolution and maintenance of coloniality are discussed (Danchin & Wagner 1997, Brown & Brown 2001): (i) Birds may live in

colonies simply because breeding sites are limited. (ii) Living in colonies provides fitness benefits to the birds, which exceed the costs of living in high densities (cost benefit hypothesis). (iii) The presence of conspecifics is used as a cue for high breeding quality of a specific site (conspecific attraction hypothesis). (iv) The reproductive success of conspecifics in the previous years is used as a cue for the breeding quality of a site (conspecific reproductive success hypothesis).

For the sociable weaver I would assume that the ultimate causes for the maintenance of coloniality are the benefits that result from the cooperative construction of the complex nest. The nest provides protection from predators, as well as thermal benefits in hot summers and cold winters (White *et al.* 1975, Bartholomew *et al.* 1976, Maclean 1973). Still, living in the protective nest does not explain, why birds would live in crowded colonies of a few hundred birds, where the high population density leads to food depletion around a colony. As shown by the model, the choice of birds to stay in large colonies could be caused by the increase in survival rate in large colonies, which balances the disadvantage of the negative effect of crowding on reproductive success. However, though the model showed that the increased survival rate alone is sufficient to explain the existence of large colonies, I would assume that several other factors add to the choice of colony size: adaptation of individual birds to a specific colony size, intercolony competition, and fitness costs of founding new colonies. All factors refer to the above given hypothesis on the evolution and maintenance of coloniality. The first three relate to the cost benefit approach: birds choose to live, where their fitness is maximised, or at least where their fitness is not smaller than in other colony sizes. The latter, fitness costs of founding new colonies, is related to the hypothesis of conspecific attraction: it is less risky for a bird to breed in a crowded colony, than to explore a new site.

In the three parts of the thesis I used different modelling approaches to address the given questions. In the first part I used a very simple abstract model, which was not designed for a specific species or system. Such abstract models are useful for understanding general mechanisms and processes in ecological systems. However, their results should be tested and validated in more detailed models, as well as in field studies. In the second and third part of the thesis, I used a model which was designed for a specific species in a specific system, i.e. the sociable weaver in semiarid savannahs of southern Africa. As models, which are designed for specific species or systems usually lack the necessary data basis for reliable parameter estimation, I used the approach of pattern oriented modelling for a realistic parameterisation of the model (Grimm *et al.* 1996, Wiegand *et al.* 2003).

All three parts have shown the benefits as well as the limitations of models. Especially the second part showed the limitation of models to make predictions about what might happen in future. However, one important task of models is to identify, where the current status of knowledge is not established enough for explaining observed patterns and for making predictions (e.g. Jeltsch *et al.* 1996, 1998). In the other two parts, the models helped to understand the consequences of observed patterns in the environment (temporal autocorrelation), as well as to understand the mechanisms

which lead to observed patterns of abundance (variation of colony sizes). In all areas of ecological research where predictions on the effect of changes in the environment should be made, a mechanistic understanding of the processes which lead to the observed patterns of abundance is a crucial precondition for making predictions (Levin 1992).

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# Zusammenfassung

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Änderungen in der Umwelt - sowohl natürliche Variabilität als auch anthropogene Änderungen - beeinflussen Populationen auf verschiedenen Zeitskalen. Wenn sie räumlich heterogen wirken, verursachen sie räumliche Variabilität in der Abundanz. In dieser Dissertation habe ich drei Themen bearbeitet, die sich auf den Effekt von Änderungen in der Umwelt auf Populationsdynamiken beziehen.

Im ersten Teil untersuchte ich an einem einfachen Populationsmodell den Effekt von positiver zeitlicher Autokorrelation im Umweltrauschen auf das Extinktionsrisiko einer Population. Der Effekt der Autokorrelation hing davon ab, wie empfindlich eine Population gegenüber singulären, katastrophenähnlichen Ereignissen schlechter Umweltbedingungen war. War die Population nur dann direkt bedroht, wenn eine Serie von schlechten Umweltbedingungen auftrat, erhöhte positive Autokorrelation das Extinktionsrisiko. Konnte eine Population auch dann aussterben, wenn schlechte Umweltbedingungen einzeln auftraten, verringerte positive Autokorrelation das Extinktionsrisiko. Diese unterschiedlichen Effekte konnten durch zwei Eigenschaften autokorrelierter Zeitreihen erklärt werden. Einerseits erhöht positive Autokorrelation die Wahrscheinlichkeit, daß in einer Zeitreihe Serien von schlechten Bedingungen auftreten. Andererseits führt die Aggregation von schlechten Jahren auch zu langen Zeiträumen mit relativ guten Bedingungen. Deshalb ist die Wahrscheinlichkeit, daß innerhalb eines bestimmten Zeitraums zumindest ein extrem schlechtes Jahr auftritt, geringer unter positiver Autokorrelation. Die Ergebnisse konnten einen Widerspruch in der Literatur aufklären, in dem unterschiedliche Effekte von autokorreliertem Umweltrauschen auf das Extinktionsrisiko gefunden wurden, obwohl sehr ähnliche Modelle verwendet wurden.

Im zweiten Teil, verglich ich zwei Methoden, die häufig verwendet werden, um den Effekt von Klimawandel auf die zukünftige Verbreitung und Abundanz von Arten vorauszusagen: Ein "Raum-ersetzt-Zeit-Ansatz" ("space for time approach"), in dem Voraussagen aufgrund der aktuellen geographischen Verbreitung und Abundanz einer Art in Relation zum Klima getroffen werden, und ein "Populationsmodell-Ansatz", der auf Korrelationen zwischen demographischen Parametern und der jährlichen Variabilität im Klimas beruht. In einer Fallstudie verglich ich die beiden Methoden, um den Effekt einer Änderung im mittleren Niederschlag auf eine Population des Siedelwebers *Philetairus socius* vorauszusagen. Der Siedelweber ist eine häufige, koloniale Vogelart in semiariden Savannen im südlichen Afrika. Im "space for time approach" verglich ich zwei Populationen des Siedelwebers in Gebieten mit stark unterschiedlichem mittleren Niederschlag. Die Untersuchung zeigte keinen Unterschied zwischen den beiden Populationen. Sowohl dieses Ergebnis als auch das weite Verbreitungsgebiet des Siedelwebers implizieren keine sensitive Reaktion der Art auf eine geringfügige Änderung im mittleren Niederschlag. Im

Unterschied dazu zeigte der "Populationsmodell-Ansatz", der auf einer Korrelation zwischen Niederschlag und dem Reproduktionserfolg des Siedlerwebers beruhte, eine sensitive Reaktion in den meisten der untersuchten Modelltypen. Die Inkonsistenz der Ergebnisse wurde in einer Kreuz-Validierung der beiden Ansätze bestätigt. Aus der Untersuchung folgte ich, daß die unterschiedlichen Ergebnisse dadurch verursacht wurden, daß die beiden Methoden unterschiedliche Zeitskalen widerspiegeln. Auf einer kurzen Zeitskala reagiert die Population sensitiv auf Änderungen im Niederschlag. Auf einer großen Zeitskala oder im räumlichen Vergleich kann die sensitive Reaktion jedoch durch eine Reihe von Mechanismen gepuffert oder kompensiert werden. Diese Mechanismen können Anpassungen im Verhalten oder in der Lebensgeschichte ("life history"), Änderungen in den Interaktionen mit andern Arten oder Unterschiede in der physikalischen Umgebung beinhalten. Diese Studie zeigt, daß ein Verständnis, wie solche Mechanismen funktionieren, und auf welcher Zeitskala sie wirken, eine wesentliche Voraussetzung ist, um Prognosen über ökologische Effekte des Klimawandels treffen zu können.

Im dritten Teil untersuchte ich, warum Kolonien des Siedlerwebers so stark in ihrer Größe variieren. Die Variabilität der Koloniegrößen ist erstaunlich, da man in Untersuchungen zur Kolonialität bei Tieren oft davon ausgeht, daß eine optimale Koloniegröße besteht, bei der die individuelle Fitneß maximiert ist. Aufgrund dieser Annahme sollten Vögel sich so im Raum ausbreiten, daß die Koloniegrößen möglichst nahe am Optimum liegen. In dieser Arbeit konnte ich jedoch anhand von Daten zum Reproduktionserfolg und zur Überlebensrate in Relation zur Koloniegröße zeigen, daß die Funktion der Fitneß in Abhängigkeit von der Koloniegröße nicht einer Optimumskurve folgt. Statt dessen überlagern sich positive und negative Effekte der Koloniegröße so, daß die Populationswachstumsrate generell nahe eins ist, und die Dichteabhängigkeit gering ist. Auf diesen Ergebnissen aufbauend zeigte ich in einem Populationsmodell, das einen evolutionären Optimierungsprozeß der Dispersal-Strategie beinhaltet, daß die spezifische Form der Fitneßfunktion zu einer Dispersal-Strategie führen kann, bei der die hohe Variabilität der Koloniegrößen aufrecht erhalten wird.

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