The effects of colony dynamics and climate on a declining population of sociable weavers, *Philetairus socius*

Michael Marais

DST/NRF Centre of Excellence at the
Percy FitzPatrick Institute of African Ornithology
University of Cape Town
Rondebosch,
South Africa 7701

Supervisors: Dr R. Covas, Dr. R. Altwegg & A/Prof. P.G. Ryan

Submitted: February 2010

Submitted in partial fulfilment of the requirements for the degree of

Master of Science in Conservation Biology

Table of Contents

Abstract

This study was conducted in order to investigate the potential reasons for population decline in colonial birds in semi-arid environments by looking at the role that colony dynamics and climatic variables may play in this. This study was carried out on a declining population of Sociable Weavers, *Philetairus socius*, monitored in 15 years from 1993-2009 on Benfontein Game Farm, Kimberley, South Africa. Twenty-four weaver colonies were divided into four groups based on the size of their colonies as well as the population trend of the colony: 1) Large declining colonies (n=8); 2) Small declining colonies (n=4); 3) Large stable colonies (n=6); and 4) Small stable colonies (n=6). I used CMR models to evaluate patterns in survival of adult birds (>1 year old). Age did not have a strong effect on survival, the effect of fieldwork on the population is minimal and emigration was not considered. Adults in large colonies had greater survival rate than birds in small colonies, and birds in stable colonies had greater survival than those in colonies with a declining trend. Adding climatic variables failed to improve the model fit, with analysis of deviance (ANODEV) suggesting that climatic variables explained only 8% of the variance in survival data. Minimum temperature was the climatic variable that has the greatest effect (negative, linked to the costs of thermoregulation), with rainfall having the second largest effect (positive, linked to increased food availability) on survival.

The number of fledglings per female in each colony was available for 1999, 2000, 2002 and 2005. Poisson regression models indicated that maximum temperature (negative) and rainfall (positive) best explained variance in reproductive success. Weavers from larger colonies and from stable colonies had fledged more chicks than birds from small and declining colonies, but reproduction was affected more by climatic conditions than by colony dynamics.

Sociable weavers from larger colonies probably have higher survival rates due to the extra vigilance in anti-predator responses and a better thermoregulatory ability. Nest predation also is important, but was not included explicitly in this study, although it was incorporated in the reproduction data. Apart from these factors, the differences in survival also is likely to be due to Allee effects in smaller colonies, such as reduced predator defense, lower thermoregulatory ability, poorer colony maintainence and lower reproductive rates in which the low growth rate cannot compensate for the loss of individuals. These findings may shed light on similar species under similar conditions.

Chapter 1: Introduction

Conservation biology is concerned with the protection of species and their habitats. There are many species that are in dire need of conservation (www.iucn.org), and these species are placed in conservation categories based on various aspects of their world population (size, spatial extent and pattern, number of sub-populations, etc.) and the trends that they show (including perceived threats; www.iucnredlist.org). The field of conservation is advancing on two fronts, supported by two sets of ideas (Caughley, 1994; Asquith, 2001): the small population paradigm, concerned with the inherently higher extinction risk small populations face (Caughley, 1992; Keller & Waller, 2002), and the declining population paradigm, which deals with the processes whereby populations are driven towards extinction by external agents (Caughley, 1994; Green, 1995; Norris, 2004). Population size and population growth rate are the two main factors influencing a species' conservation status (www.iucnredlist.org).

Birdlife International has estimated that approximately 12% of the 9946 bird species on earth are threatened with extinction (www.birdlife.org, 2009), and it is estimated that 21% of these birds are extinction prone (Sekercioglu et al. 2004).Although this sounds alarming, the situation is much more severe for other vertebrate taxa, while for invertebrate taxa, the lack of comprehensive data prevents a proper evaluation of endangerment (Norris, 2004). Diagnosing the factors that cause a population to decline is a principle component of nearly all projects intending to save threatened species from extinction (Green, 1995; Norris, 2004).

Population dynamics

In order to diagnose declines and their causes, it is important to consider the population ecology of a species. The study of a species' population dynamics is concerned with the fluctuations of population sizes and the demographics of the population, as well as the biotic and abiotic factors driving these fluctuations. Populations increase through births and immigration and decrease through deaths and emigration. Their dynamics are determined by the relationship between the size of the population and the per capita growth rate (Sibly et al., 2005). Population growth in mammals, birds, fish and insects, generally tends to be high at low population densities and low at high population densities (Sibly et al., 2005). However, small populations may falter due to Allee effects, a syndrome that causes poor performance among small populations (Courchamp et al. 1999).

Population growth rate frequently is considered to be the main natural response variable to be used in the statistical analysis of the factors that may influence the population dynamics of a particular species (Godfray & Rees 2002). Although factors affecting population growth rates have been a major focus of conservation biology and population ecology for several decades, surprisingly few generalizations have been developed that would allow us to predict variation in the growth rates of natural populations (Saether & Engen, 2002). The estimation of population growth rate using population census data faces several challenges with regards to its precision. The first challenge arises from the fact that these data are often collected over relatively short time periods, usually 5-10 years, with studies rarely longer than 30 years (Humbert et al. 2009). Other challenges include uneven time intervals arising from monetary or logistical constraints, environmental noise, estimation error, and the choice of statistical method to analyse the data (Humbert et al. 2009). Limited sample sizes may also pose major problems, especially in terms of space as populations are often divided into smaller sub-populations that may have slightly different characteristics.

The balance between the loss of individuals through emigration and mortality and the recruitment of new breeders through immigration and reproduction determines local population sizes (Pulliam 1988). Populations can be divided into smaller sub-populations on a smaller spatial scale and these populations may differ in their life history components and thus make up source or sink populations depending on their success or overall fitness (Pulliam, 1988; Opdam, 1991) The biotic and abiotic conditions present within a particular environment will determine if the area is favourable or unfavourable and whether or not the population will increase or decrease. With survival and reproduction being the factors that typically have the largest influence on population size, factors that affect these two traits need to be considered when analysing possible reasons for a decline in population size.

There are many factors that affect survival and reproduction as well as the distribution of a species, ranging from limited food or habitat availability, either through competition or poor production due to environmental factors, to predation and disease (Grosbois et al. 2008). Humans may also play an important role in population fluctuations through activities such as harvesting and habitat degradation. Whether it is stochastic events or density dependent effects that cause population fluctuations, quantifying the sources of these fluctuations may provide insights into the various underlying processes of population dynamics and can play a direct role in the conservation of wildlife (Altwegg et al., 2003, Bond et al., 2009). Understanding which factors influence population dynamics may also help us determine how populations could respond under environmental change (Grosbois et al. 2008, Karell et al. 2009). Fluctuations in population size often seem to be stochastic, but this may simply result from ignorance regarding the detailed causes of dispersal, reproduction and mortality (Lande et al., 2003).

The role of climate in population dynamics

Although many populations are affected by climatic variation (Stenseth et al. 2002, Walther et al. 2002, Grosbois et al 2008), relatively little is known about environmental forcing of the factors affecting survival of birds in arid regions where unpredictable, variable rainfall is the dominant environmental variable (Altwegg & Anderson, 2009). The amount and variability of rainfall in these regions is an important determinant of survival in several arid-zone bird species (Saether et al. 2004, Altwegg & Anderson, 2009). Breeding success may be affected by rainfall, through its influence on food availability (Covas et al 2008, Altwegg & Anderson, 2009) and hence understanding how climatic variables affect these parameters is crucial to get a better grasp on population dynamics. Knowing the effect of climatic variables on survival and breeding success is essential to infer population responses to different climatic scenarios (Grosbois & Thompson, 2005)

With a better grasp on the effects that climatic variables have on populations, and a basic knowledge of the average growth rate of the species, it may be possible to model population size and thus conduct less frequent surveys (Jonzen, et al. 2010). However, population models lack real world accuracy and should thus not be too heavily relied upon for important conservation actions. The expected rate of change on the growth rate of a population is an important measure when attempting to determine the 'health' of a population as well as potential management strategies (Nichols & Hines 2002). Reducing field surveys will save time and money. However, if we want to produce accurate estimates, it is vital to understand the relationship between climatic factors and population growth rate. Due to the fact that there are so many variables that could affect population growth rate, the most important variables will need to be determined.

Reproduction and the factors affecting it are important to consider when investigating potential reasons for population fluctuations. The amount of available energy to the species is a major constraint for reproduction (Brommer et al. 2002). In arid zones, rainfall is a major stimulus for breeding initiation and fecundity in many birds (Lloyd, 1999). For example, nine out of 11 arid zone bird species studied in the Nama Karoo biome in South Africa showed a considerable increase in breeding activity and clutch size after appreciable rainfall (Lloyd, 1999).

The sociable weaver as a study species

The sociable weaver, *Philetairus socius*, is a passerine endemic to the semi-arid savanna regions of South Africa and Namibia. Rainfall plays an important role in determining the amount of available plant matter for food and nest building, as well as influencing the local insect populations which provide additional food (Maclean, 1973a). Sociable weavers are obligate colonial birds, building large communal nests in *Acacia erioloba* trees and man made structures, with colonies varying from 2-500 birds (Maclean, 1973b). The communal nests have individual nest chambers in which the weavers breed and roost throughout the year (Covas et al., 2002). Body condition, morphology, survival and reproduction have been found to differ according to colony size (Spottiswoode 2007, 2009, Brown et al. 2003).

Compared to the outside temperature, which may vary substantially, sociable weavers maintain the temperature of nest chambers within a small range of only 7-8^{o}C (Bartholomew et al. 1976). Thermoregulation is done passively by moving to cooler chambers during the day and grouping together and actively keeping warm at night, which can be energetically costly, although this cost is inversely related to the number of birds in the colony (Bartholomew et al. 1976). Thus, minimum and maximum temperatures, as well as colony size should influence the cost of thermoregulation, with possible effects on survival and reproduction. This makes the sociable weaver a good study subject to consider the effects of varying temperatures. Apart from climate, other factors affecting reproduction in sociable weavers include predators such as snakes, which prey on eggs and juveniles, as well as parasites (Maclean, 1973c). Colony size also has implications with regards to the Allee effect, with small colonies being more likely to suffer from potential extinction (Courchamp et al. 1999), as in the small population paradigm (Caughley, 1994).

The social structure of sociable weavers plays an important role in reproduction in terms of cooperative breeding (Covas et al. 2004b). Survival is higher in larger colonies than in small and medium colonies (Brown et al. 2003). However, these asymmetries may generate colony population dynamics that are size specific and this should be taken into account (Serrano et al. 2005). Dispersal also may be related to colony size. For example, in lesser kestrels (*Falco naumanni*), smaller colonies show higher rates of dispersal (Serrano et al. 2005), while in sociable weavers, dispersal usually occurs between colonies of similar sizes (Brown et al. 2003).

Estimating survival and reproduction

Survival estimators are more robust to partial failure of its assumptions than estimators of population size are, when estimating population size from capture-mark-recapture data, although population size is often seen as the best indicator for population health.

(Lebreton et al., 1992). When natural populations are studied, individuals may often go undetected in sampling occasions, or may have moved out of the area where the study is being conducted and are thus not observed during sampling (Thompson 2002, Altwegg et al. 2003). In cases like this, these unobserved individuals would be falsely counted as individuals that have died (Thompson 2002, Altwegg et al., 2003). Capture mark recapture techniques control for variation in recapture success by estimating recapture probability separate from survival probability (Lebreton 1992; Nichols 1992).

Since their rapid development in the 1980s the use of life history parameters in population dynamics studies have become increasingly important in ecological studies (Lebreton et al., 1992). The capture-mark-recapture framework is essentially concerned with detecting and analyzing differences in survival and/or recruitment and ultimately fitness (Lebreton et al., 1992, Nichols, 1992). The probability of survival often tends to vary with individual characteristics such as sex, age, mass, genotype, phenotype, competition and predation and also as a function of abiotic and biotic environmental variables (Lebreton et al., 1992). Therefore, testing hypotheses concerned with the survival process and estimation of survival rates are vital to understand animal population dynamics (Lebreton et al., 1992). In order to estimate survival parameters under natural conditions, individually marked animals need to be followed through time (Lebreton et al. 1992, Nichols 1992).

Understanding a declining population

The population of sociable weavers on Benfontein Game Farm near Kimberley (Northern Cape, South Africa) has decreased by roughly 4% per year over the last 15 years (Figure 1). Some colonies have declined rapidly, others had only declined slightly, while others have remained stable or even increased slightly. Possible reasons for this decline include the effects of climate, emigration, inherent dynamics linked to colony size or the effects of fieldwork on the colonies.

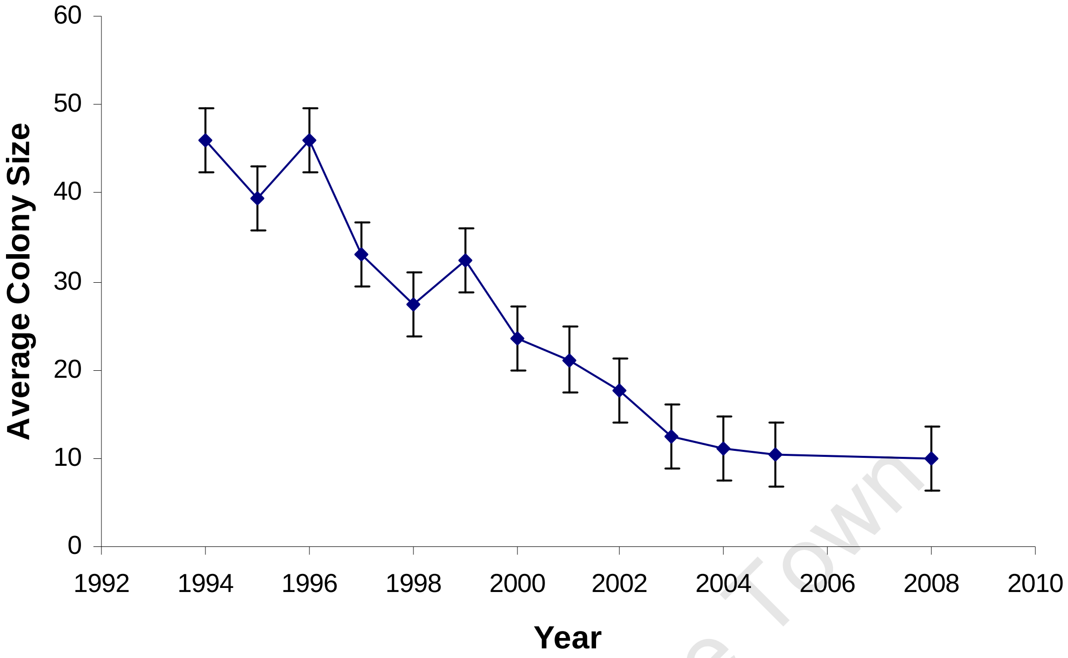


Figure 1: Changes in average colony size from 1994 to 2008 showing standard error.

Many studies have been conducted on the sociable weaver population on Benfontein Game Farm since 1993 to investigate factors affecting breeding and survival in these colonies (Brown et al., 2003; Covas et al., 2004a, b; 2006; 2008; Spottiswoode, 2007; 2009). However, these studies have focused mostly on questions related to the species' cooperative breeding system and relatively little attention has been given to their population dynamics and the environmental factors affecting them. As these birds seem to be affected by the local climate and their colony dynamics, I investigate these two factors in conjunction and compare declining and stable colonies to investigate potential reasons for the overall population decline. More specifically, I investigate the effect of climatic (rainfall and extreme temperatures), demographic and social parameters on the weavers' survival and reproductive rates. I hypothesize that as it is an arid environment, rainfall is the climatic variable that is most important in the performance of the population, with minimum temperature having a lesser effect and maximum temperature having little influence. I also hypothesize that birds from larger colonies will have higher rates of survival and reproduction than those from smaller colonies, and that weavers from declining colonies will have lower rates than those from stable colonies.

Chapter 2: Methods

The study was conducted at Benfontein Game Farm, 6 km southeast of Kimberley, in the Northern Cape, South Africa. The vegetation in the area is Kalahari sandveld, dominated by open *Acacia* savanna and *Stipagrostis* grasses This region is semi-arid and receives an average rainfall of 431 ± 127 mm per year, with temperatures ranging below 0^{o}C in winter to above 40^{o}C in summer (South African Weather Service). The study area covers approximately 15 km^2 of open savanna and contains approximately 25 sociable weaver colonies.

A capture-mark-recapture study has been conducted on sociable weavers from selected colonies at Benfontein Game Farm from July 1993 to September 2009, with the exception of 1997, 2005, 2006 and 2007. Weavers on the reserve have been captured using mist nets placed around the nest tree before dawn. This method catches at least 70% of the birds as they leave their nest (Covas et al., 2002). In order to estimate the numbers of birds in a colony, two counters were present, one on each side of the nest. Any birds that managed to escape were counted and added to the number of birds caught to estimate total colony size. Captured birds were ringed, measured (mass, wing and tarsus) and aged as either adult or juvenile (birds up to 4 months old). Ringed birds were recorded as present at a specific colony and measured. Sociable weavers are monomorphic (Doutrelant et al. 2004), so sexing is only possible through genetic analyses.

Survival

I estimated survival rates among adult birds (those captured in adult plumage). Of the 9814 captures, Only 9 birds were injured or killed during handling; they were removed from the data set on the last capture so that their death was not treated as a natural mortality, but the data on these birds up to the last capture are still used in the analyses.

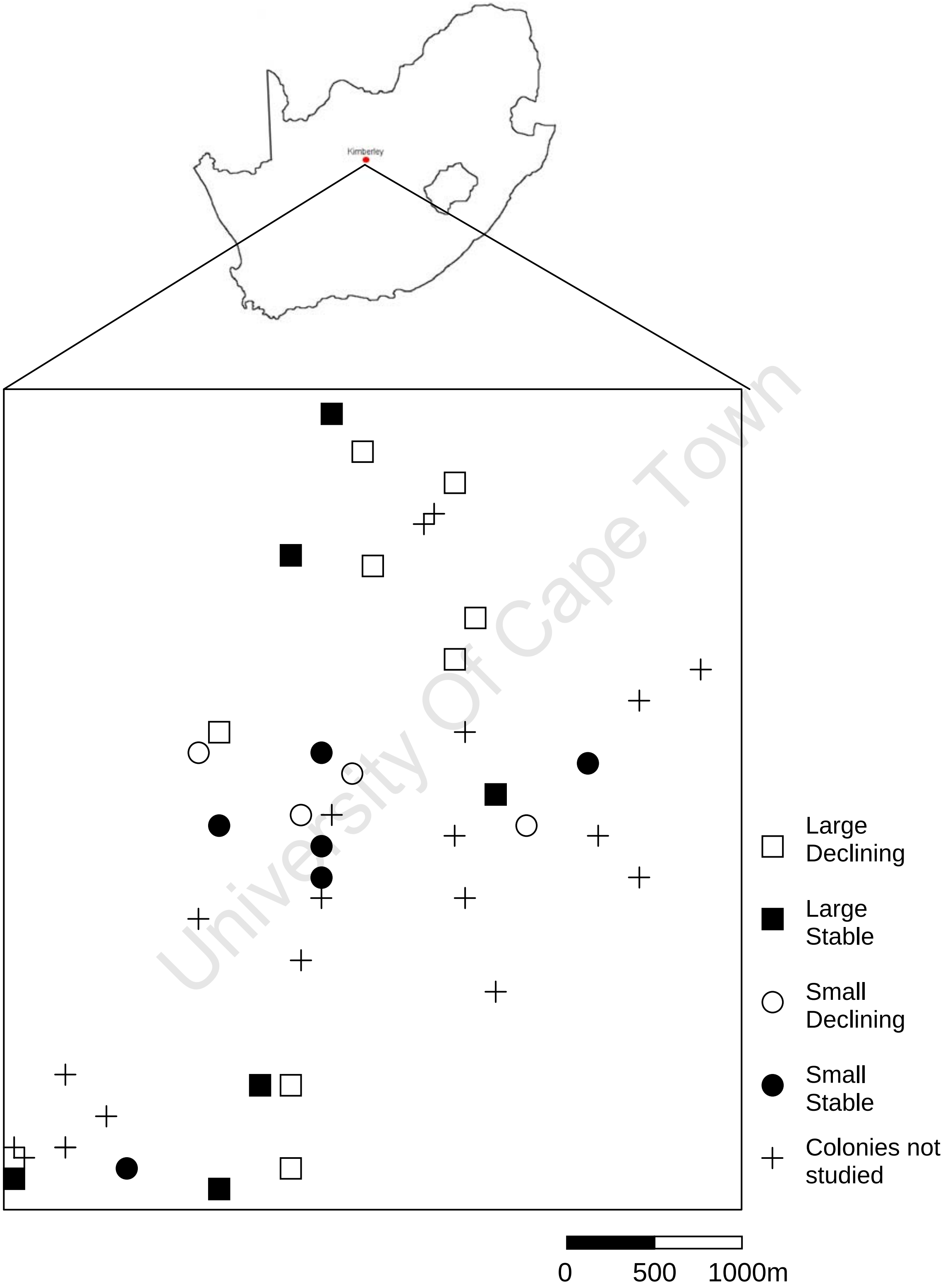


Figure 2: Map of South Africa showing location of Kimberley with a map of Benfontein Game Farm showing location of colonies. Area of map is 20 km^2

Birds from colonies that were not being studied were removed from the dataset. Individuals that were recorded at more than one colony for the duration of the study were removed from the dataset to avoid any possible errors that these individuals may have introduced into the analysis. These individuals made up <5% of the total.

My analysis included 6788 birds that were being studied from 24 colonies. Most of the 13 capture occasions were separated by intervals of approximately 1 year (1,083; 1; 1; 2,25; 0.83; 1; 1; 1; 0,916; 1,083; 4,083 and 0,83 years). These intervals were included in the CMR models.

I used program MARK 5.1 (White & Burnham, 1999) to estimate survival, using the general methods of Lebreton et al. (1992). These methods correct for the fact that not all individuals are captured every year by estimating recapture probabilities. I used the general notation of Lebreton et al. (1992), where Phi = survival probability P = recapture probability, with t indicating time dependence and other annotations such as age, trend and size dividing individuals into groups based on various criteria.

Model selection is an important step in the analysis of capture-mark-recapture data, with the biology of the population being studied driving the selection of a suitable class of models on which the data analysis should be based (Lebreton et al., 1992). As the number of parameters used in the model increases, so too does the sampling variance (Nichols, 1992). In order to remain parsimonious and reduce sampling variance, it is important to consider the number of parameters and select a suitable model with the minimal number of parameters (Nichols, 1992) Goodness of fit tests make sure that the models fit generally and that the assumptions of the model are not violated by the data. Once these assumptions have been met, model selection can take place (Lebreton et al., 1992).

Model selection is based on Akaike's Information Criterion (AIC) values. Akaike (1973) found a relationship between maximum likelihood and Kullback-Liebler information, which made it possible to combine model selection and estimation in a single theoretical framework (Anderson et al. 2000). The model with the lowest AIC value is selected as the best model for the available empirical data (Anderson et al. 2000). Values of AIC can be adjusted to account for sample size (AIC_c) or for overdispersion (QAIC).

For the preliminary analysis, the effect of age was tested to see whether the survival was different between fledglings and adults. I conducted a median ĉ goodness of fit (GOF) test on the last model in Table 1, the most general model, in order to see how well the model fitted the data. I then categorised weaver colonies based on their size and long-term trend of the colony. The size of the colony was either small or large, while the trend of the colony was either declining or stable. In order to decide which colonies belong to which of the four groups, I needed to construct boundaries so that each colony would fall within a certain group while trying to ensure that groups contained a roughly balanced number of colonies.

The initial colony size, which was the size of the colony at its first year of counting, ranging from 1994 to 1999, was used to categorise colonies as large or small (Figure 3). These were then combined with data on colony trends to create four groups: large-stable, large-declining, small-stable and small-declining. In order to obtain roughly equal numbers of colonies in each of these groups, colonies with <29 birds were deemed to be small (n=10), with colonies ≥32 birds large (n=14).

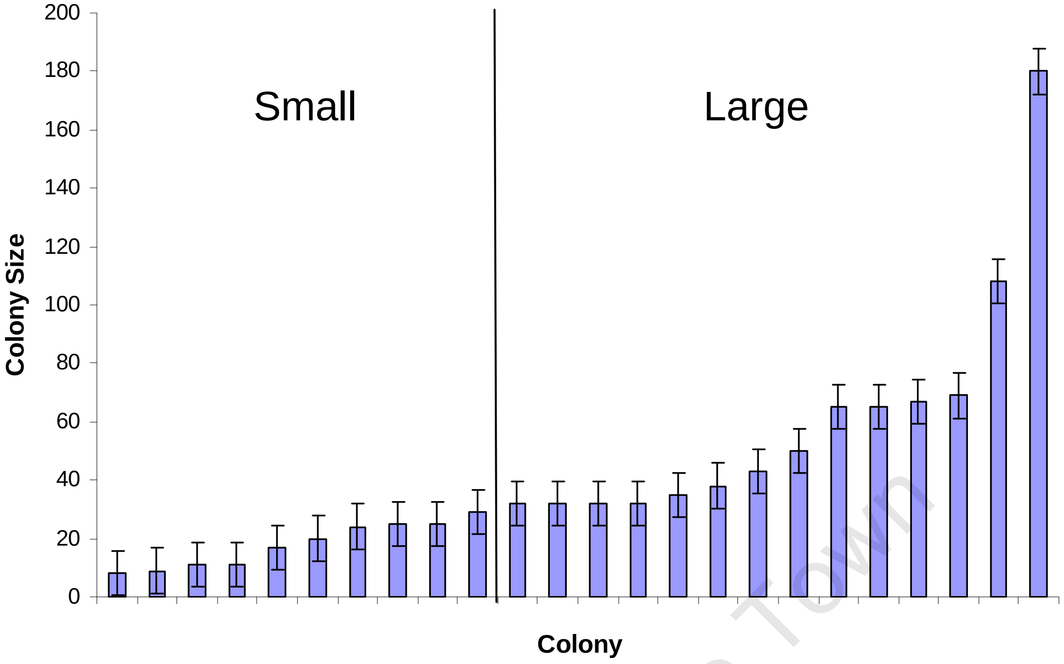


Figure 3: Distribution of sociable weaver colony sizes in the study area at Benfontein Game Farm, Kimberly, showing the division of small (S) and large (L) colonies, with error bars showing standard error.

To identify declining or stable colonies, I estimated the log of the slope of the change in colony size from 1993-2009 (Figure 4). To obtain sample groups of similar sizes colonies with a slope >-0.082 were placed in the stable group and <-0.095 in the declining group.

The resultant groups had 8 large declining colonies, 4 small declining, 6 large stable colonies and 6 small stable colonies.

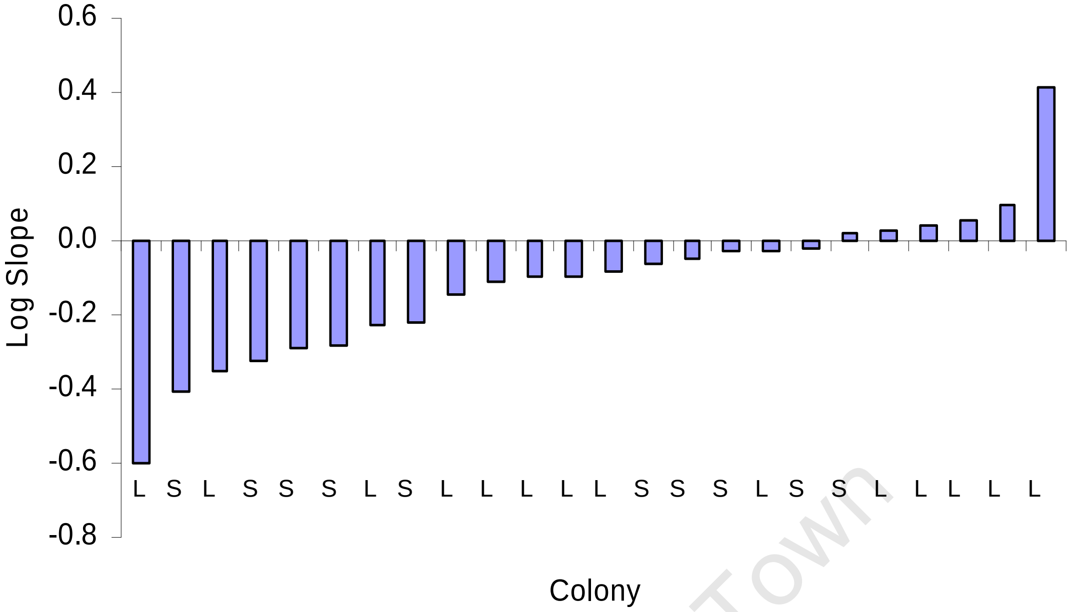


Figure 4: Distribution of log slopes of sociable weavers at Benfontein Game Farm, based on regular surveys from 1993 to 2009, with error bars showing standard error and X-axis labels showing Large (L) or Small (S) colonies

The initial analyses tested the possible effects of size and trend of colonies on survival of individuals to obtain the most parsimonious model. This model was then used to explore the effects of varying climatic conditions on survival. Weather data recorded at Kimberley airport by the South African Weather Service were used to estimate the maximum and minimum temperatures during a given capture interval and annual rainfall to include as environmental covariates. The rainfall values were adjusted to the length of a capture interval to give average rainfall per one year interval and thus allow for comparison. I examined the effect that each of these climatic variables may have on the population as a whole, or in interaction with colony size and trend.

I used an analysis of deviance (ANODEV) to determine how much of the temporal variation in survival could be attributed to each covariate. This subtracts the covariate model deviance from the constant model deviance and divides this by the number obtained from subtracting the global model deviance from the constant model deviance.

V = [deviance(constant model) – deviance(covariate model)]/[deviance(constant model) – deviance(time-dependent model)] and this can be done using program MARK 5.1 (White & Burnham, 1999).

Reproduction

Reproduction data on the sociable weaver colonies on Benfontein Game Farm were collected in 1999, 2000, 2002 and 2005 for all but two of the colonies used in the analysis of survival. Data from one additional colony also were included. These data were analysed using a generalized linear mixed effects model assuming a Poisson distribution and log link function. In order to get the number of fledglings per female rather than per colony, I added the logarithm of the number of females (based on annual censuses and assuming a 50:50 sex ratio; Doutrelant et al 2004) present in a specific year as an offset to all models. It was necessary to log the number of females because the model used a log link function. Year and colony were added as random effects to account for the non-independence among colonies that experienced the same climatic conditions in a given year, and for the fact that the same colonies were studied in several years. I used procedure Lmer in R 2.9.2, which approximates maximum likelihood and from these data, I also calculated the delta AIC and the various AIC weights (Anderson et al. 2000).

Possible effects of fieldwork

One possible reason for the overall decline in sociable weavers at Benfontein is the effect of the fieldwork on the weavers. Few birds were killed or injured during handling, but disturbance caused by regularly capturing birds and checking nest contents may encourage birds to emigrate. To assess whether this might be a problem in this study, I compared the performance of colonies that were not studied intensively to core study colonies. Data for the former colonies were only available for two years, 2005 and 2009, which limited the power of this exercise.

Chapter 3: Results

Survival

The results from the initial survival analysis showed that, although the AIC values were close, the best supported model had no age effect and as such, age did not have a strong effect(Table 1). This meant that all individuals could be treated as one group with regards to age. The results of the median ĉ test gave a median ĉ value of 1.342 (95% CI 1.262 - 1.352), which indicated a relatively good fit of the model to the data.

Table 1: Summary of model selection looking at the effect of age on survival of sociable weavers on Benfontein Game Farm. Ranked according to AIC_c, AIC weights give relative support in relation to other models.

Model	AIC_c	Delta AIC_c	AIC_c Weights	No. Parameters	Deviance
Phi(t) P(t)	10511.62	0	0.5332	25	1285.759
Phi (Age + t) P (t)	10512.25	0.6276	0.38959	26	1284.367
Phi(Age) P(t)	10515.49	3.8704	0.07699	38	1263.315
Phi(Age × t) P(t)	10527.22	15.6024	0.00022	49	1252.68

Applying this model to the four different groups of colonies showed that weavers from large colonies had a greater survival than those from small colonies, whereas birds from stable colonies had greater survival than birds from declining colonies (Figure 5). Weavers from large declining colonies had similar survival rates to birds from small stable colonies.

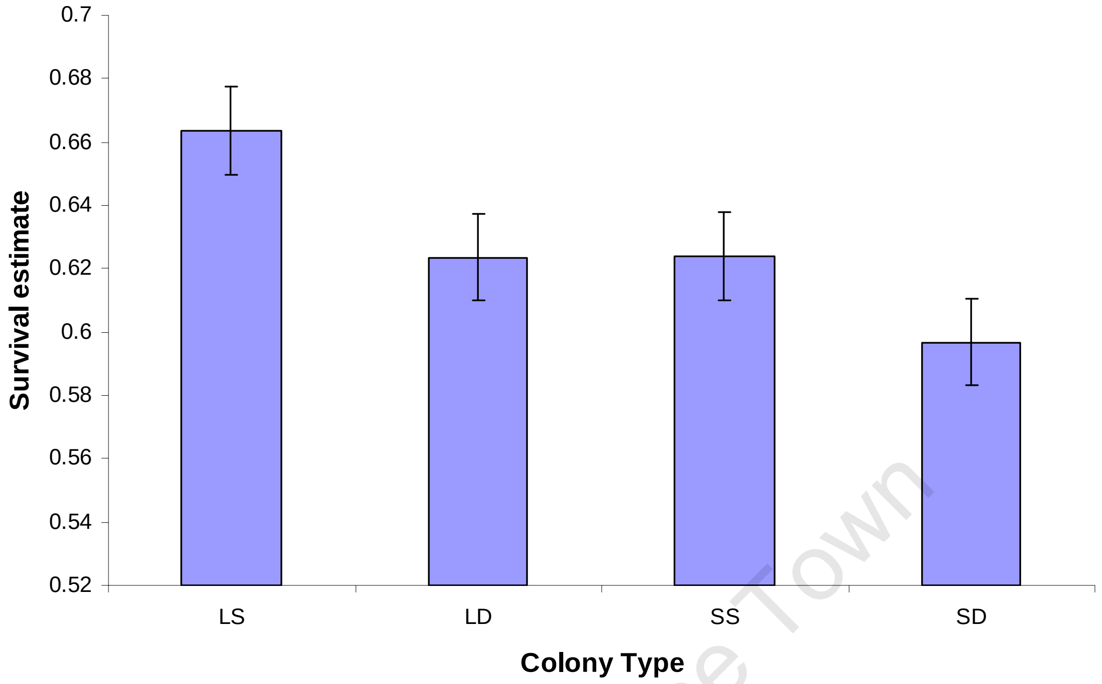


Figure 5: Survival estimates for the four different colony types on Benfontein Game Farm (Large Stable, Large Declining, Small Stable and Small Declining colonies), with error bars showing standard error.

The most parsimonious model, Phi (Size + Trend + t) P (Size + Trend + Trend*t + Size*t), incorporates colony size, trend and time (Table 2). There is a model that better fits the data than this model, but it has 20 additional parameters and this model is thus not considered to be a better model. Various other models were tested and the best-fitting of these are shown in Table 2.

Models containing the climatic variables did not fit the data as well as the most parsimonious model (Table 3). Those models with climatic variables had delta QAICs of more than 60 and thus carried no QAIC weight and thus had a model likelihood of 0.

Table 2: Summary of model selection looking at the effect Trend and Size on survival of sociable weavers on Benfontein. Models ranked according to QAICc, AIC weights give relative support in relation to other models, size divides colony into large or small groups, trend divides colonies into declining or stable groups.

Model	QAICc	Delta QAICc	QAICc Weights	Model Likelihood	Number of Parameters	QDeviance
Phi (Size, t) P (Size, Trend, t)	6243.5	0	0.32510	1	70	750.43
Phi (Size + Trend + t) P (Size + Trend + t + trend x t + size x t)	6243.9	0.3412	0.27411	0.8432	50	791.86
Phi (Size + Trend + t) P (Size + Trend + t + size x trend + trend x t + size x t)	6244.9	1.3392	0.16642	0.5119	51	790.81
Phi (Size + Trend + t + Size x Trend) P (Size + Trend + t + trend x t + size x t)	6245.9	2.3345	0.10118	0.3112	51	791.81
Phi (Trend + t) P (Size + Trend + t + Trend x t + Size x t)	6247.2	3.6348	0.05281	0.1624	49	797.20
Phi (Size + t) P (Size + Trend + t + Trend x t + Size x t)	6249.0	5.4575	0.02123	0.0653	49	799.02
Phi (Size + t) P (Size + Trend + t + Trend x t + Size x t)	6249.0	5.4575	0.02123	0.0653	49	799.02
Phi (Size + Trend + t + Size x t) P (Size + Trend + t + Trend x t + Size x t)	6249.3	5.7259	0.01856	0.0571	61	774.70
Phi (Size + Trend + t + Size x Trend + Size x t) P (Size + Trend + t + Trend x t + Size x t)	6250.8	7.2789	0.00854	0.0263	62	774.19
Phi (t) P (Size + Trend + t + Trend x t + Size x t)	6251.2	7.6461	0.00711	0.0219	48	803.25
Phi (Trend, t) P (Size, Trend, t)	6253.3	9.7813	0.00244	0.0075	70	760.21
Phi (Size + t + Size x t) P (Size + Trend + t + Trend x t + Size x t)	6254.7	11.1506	0.00123	0.0038	60	782.17
Phi (Size + Trend + t + Size x Trend + Trend x t) P (Size + Trend + t + Trend x t + Size x t)	6262.0	18.4574	0.00003	0.0001	62	785.37

Table 3: Summary of model selection looking at the effect Trend and Size combined with climatic variables on survival of sociable weavers on Benfontein. Ranked according to QAICc, QAICc weights give relative support of model in relation to other models, size divides colonies into large or small groups, trend divides colonies into declining or stable groups

Model	**QAICc**	**Delta QAICc**	**QAICc Weights**	**Number of Parameters**	**QDeviance**
Phi (Size + Trend + t) - **Global Model**	6243.89	0	1	50	791.858
Phi (Size + Trend + Trend x Min Temp)	6309.01	65.123	0	41	875.350
Phi (Size + Trend + Min Temp)	6309.65	65.764	0	40	878.028
Phi (Size + Trend + Size x Rainfall)	6309.77	65.876	0	41	876.104
Phi (Size + Trend + Size x Min Temp)	6310.24	66.352	0	41	876.579
Phi (Size + Trend + Trend x Size x Min Temp)	6310.44	66.554	0	43	872.706
Phi (Size + Trend + Max Temp)	6311.51	67.620	0	40	879.881
{Phi (Size + Trend) - **Constant Model**	6311.94	68.046	0	39	882.346
Phi (Size + Trend + Trend x Size x Rainfall)	6312.80	68.912	0	43	875.064
Phi (Size + Trend + Trend x Max Temp)	6312.82	68.935	0	41	879.162
Phi (Size + Trend + Rainfall)	6312.96	69.068	0	40	881.332
Phi (Size + Trend + Size x Max Temp)	6313.54	69.650	0	41	879.877
Phi (Size + Trend + Trend x Rainfall)	6314.40	70.520	0	41	880.746

Little variance in survival could be attributed to climatic variables. Minimum temperature had the greatest effect, with a negative correlation, attributing 7.7%, while maximum temperature also had a negative correlation but only explained for 3.5% and rainfall, which had a positive correlation and explained 6.8% of the observed variance.

Reproduction

The average number of fledglings per female sociable weaver varied greatly between years, peaking at 1.147 in 1999, and only 0.0168 in 2002 (Figure 6). The average number of offspring per female for the duration of the reproduction data collection was 0.646.

Reproductive output was best correlated with maximum temperature (negative) and rainfall (positive; Table 4; Figure 7). Minimum temperature also had a negative impact on reproduction (Table 4). Colony trend and size had less of an affect on reproduction than climatic variables, although there were still clear differences between the four colony types as well as between different colony sizes and trends (Figure 8, 9).

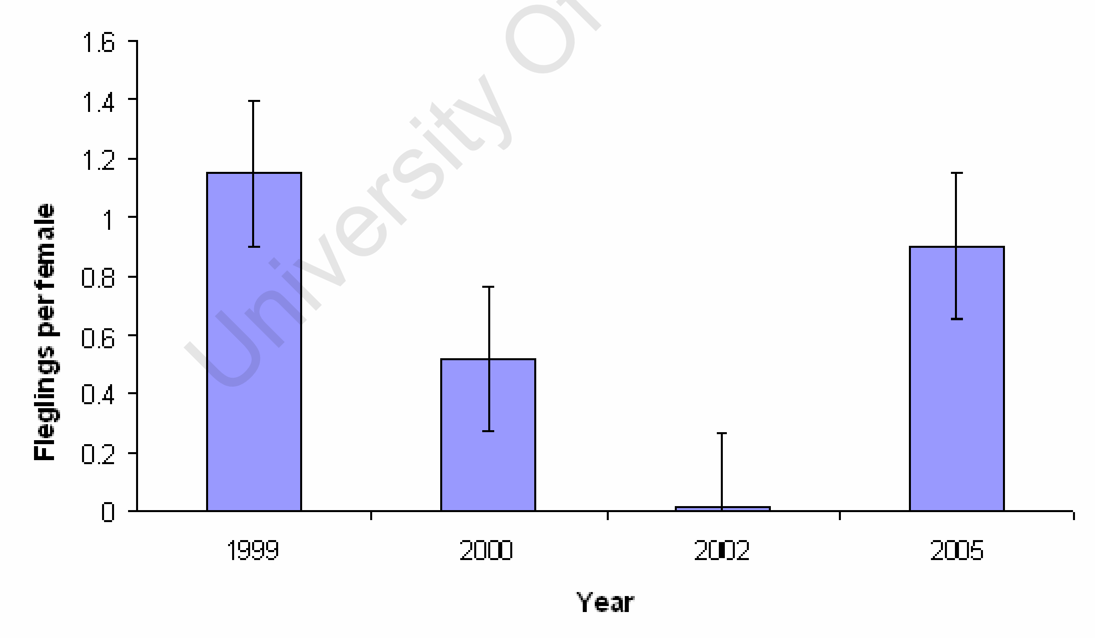
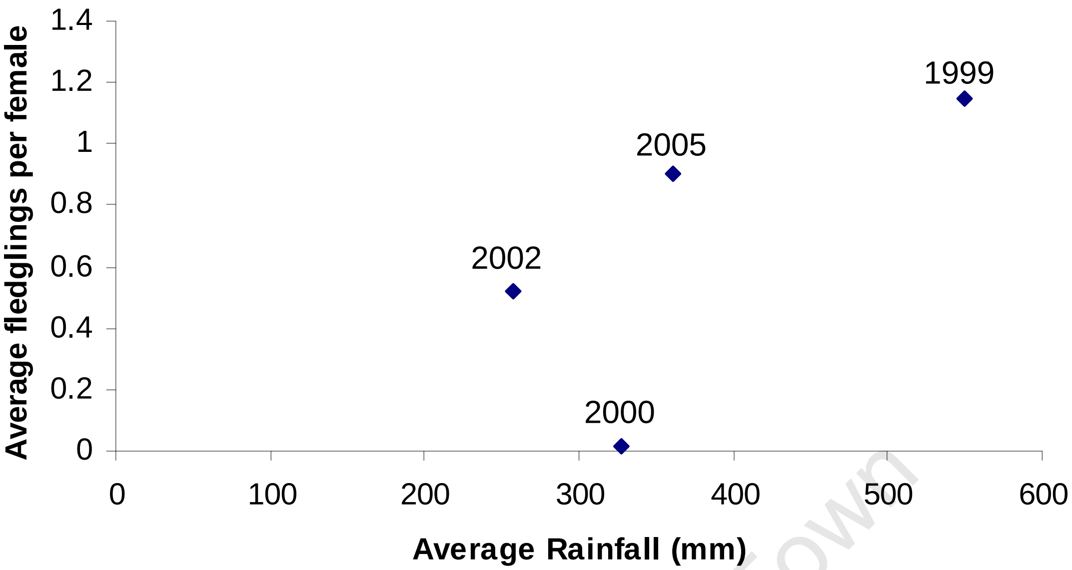


Figure 6: Number of fledglings per female sociable weaver recorded at 14 colonies at Benfontein Game Farm in four years from 1999 to 2005, with error bars showing standard error

.

Table 4: Summary of model selection results looking at effect of trend, size and climate on reproduction. Models ranked by AIC weights.

Model	AIC	Delta AIC	Deviance	No. Parameters	AIC Weight
Max	185.1	-2.5	177.1	4	0.4633
Rain	186.5	-1.1	178.5	4	0.2300
No Covariate	187.6	0	181.6	3	0.1327
Size	189.0	1.4	181.0	4	0.0659
Min	189.4	1.8	181.4	4	0.0539
Trend	189.4	1.8	181.4	4	0.0539



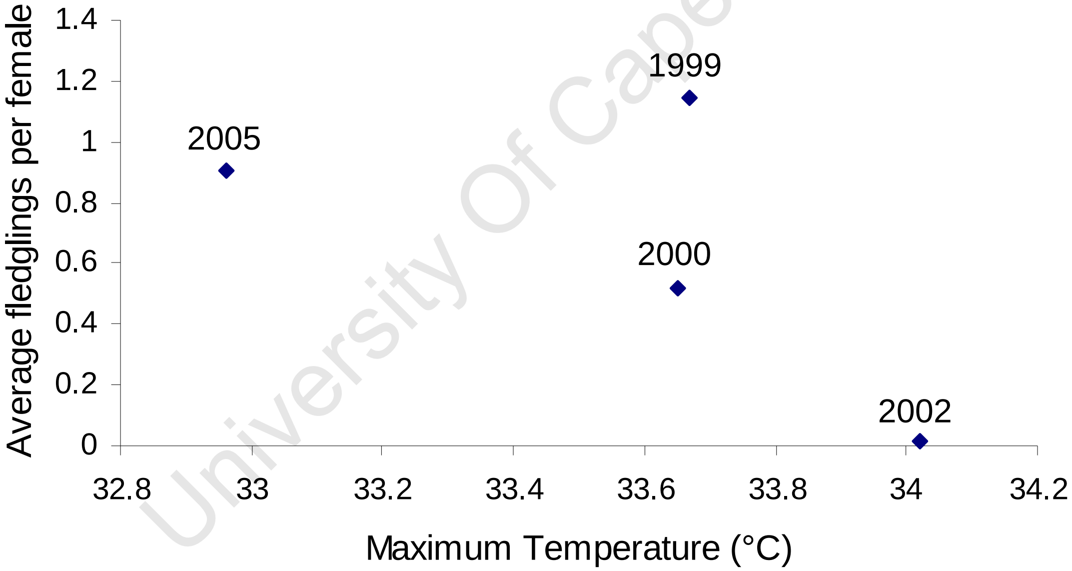


Figure 7: Average rainfall and maximum temperatures on Benfontein Game Farm between 1999 and 2005 plotted against the average number of fledglings per female in each year.

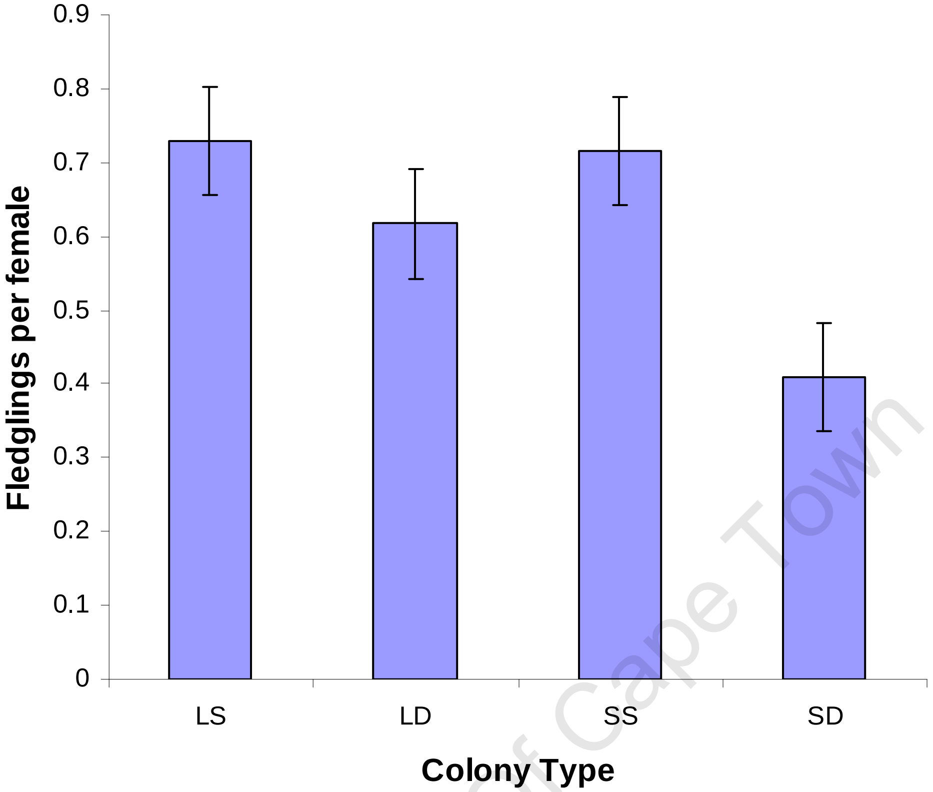


Figure 8: Fledglings per female for each colony type in four years between 1999 and 2005 on Benfontein Game Farm, with error bars showing standard error (LS – Large stable; LD – Large Declining; SS – Small Stable; SD – Small Declining).

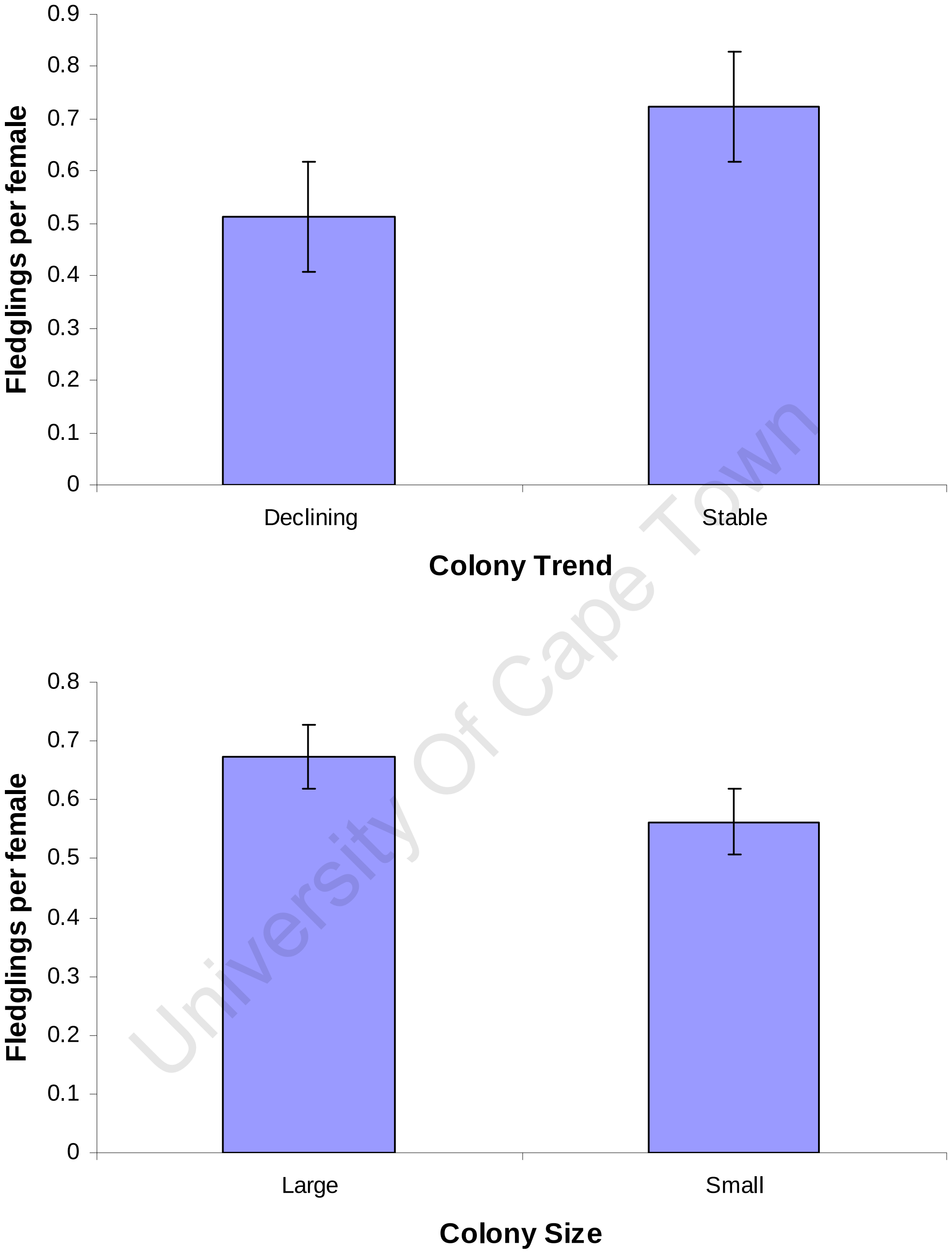


Figure 9: Fledglings per female on Benfontein Game Farm by colony trend (stable or declining) and colony size (large or small), with error bars showing standard error.

Possible effects of fieldwork

By looking at the changes in colony size over the two years of non-intensive study, compared to intensively studied colonies of similar sizes, it seems that the effects of the fieldwork on the colonies appears to be minimal (Figure 10). Only three out of the 11 colonies showed an increase in number, with six of the eight remaining colonies going extinct. This data indicated that the average colony size decreased from 14.9 in 2005 to 7.9 in 2009, which relates to a decline of 13% per year.

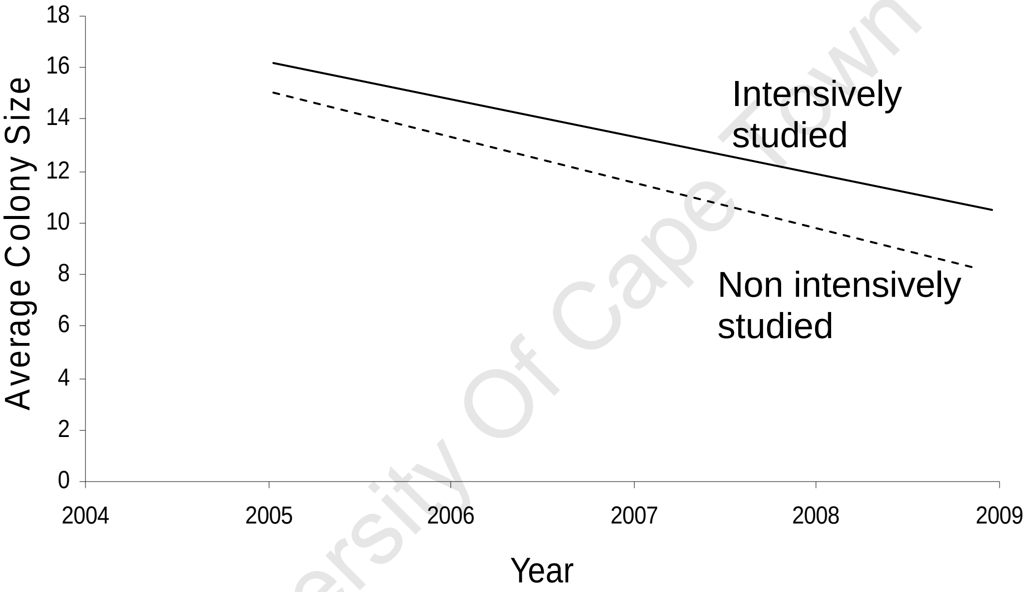


Figure 10: Decline in average colony size showing the difference between intensively and non-intensively studied colonies of similar

Chapter 4: Discussion

The main focus of this study was to determine the reasons for the population decline, and the role that colony dynamics and climatic variables may play in this. The main findings of the study showed that there are differences between the colonies with regards to survival and reproduction. Survival was higher for colonies that were larger colonies, which is in accordance with Brown et al. (2003). Survival was higher in stable colonies. Reproduction was higher for larger colonies and for stable colonies. Climate was seen to have an effect on both survival and reproduction and has thus played a role in the population decline, which supports the hypotheses relating to climate.

The higher apparent survival of weavers in larger colonies may be due to extra vigilance against predators as well as benefits to fledglings brought about by living in larger colonies (Brown et al., 2003). Larger colonies also have a more chambers and better insulation, reducing the costs of thermoregulation (White et al., 1975). These benefits are reduced in small colonies, suggesting an Allee effect linked to small colony size that might account for the lower adult survival rate in small colonies. Smaller colonies are likely to suffer due to a reduced thermoregulatory ability, reduced predator detection, decreased nest keeping and lower growth rates.

A thorough assessment of movement between colonies is necessary to interpret these results, because emigration may account for the lower apparent survival estimates in colonies that are small and/or declining. There may also be negative effects to living in larger colonies such as an increased parasite load, greater attraction to predators and the possibility of depleting the resources around the colony (Spottiswoode et al. 2007; Brown et al. 2003). The slight difference in survival rates between the various colonies may translate to large effects on lifespan (Brown et al., 2003)

Climate plays a small role in determining survival. Minimum temperature is the climatic variable that has the greatest effect on survival, and this can be partly attributed to the energy loss suffered during thermoregulation (White et al. 1975) as winter minimums can get to below freezing. The minimum temperatures may also have a negative impact on plant growth and insect activity. Of the climatic variables, rainfall had the second largest effect on survival. Late breeding season rainfall is observed to improve survival of blue cranes in arid South African environments (Altwegg et al., 2009) and migrating birds overwintering in arid environments (Kanyamibwa et al., 1990) and rainfall may have a similar effect here. The effect of rainfall on survival could be attributed to the amount of available food, which is closely related to rainfall (Brommer et al 2002; Altwegg et al., 2009). Maximum temperature had very little to no effect on survival, which may indicate that thermoregulation is more energetically costly at low temperatures than high temperatures for this particular species.

By comparing the survival data from declining and stable colonies, it would appear that the differences in survival are what are driving the population decline, although this can not be looked at in isolation. The reasons for the level of decline relating to colony trend are less obvious than those for colony size, and may be attributed to factors such as emigration of birds looking for colonies with higher survival. Looked at in isolation, the higher survival rates in stable colonies allows for the colonies to stay at roughly the same size, while the colonies that exhibit a decline, have a lower survival rate and are thus not able to maintain colony size and will eventually become extinct or abandoned.

Colony size is likely to influence reproductive success through the effect of helpers, which may become more noticeable in years of adverse conditions (Covas et al., 2008). This study found a positive correlation between colony size and reproductive success, unlike the Covas et al. (2008) study which found a negative correlation between the two, although in years of adverse conditions, the larger colonies had higher reproductive success due to the effect of increased numbers of helpers (Covas et al., 2008).

Several South African arid-zone bird species have shown a positive correlation between reproductive success and rainfall (Lloyd, 1999). The length and timing of the breeding season is dependant on the integrated effect that temperature and rainfall have on the vegetation (Lloyd, 1999). Blue cranes have shown a positive correlation between rainfall and reproduction in the early breeding season (Altwegg et al., 2009). The effects of climate on reproductive success are thus important, and could mean that smaller colonies will be adversely affected in terms of reproduction by a few years of bad weather, and subsequently unable to increase in size. Reproductive success was negatively correlated to maximum temperature and this is likely to be due to increased energy loss through thermoregulation and juvenile mortality due to heat stress and dehydration, as maximum temperatures can reach over 40°C and water may be scarce. In adverse climatic conditions, some birds may reduce their clutch sizes or not breed at all (Lloyd, 1990).

Snakes, in particular Cape cobras, *Naja nivea*, and boomslangs, *Dyspholidus typus*, are the main nest predators of sociable weavers, taking an average of 70% of all nesting attempts, with some colonies more prone to predation than others (Covas et al., 2008). This results in a major reduction in the reproductive success in colonies where nest predation by snakes is common. In the case of reduced reproductive success due to nest predation, smaller colonies are likely to suffer more than large colonies directly due to low numbers (100% of juveniles predated, poor defense) or indirectly through the colonies' inability to recover.

Combining survival and reproduction data is important to get an understanding of why the population is declining. Large colonies have higher rates of survival and reproduction than small colonies. In years of adverse climatic conditions, these rates are likely to decrease, with reproduction being more heavily reduced. In 2002, temperature was at its highest and rainfall was relatively low, and the observed reproductive success was at its lowest (0.0168 fledglings per female). Colonies with higher rates may have a buffering capacity, and be able to pass through these bad periods relatively unaffected. However, colonies that have lower rates may be pushed to a point from which they cannot recover due to their low reproductive and survival rates and will thus continue to decline until they become extinct. Although small stable colonies have similar survival rates to large declining colonies, it is likely that the higher reproduction rates in the small stable colonies prevent them from going extinct. The colonies have been grouped, and looking at these colonies individually may give further insight into what level of survival is required for a colony to stay stable or to increase in size.

Survival and reproduction are not the only parameters affecting populations, and emigration and immigration will also affect the population and the decline cannot be entirely attributed to differences in survival and reproduction. Birds are highly mobile organisms and the effects of movement should be always considered, especially when studying sub-populations. Emigration may be one of the reasons for the observed colony decline; sociable weavers may emigrate from declining colonies, while better colonies may have higher rates of immigration. Sociable weavers tend to move to colonies of similar sizes to the colonies from which they came (Brown et al., 2003). With the influence of several years of poor climatic conditions on reproduction potentially resulting in a reduction in colony size, the resulting survival in these colonies could be reduced due to the small colony size, and this may result in a downward spiral towards extinction.

A potential reason for the decline of the declining colonies may be that birds tend to leave those colonies in an attempt to find a colony in which their survival and reproductive success may be improved. Reproductive success in one colony or site may play a role in the selection of a breeding habitat for some individuals in the following year among some passerine bird species (Brown & Brown, 1996; Danchin et al., 1998; Brown et al., 2000), resulting in good habitats showing an increase in numbers relative to poorer habitats. This may result in the stable colony numbers increasing and these individuals will benefit from the advantages of living in a larger colony. Unfortunately, this study was unable to look at the effects of emigration on the population as a whole, so it is unknown whether the values obtained here correspond to increased mortality or increased emigration or more likely, a combination of both. Emigration would need to be studied to look at what proportion of the decline can be attributed directly to survival and recruitment.

Another aspect worth considering is the effect that minimum and maximum temperatures may have on the activity of snakes. Being reptiles, snakes are affected by the external temperature (Maclean, 1973c). Since the activity of snakes will be lower at cooler temperatures, it is likely that the warmer temperatures will allow for increased nest predation of juveniles and thus, a reduction in reproductive output. A colony that suffers from regular predation is likely to have a severely reduced reproductive output, which will result in the colony not being able to grow and eventually becoming extinct. The fact that maximum temperature has a negative correlation to reproduction may be due to the fact that snakes are more active at these higher temperatures, although it may also be to other factors such as chicks dying from thirst or heat stress. Some of the declining colonies may attribute their declines to resident nest predators. Predators and parasites should be incorporated into the study in order to determine more precisely which factors have what kind of influence on survival and reproduction.

This was a correlative study, and although such studies are a key part of ecological research, they suffer from confounding of their variables even in simple systems (Krebs & Berteaux, 2006). In this study, the relationship between the survival/reproduction was compared with potential explanatory variables, but causality cannot be determined. The results merely give an indication of the potential impacts that colony size and trend as well as climatic conditions may have on the weaver populations.

A further confounding factor may be the effect of disturbance caused by the fieldwork, since the repeated capture of the colonies for monitoring purposes could have disturbed the residents or even directly decrease their survival or reproductive success. From the results on the colonies that were not intensively studied (i.e. where the number of nest chambers was simply counted on different years and captured the residents on a single occasion), it appears that these colonies are declining at a faster rate than the colonies that were studied more intensively. However, the data on the colonies that were studied non-intensively was only collected in two years, over a period of 5 years, compared to the more extensive data collection on the intensively studied colonies. In addition, most low-disturbance colonies were small (<29 individuals), and so colony size may have had an effect in their poor performance. When these colonies were compared to intensively studied colonies of similar sizes, the decline was still faster in the non-intensively studied colonies, which indicates that the effect of fieldwork on the study species is minimal.

Finally, it is clear that there are differences in both survival and reproduction when comparing the different colony types, as well as between the different colony sizes and trends. This may have important implications for other colonial species in semi-arid environments. Although the optimal colony size or the threshold at which colonies begin to decline is not specifically known, it is evident that this species is affected by colony size and colony trend to a lesser extent. This is likely to be similar for some other colonial, cooperative, semi-arid passerine endemics. In similar species, it is likely that climatic variables may play similar roles, although this is not always the case (Lloyd, 1990). The diet of the species is likely to play an important role, as food availability is an important consideration, and the extent to which it is linked to rainfall and temperature will determine the effects of climate on survival and reproduction to an extent. Other species are likely to have unique factors affecting them that may also require investigation.

Chapter 5: Conclusions

The findings in this study are similar to other studies showing that natural populations can be driven by stochastic environmental factors, and often different parts of the population may be affected by different factors (Altwegg et al., 2003; Gaillard et al., 2000; Saether et al., 2000). By separating the different colonies into groups, it is possible to get an understanding of how the life history traits may vary with colony size. However, these groupings may have lumped data together that could have required separate analysis to produce more specific results.

It is clear that the sociable weaver population in the study area has been declining for the past few years. It appears that living in larger or more stable colonies confers the advantages necessary for the population to survive adverse climatic conditions. While much of this decline may be attributed to colony dynamics and climatic conditions, there are still other potential reasons that could contribute to their decline. Emigration should be studied to estimate how many of the assumed mortalities may simply be birds that have moved off to other sites. If emigration is an important factor, further investigations into the possible reasons for this movement should prove valuable in understanding the population decline. This may require a study of the vegetation, predators and parasites in various sites. Although the effects of fieldwork appear to be minimal just by observations, a more detailed analysis of the effect of the fieldwork on the population is required.

This study showed that the population dynamics of sociable weavers are affected by colony size and trend, as well as by climatic variables, which affect survival or reproduction in different ways. With an increasing focus on global change, there is a need to better understand the effects of climate on natural processes. Climate change scenarios for this region predict that summer rainfall will increase, but the rainfall variability will also increase (Altwegg et al., 2009). In combination with the possible temperature increase, these changes are likely to negatively affect reproduction, with minimal effect on survival, although climatic predictions are still relatively uncertain and the net effect on the population is thus uncertain.

Fortunately, the sociable weaver is not in any danger of extinction at present, and no conservation strategies are necessary. However, studies like this one provide insights into the causes of population declines, allowing for more efficient use of scarce resources for conservation and speeding up the conservation process.

References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle In B.N. Petrov & F. Csaki, editors, 267-281. Second International Symposium on Information Theory. Akademiai Kiado, Budapest.

Altwegg, R., Anderson, M.D. 2009. Rainfall in arid zones: possible effects of climate change on the population ecology of blue cranes. Functional Ecology 23 (5), 1014-1021.

Altwegg, R., Underhill, L.G. 2006. Apparent survival rates of Cape Sugarbirds *Promerops cafer* at a breeding and a non-breeding site. Ostrich 77, 220–224.

Altwegg, R., Roulin, A., Kestenholz, M. & Jenni, L. 2003. Variation and covariation in survival, dispersal, and population size in barn owls *Tyto alba*. Journal of Animal Ecology 72, 391-399.

Anderson, D.R., Burnham, K.P. & Thompson, W.L. 2000. Null hypothesis testing: problems, prevalence and an alternative. Journal of Wildlife Management 64, 912-923.

Asquith, N.M. 2001. Misdirections in conservation biology. Conservation Biology 15, 345–352.

Bartholomew, G.A., White, F.N. & Howell, T.R. 1976. The thermal significance of the nest of the sociable weaver, *Philetairus socius*: summer observations. Ibis 118, 402-411.

Bond, J.C., Iverson S.A., Maccallum N.B., Smith C.M., Bruner H.J., Esler D. 2009. Variation in breeding season survival of female Harlequin Ducks. Journal of Wildlife Management 73, 965-972.

Brommer, J.E., Pietiainen, H. & Kolunen, H. 2002. Reproduction and survival in a variable environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. Auk 119, 544-550.

Brown, C.R. & Brown, M.B. 1996. Coloniality in the cliff swallow: the effect of group size on social behaviour. University of Chicago Press, Chicago.

Brown, C.R., Brown, M.B. & Danchin. E. 2000. Breeding habitat selection in Cliff Swallows: The effect of conspecific reproductive success on colony choice. Journal of Animal Ecology 69, 133-142.

Brown, C.R., Covas, R., Anderson, M.A., Bomberger Brown, M. 2003. Multistate estimates of survival and movement in relation to colony size in the Sociable Weaver. Behavioral Ecology 14, 463-471.

Calvo, B. & Furness, R.W. 1992. A review of the use and effects of marks and devices on birds. Ringing & Migration 13, 129-151.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63, 215-244.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. 1999. Inverse density dependence and the Allee effect. Trends in Ecology and Evolution 14, 405-410

Covas, R, Brown, C,R,, Anderson, M.D., Bomberger Brown, M. 2002. Stabilising selection on body mass in the Sociable Weaver. Proceedings of the Royal Society of London B 269, 1905-1909.

Covas, R., Brown, C.R., Anderson, M.D., Bomberger Brown, M. 2004a. Juvenile and adult survival in the Sociable Weaver (*Philetairus socius*), a southern-temperate colonial cooperative breeder in Africa. Auk 121, 1199-1207.

Covas, R., Doutrelant, C., du Plessis, M.A. 2004b. Experimental evidence of a link between breeding conditions and the decision to breed or to help in a colonial cooperative bird. Proceedings of the Royal Society of London B 271, 827-832.

Covas, R., Dalecky, A., Caizergues, A., Doutrelant, C. 2006. Kin associations and direct vs indirect fitness benefits in colonial cooperatively breeding Sociable Weavers, *Philetairus socius*. Behavioural Ecology and Sociobiology 60, 323-331.

Covas, R., du Plessis, M.A., Doutrelant, C. 2008. Helpers in colonial cooperatively breeding Sociable Weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. Behavioural Ecology and Sociobiology 63, 103-112.

Danchin , E., Boulinier, T. & Massot, M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the evolution of coloniality. Ecology 79, 2415-2428.

de Swardt, D.H. & Peach, W.J. 2001. Annual survival of Gurney's Sugarbird, *Promerops gurneyi*. Ostrich 72, 206–209.

Doutrelant, C., Covas, R., Caizergues, A. & duPlessis, M. A. 2004. Unexpected sex ratio adjustment in a colonial cooperative bird: pairs with helpers produce more of the helping sex whereas pairs without helpers do not. Behavioural Ecology & Sociobiology 56, 149-154.

Gaillard, J.-M., Festa-Bianchet, M., Yoccoz, N.G., Loison, A. & Toigo, C. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31, 367–393.

Godfray, C.H.J & Rees. M. 2002. Growth rates: Issues and an application. Philosophical Transactions of the Royal Society, London B 357, 1307-1319.

Green, R.E. 1995. Diagnosing the causes of bird population declines. Ibis 137, 47–55.

Grosbois, V., Gimenez, O., Gaillard, J.M., Pradel, R., Barbraud, C., Clobert, J., Moller, A.P. & Weimerskirch, H. 2008. Assessing the impact of climate variation on survival in vertebrate populations. Biological Reviews 83, 357-399.

Grosbois, V. & Thompson, P.M. 2005. North Atlantic climate variation influences survival in adult fulmars. Oikos 109, 273-290.

Humbert, J., Mills, L.S., Horne, J.S. & Dennis, B. 2009. A better way to estimate population trends. Oikos 118, 1940-1946.

Jonzen, N., Pople, T., Knape, J. & Skold, M. 2010. Stochastic demography and population dynamics in the red kangaroo *Macropus rufus*. Journal of Animal Ecology 79, 109-116.

Kanyamibwa, S., Schierer, A., Pradel, R. & Lebreton, J.D. (1990) Changes in adult annual survival rates in a western European population of the White Stork Ciconia ciconia. Ibis 132, 27–35.

Karell, P., Ahola, K., Karstinen, T., Zolei, A. & Brommer, J.E. 2009. Population dynamics in a cyclic environment: consequences of cyclic food abundances on tawny owl reproduction and survival. Journal of Animal Ecology 78, 1050-1062.

Keller, L.F. & Waller, D.M. 2002. Inbreeding effects in wild populations. Trends in Ecology and Evolution 17, 230–241.

Krebs, C.J. & Berteaux, D. 2006. Problems and pitfalls in relating climate variability to population dynamics. Climate Research 32, 143-149.

Lande, R., Engen, S. & Saether, B.E. 2003. Stochastic population dynamics in ecology and conservation. Oxford University Press, Oxford.

Lebreton, J. D., Burnham, K. P., Clobert, J. & Anderson, D. R. 1992 Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62, 67–118.

Lloyd, P. 1999. Rainfall as a breeding stimulus and clutch-size determinant in South African arid-zone birds. Ibis 141, 637-643

Maclean, G. L. 1973a. The sociable weaver, part 5: Food, feeding and general behaviour. Ostrich 44, 254-261.

Maclean, G. L. 1973b. The sociable weaver, part 2: Nest architecture and social organisation. Ostrich 44, 191-218.

Maclean, G. L. 1973c. The sociable weaver, part 4: predators, parasites and symbionts. Ostrich 44, 241–253.

Nichols, J.D. 1992. Capture-recapture models: using marked animals to study population dynamics. BioScience 42, 94–102.

Nichols, J.D. & Hines, J.E. 2002. Approaches for the direct estimation of k, and demographic contributions to k , using capture-recapture data. Journal of Applied Statistics, 29, 539-568.

Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology 41, 413–426.

Opdam, P. 1991. Metapopulation theory and habitat fragmentation: A review of Holarctic breeding bird studies. Landscape Ecology 5, 93-106.

Pulliam, H.R. 1988. Sources, sinks and population regulation. American Naturalist 132, 652–661.

R Development Core Team 2008. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Saether, B. & Engen, S. 2002. Pattern of variation in avian population growth rates. Philosophical Transactions of the Royal Society, London B 357, 1185-1195.

Sæther, B.-E., Tufto, J., Engen, S., Jerstad, K., Røstad, O.W. & Skåtan, J.E. 2000. Population dynamical consequences of climate change for a small temperate songbird. Science 287, 854–856.

Sæther, B.E., Sutherland, W.J. & Engen, S. 2004 Climate influences on avian population dynamics. Advances in Ecological Research 35, 185–209.

Sekercioglu, C.H., Daily, G.C. & Ehrlich, P.R. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences 101, 18042-18047.

Serrano, D., Oro, D., Ursua, E. & Tella, J.L. 2005. Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. American Naturalist 166, 22-31.

Sibly, R.M., Barker, D., Denham, M.C., Hone, J. & Page, M. 2005. On the regulation of populations of mammals, birds, fish and insects. Science 309, 607-610

Spottiswoode, C.N. 2007. Phenotypic sorting in morphology and reproductive investment among sociable weaver colonies. Oecologia 154, 589–600.

Spottiswoode, C.N. 2009. Fine-scale life-history variation in sociable weavers in relation to colony size. Journal of Animal Ecology 78, 504-512.

Stenseth, N.C., Mysterud, A., Ottersen, G., Hurrell, J.W., Chan, K. & Lima, M. 2002. Ecological effects of climate fluctuations. Science 297, 1292-1296.

Thompson, W.L. 2002. Towards reliable bird surveys: Accounting for individuals present but not detected. Auk 119, 18-25

Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. Nature 416, 389-395.

White, G.C. & Burnham, K.P. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46, 120–139.

White, F. N., Bartholomew, G. A. & Howell, T. R. 1975. The thermal significance of the nest of the sociable weaver *Philetairus socius*: winter observations. Ibis 117, 171-179.

www.birdlife.org – visited 10/02/10

www.iucn.org – visited 22/01/10

www.iucnredlist.org – visited 22/01/10