Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation

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Abstract Population trends are determined by gains through reproduction and immigration, and losses through mortality and emigration. These demographic quantities and resulting population dynamics are affected by different external and internal drivers. We examined how these demographic quantities were affected by weather, research-induced disturbance, local density, colony site and year in a metapopulation of 17 sociable weaver (*Philetairus socius*) colonies over 17 years of study (4 years for reproduction). Most colonies declined, but at different rates. The four demographic quantities were related to different drivers. Survival strongly varied among years and colonies and was positively related to rainfall and negatively related to extreme temperature (together explaining 30 % of variation) and disturbance (measured as number of captures conducted at a colony; 7 %). There was a trend for a positive relationship between reproduction and rainfall (50 %). Movement was mainly related to local density: individuals were more likely to emigrate from small to large colonies and from colonies that were either well below or above their long-term mean. They were more likely to immigrate into colonies that were nearby, and below their mean size. We then quantified the effects of these relationships on metapopulation dynamics using a multi-site matrix projection model. Rainfall was potentially a strong driver of metapopulation dynamics. In addition, field-work disturbance might have contributed to the decline of this metapopulation but could not explain its full magnitude. Hence, through a combination of analytical methods we were able to obtain information on the main drivers affecting dynamics in a declining metapopulation.

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Introduction

Variation in population size is determined by additions through recruitment and immigration, and losses due to mortality and emigration. A more mechanistic understanding of population dynamics can therefore be gained from examining how different drivers affect these components to cause an overall change in population size (Morris and Doak 2002).

Such extrinsic drivers can broadly be classified into direct human-induced drivers, such as land-use change, disturbance, or direct exploitation, and environmental drivers such as climate or changes in the biotic environment. External drivers generally affect different demographic rates in different ways. For example, young individuals may be more susceptible to environmental drivers (Gaillard et al. 2000; Altwegg et al. 2005), and generally the demographic rates exhibiting the highest sensitivity/elasticity also tend to exhibit the least variation (Pfister 1998; Gaillard and Yoccoz 2003). Furthermore, population dynamics are not only the result of extrinsic stochastic effects but are also influenced by intrinsic processes that depend on population density and age structure (Lande et al. 2003).

One of the key intrinsic processes is density, which can affect demographic rates negatively or positively. Negative density effects on fitness generally keep natural populations bounded (Turchin 1995). However, declining populations eventually become small populations, which can be subject to positive density effects known as Allee effects (Courchamp et al. 2008). Allee effects increase extinction risk of small populations by lowering fitness at small population sizes (Kuussaari et al. 1998). In addition, most populations are connected to others through the exchange of individuals. Theoretically, small amounts of density-dependent dispersal can greatly affect the dynamics of metapopulations (Sæther et al. 1999). Increased emigration at low population densities constitutes an Allee effect and can cause sudden collapses of local populations, while immigration into small populations improves their persistence (Ims and Yoccoz 1997). Extrinsic and intrinsic effects can interact in complex ways (Coulson et al. 2001). A population model is thus required if we want to understand the overall effects of these drivers on a particular population.

We studied the demographic mechanisms of colony dynamics in a metapopulation of sociable weavers (*Philetairus socius*) in South Africa. These weavers are an obligate colonial species that inhabit the semi-arid savannas of southern Africa where they build large communal haystack-like nests, usually in acacia trees (Maclean 1973; Covas

et al. 2008). Here, we examined survival, reproduction, immigration and emigration in a set of 17 colonies making up local populations in a metapopulation of sociable weavers. The metapopulation we studied consisted of colonies that ranged widely in size and rate of change, with most of them declining over the 17 years of our study. This collection of local populations allows us to examine the demographic mechanisms behind population decline, and how it is affected by extrinsic and intrinsic drivers.

Materials and methods

We studied sociable weavers at 17 colonies on Benfontein Game Farm, near Kimberley, South Africa (Fig. 1); see Covas et al. (2004, 2008) and Spottiswoode (2007, 2009) for detailed field methods. Our study area covers ca. 15 km^2 and consists of a flat, open savannah landscape with homogeneous weather conditions across the study area. The study area contained further colonies that we did not study in enough detail to be able to include them here (also shown in Fig. 1). Our results thus apply to the studied populations and not necessarily to the dynamics of sociable weavers at the landscape level.

Nine of the 17 colonies included in this study were studied from 1993 to 2009, two from 1994 to 2009, two from 1995 to 2009, and the remaining four from 1999 to 2009. No adults were captured in the 1998 breeding season, and from 2005 to 2007. In total, our analysis included 4,295
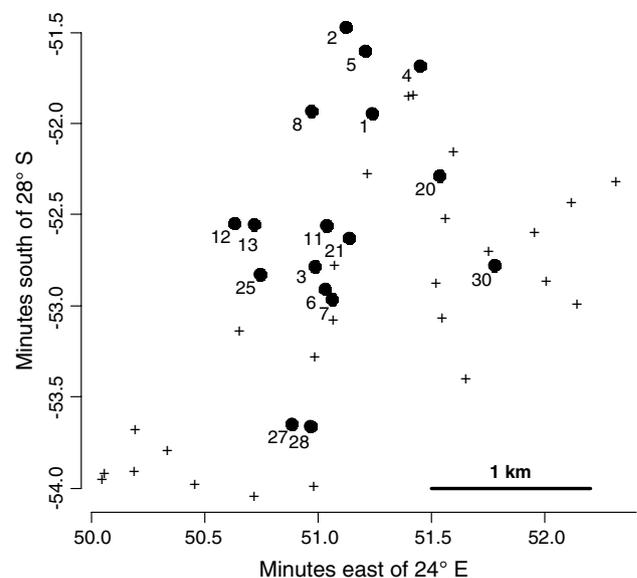

Fig. 1 Schematic map of the locations of sociable weaver colonies on Benfontein Farm near Kimberley, South Africa. The *filled circles* represent colonies included in this study, and their *number*s correspond to the panel in Fig. 3 where their dynamics are displayed. *Crosses* are other colonies that did not form part of this study

captures of 2,385 adult sociable weavers. Of those, 133 individuals were captured in two different colonies during the study, and five individuals in three different colonies. Movements were observed for 73 out of the 272 possible transitions among the 17 colonies, with a maximum of seven individuals observed making the same transition.

The colonies were subject to one to five full captures per season (one or two captures in 77 % of the occasions) by flushing all individuals into mist nets set up before dawn. Individual adults were also captured with a hand net in the nest. However, not all colonies were studied every year: we made no captures in 14 out of the 191 colony-year combinations. The analyses conducted here required that breeding success was known for the entire breeding season (which in this species can last up to 9 months). Such total reproductive output was available for four years in 11 (in 1999 and 2002), 14 (2000), or ten (in 2005) colonies. We estimated colony sizes during capture events as the number of individuals caught plus the number observed to avoid the mist nets, which usually comprised only a few individuals.

Statistical analyses

We estimated survival and movement of adult sociable weavers using multi-state capture-mark-recapture models (Spendelow et al. 1995; Lebreton and Pradel 2002), defining residence at each colony as a separate state. Throughout the manuscript, we refer to 'survival' as the probability of surviving and staying in one of the studied colonies.

The number of possible transitions among n states is $n \times (n - 1)$. Since we had 17 colonies, there were 272 possible transitions, not all of which were separately estimable. Instead we used as our starting model one where the movement probability between pairs of colonies was constrained to be a linear function of distance between them (ranging from 100 to 3,700 m). The starting model also allowed for full colony and year effects, including their interaction, on survival. The recapture probabilities were allowed to vary over the years and as a linear (on the logit scale) function of the number of capture sessions conducted at each colony each year.

Goodness-of-fit, model fitting, model selection, and analysis of deviance

The capture-mark-recapture statistical modelling framework we used assumes equal survival, recapture and movement probabilities among individuals within groups. The data on movement were too sparse to test the assumption of homogeneity of movement probabilities, but we tested the other two assumptions using a standard goodness-of-fit for the time-dependent Cormack-Jolly-Seber model implemented in program U-CARE (Choquet et al. 2009). For this test, we treated the colonies as groups and assigned the individuals that had moved to the colony at which they were initially encountered. This model is similar to our general model (model 1; Table 1) except that it ignores movement. The standard tests 2 and 3 in U-CARE showed

Table 1 Summary of model selection for survival in and movement among 17 sociable weaver colonies near Kimberley, South Africa

Model		AIC_c	ΔAIC_c	w_i	K	Deviance
1	$\Phi_{\text{year} \times \text{colony}} \, \psi_{\text{distance}}$	8,550.197	29.070	0	180	2,654.304
2	$\Phi_{\text{year}} \, \psi_{\text{distance}}$	8,551.389	30.263	0	27	2,978.077
3	$\Phi_{\text{year} + \text{colony}} \, \psi_{\text{distance}}$	8,575.023	53.896	0	44	2,967.094
4	$\Phi_{\text{weather}} \, \psi_{\text{distance}}$	8,621.401	100.275	0	20	3,062.258
5	$\Phi_{\text{disturbance}} \, \psi_{\text{distance}}$	8,632.737	82.540	0	21	3,071.572
6	$\Phi_{.} \, \psi_{\text{distance}}$	8,651.604	130.477	0	17	3,098.518
7	$\Phi_{\text{density}} \, \psi_{\text{distance}}$	8,656.382	135.255	0	21	3,096.422
8	$\Phi_{\text{colony}} \, \psi_{\text{distance}}$	8,657.587	136.460	0	33	3,086.605
9	$\Phi_{\text{year}} \, \psi_{\text{distance} + \text{density}}^{2}$	8,521.127	0.000	0.79	32	2,937.664
10	$\Phi_{\text{year}} \, \psi_{\text{distance} + \text{density} + \text{allee} + \text{disturbance}}^{2}$	8,523.735	2.608	0.21	37	2,930.096
11	$\Phi_{\text{year}} \, \psi_{\text{distance} + \text{allee}}$	8,545.747	24.620	0	29	2,968.378
12	$\Phi_{\text{year}} \, \psi_{\text{distance} + \text{disturbance}}$	8,547.844	26.717	0	31	2,966.413
13	$\Phi_{\text{year}} \, \psi_{\text{distance} + \text{weather}}$	8,550.661	29.534	0	30	2,971.261

The models are multi-state capture-mark-recapture models treating each colony as a separate state. The models consisted of three parts describing survival (Φ), movement (ψ), and recapture. The structure of the recapture model was the same for all models, and included variation among years and the effects of the number of full captures conducted at each colony in a particular year. The recapture model also accounted for the fact that no capture effort was made at some colonies in some years, by allowing the recapture probability to be zero in these cases. Model selection was based on the sample-size adjusted Akaike's information criterion (AIC_c)

ΔAIC_c Difference in AIC_c between the current model and the best, w_i Akaike weight (i.e. the relative support a model has from the data compared to the other models in the set)

no indication of a lack of fit for this model ($\chi^2 = 200.14$, $df = 297$). Likewise, the median-$\hat{c}$ procedure in program MARK (White and Burnham 1999) also indicated little overdispersion ($\hat{c} = 1.12$), and we concluded that these models fitted our data well.

We fitted all models using program MARK 6.0 (White and Burnham 1999), and evaluated model performance based on the sample size-adjusted Akaike's information criterion (AIC_c) (Burnham and Anderson 2002). With multistate models, the likelihood function can converge on local optima, and we therefore fitted some key models using the simulated annealing methods provided in program MARK (White and Burnham 1999). For the other models, we used the faster default method based on the Newton–Raphson algorithm, but used starting values obtained from a model fitted by simulated annealing for parameters that were shared between the models.

We examined the effect of the covariates on survival using ultra-structural models, i.e. by fitting models that assume survival is a deterministic function of the covariate(s) in question (described in detail in the following section). With a lot of spatiotemporal variation in survival, as we found in our study, this approach has inflated power (Link 1999). We therefore used analyses of deviance (ANODEV) (Skalski et al. 1993; Grosbois et al. 2008) to calculate the proportion of deviance explained by each (set of) covariate(s), rather than relying on AIC_c alone. The amount of spatiotemporal variation (deviance) in survival explained by a covariate is $(DEV. - DEV_{cov})/(DEV. - DEV_{year \times colony})$, where $DEV.$ is the deviance of the constant model, DEV_{cov} is the deviance of the model including covariates, and $DEV_{year \times colony}$ is the deviance of the model allowing for interactive colony and year effects (and thus full spatiotemporal variation). Using the fully spatiotemporal model as reference, ANODEV estimates the proportion of spatiotemporal variation explained by covariates. However, all colonies experienced the same weather in a given year and weather covariates therefore only varied among years. For these covariates, the relevant model for comparison is therefore the one including a year effect only (replacing $DEV_{year \times colony}$ by DEV_{year}). See Appendix 1 in the Electronic Supplementary Information for more details. For reproduction, we also examined mean colony size as a covariate that only varied spatially, i.e. among colonies but not among years. For this comparison, the reference model was thus the one allowing for colony-specific reproduction.

Correlates of survival, reproduction and movement

Our goals were twofold. We first wanted to quantify the spatio-temporal (i.e. among year, colony, and their interaction) variation in demographic rates, and then search for covariates that potentially explained this variation. For

these covariates, we were interested in the effects of population density, weather, and researcher-induced disturbance on survival, reproduction, and movement. Each of these effects could be specified using a range of actual measured covariates. With three types of demographic parameters, the candidate model set could potentially be large and lead to spurious results (Burnham and Anderson 2002). We therefore carefully prepared a small set of candidate models that appeared plausible given our knowledge of the system and the factors that were previously found to affect survival, movement and reproduction in this species (Covas et al. 2002, 2008; Brown et al. 2003). As a general strategy to limit the number of models to be fitted, we chose one model capturing each of the effects (population density, weather, and disturbance) as a combination of several covariates, i.e. by always entering several conceptually related covariates together. We did not consider interactions between covariates since we had no clear hypotheses for any of them to be important. To further keep the number of candidate model set small in the capture-mark-recapture analysis, we made an a priori decision to first examine variation in survival and then, using the best structure for the survival parameters, examine factors potentially affecting movement. The full set of candidate models is shown in Tables 1 and 2.

Survival

The population density effect consisted of mean colony size over the study period, linear and quadratic effects of relative colony size, and an Allee effect. Class of mean colony size (<30, 30–60 individuals, >60) has been found to correlate with survival in this population (Brown et al. 2003), and here we revisit this result by examining the effect of mean colony size as a continuous linear covariate. For relative colony size, we used the difference between the size of a colony in a given year and its mean size as a linear covariate. The rationale for including relative colony size was that if colony size is governed by local conditions in the long run, density effects should be evident in relation to average colony size, rather than as absolute numbers. Finally, we included an Allee effect as a factor with two levels distinguishing between colony sizes of <15 and ≥15 individuals in a particular year. The threshold value of 15 was chosen based on observations in the field, as some colonies rapidly went extinct after declining to this level. The overall colony effect therefore consisted of three parameters capturing these three covariates.

We expected survival of sociable weavers to be affected by weather, characterised by the following covariates: total rainfall, and minimum and maximum temperature during the time interval. Rainfall is a dominating environmental variable in arid and semi-arid environments

Table 2 Effects of covariates on reproduction in sociable weavers near Kimberley, South Africa in 1999, 2000, 2002 and 2005

	Model	Δ AIC$_c$	w_i	K	Deviance	% Dev. expl.	F	df cov.	df error	P
1	Colony × year			46	143.35					
2	Colony	138.80	0	17	465.05	34.12	0.57	17	28	0.88
3	Year	0	1	4	352.25	57.22	6.84	4	41	<0.01
4	Intercept only	273.38	0	1	631.63					
5	Rainfall	126.29	0	2	482.54	53.36	2.29	1	2	0.27
6	Minimum temperature	195.71	0	2	551.96	28.52	0.80	1	2	0.47
7	Maximum temperature	219.60	0	2	575.85	19.97	0.50	1	2	0.55
8	Mean colony size	275.17	0	2	631.42	0.13	0.02	1	15	0.89
9	Allee effect	271.79	0	2	628.05	0.73	0.33	1	44	0.57
10	Relative colony size^2	221.96	0	3	576.21	11.35	2.59	2	43	0.09
11	Number of full captures	272.02	0	2	628.27	0.69	0.31	1	44	0.58
12	Captures at nest	266.77	0	2	623.02	1.76	0.79	1	44	0.38

The models are generalized linear models with log link function and Poisson errors. We fitted models with one covariate at the time and then used an analysis of deviance (ANODEV) to calculate the amount of deviance explained (*Dev. expl.*) by each covariate. Since we only had one measure of reproduction per colony and year, model 1 fitted the data perfectly. Model 4, on the other hand, had no explanatory power. All other models fell between these two. Weather covariates (models 5–7) varied among years but not colony (since all colonies experienced the same weather), and the baseline model for the ANODEV was therefore the model with full year dependence (model 3). Similarly, mean colony size (model 8) varied among colonies but not years, and the relevant baseline model is model 2. Models 9–12 include covariates that vary across colonies and years and use model 1 as baseline model. For other abbreviations, see Table 1

(Noy-Meir 1973) governing vegetation growth and ultimately resources for the weavers. As our time intervals were unequal, we divided the total rainfall by the length of the time interval so that they corresponded to annual values. Weavers are likely to be sensitive to very high or low temperatures (minimum winter temperatures are often below 0 °C). They tend to seek refuge in the nest structure at such times. We used weather data collected by the South African Weather Service at Kimberley airport, 12 km from the centre of the study site.

The disturbance effect consisted of four parameters capturing the following effects. The first was the number of full capture events conducted at each colony in a given year. Second, we included the number of birds caught using hand nets at the nest as a further measure of disturbance. Third, we included whether or not the colony had been monitored for breeding success. Finally, in some colonies in 2000 we used a type of metal colour ring that turned out to harm the birds because this softer metal was deformed by the contact with the hard stainless steel identity ring. This effect would perhaps best be included as an individual-level effect, but all captured birds (some of which were ringed earlier with regular rings) in the affected colonies received these rings, and they were later removed as individuals were recaptured. Including this effect at the level of an individual would entail defining more states, which was not practical in the present analysis. We therefore included this covariate as a one-off effect on survival between 2000 and 2001 in the affected colonies, thus just using one parameter.

In five colonies, the supporting part of the tree collapsed during our study period, destroying part or all of the nest structure. In a preliminary analysis we examined whether this negatively affected survival in the affected colony during the year following collapse, but found no effect.

Movement

In addition to distance among colonies, which was included in all models, we examined the effects of colony size, Allee effects, disturbance at the colony of origin, weather, and colony collapse following similar procedures as with the covariates for survival.

The model describing population density effects included linear and squared effects of relative colony size both at the origin and destination in a particular year. We hypothesized that individuals were more likely to emigrate from and less likely to immigrate to colonies that are far above or far below their average sizes. In addition, this model also included the absolute difference between the sizes of the colony at the origin and destination in a particular year. We included this effect to see whether weavers preferably moved from smaller to larger colonies or the other way round.

Even though the model described in the previous paragraph includes an Allee effect by potentially allowing for higher emigration out of colonies in years when they are far below their average size, we considered a separate model where we allowed movement rates to differ between emigration from and immigration to colonies that were below 15 individuals in a particular year. We included this

model in our candidate set to see whether movement could account for the observed collapse of small colonies.

The model describing a disturbance effect on movement included the number of total captures made at a colony in a particular year, the number of captures made at the nest (which is related to the time researchers spent at the colony), and whether or not a colony was being monitored for reproduction.

We considered a model where movement depended on rainfall, and minimum and maximum temperatures. We hypothesized that harsh environmental conditions could affect metapopulation dynamics by changing movement probabilities.

Reproduction

We used the number of fledglings produced in a colony in a particular year as a measure of reproduction, and analysed its relationship to covariates using generalized linear models with log link function and Poisson errors. For the population model (below) we needed the number of fledglings produced per female, rather than per colony. We therefore added the logarithm of the number of females as an offset (covariate with coefficient fixed to 1) to all models, assuming that half of the adults at a colony were females (Doutrelant et al. 2004). Just as for the effects of covariates on survival, we used ANODEV to calculate the amount of variation in reproduction explained by particular covariates. Since the reproduction data were more limited than the capture-mark-recapture data, we considered simpler candidate models with only one covariate at a time (Table 2). In particular, we only had reproduction data for 4 years and therefore limited power to examine potential drivers of temporal variation in reproduction. However, it turned out that the 4 years differed substantially in their weather (range of observed values: rainfall 131–579 mm, mean minimum temperature 6.9–8.8 °C, and mean maximum temperature 31.9–33.7 °C) and variation in weather, particularly rainfall, has been previously shown to exert a strong effect on reproductive performance and success in this population (Covas et al. 2008).

Metapopulation dynamics

Next, we examined how well the estimated demographic rates reproduced the observed colony trends using a matrix-projection metapopulation model (Caswell 2001; Runge et al. 2006). This model is an extension of a single-population matrix projection model and explicitly accounts for local population (or colony in our case) dynamics and movement among them.

Let $\boldsymbol{n}_{t-1}$ be a vector of length p describing the sizes of all p colonies in year $t-1$. In our case $p = 17$. The model then predicts $\boldsymbol{n}_t$ using the projection matrix A:

$$\boldsymbol{n}_t = A\boldsymbol{n}_{t-1} \tag{1}$$

where

$$A = \begin{bmatrix} R^{11} & \cdots & R^{p1} \\ \vdots & \ddots & \vdots \\ R^{1p} & \cdots & R^{pp} \end{bmatrix} \tag{2}$$

and

$$R^{rs} = \emptyset_A^{rs} + \beta^r \emptyset_J^{rs}. \tag{3}$$

R^{rs} is the contribution of colony r to colony s. If $r = s$, R is the rate of self-recruitment and self-retention. $\emptyset_A^{rs}$ is the probability of an adult bird in colony r surviving and moving to colony s (or staying in the same colony if $r = s$). Analogously, $\emptyset_J^{rs}$ is the probability of a juvenile bird in colony r surviving and moving to colony s. The number of female fledglings produced per female in colony r is β^r. We assume a pre-breeding survey in the model so we can compare the projections to the actual counts that were made at the start of each breeding season. We further assume that females mature at 1 year of age.

Runge et al. (2006) show how this model can be used to project long-term dynamics and to determine whether local populations are sources or sinks. Here, we use the model for a slightly different purpose, namely (1) to project colony development forward from the first census to examine the impact at the metapopulation level of factors affecting demographic rates for the duration of our study, and (2) to examine which demographic rates are the most important ones for overall population dynamics over this time period. We carried out a transient sensitivity analysis by increasing each demographic rate in turn by 0.001 and calculating the resulting change in the total final population size. We also carried out a proportional perturbation (elasticity) analysis similar to the sensitivity analysis except that we increased each demographic rate by 1 %. To examine how the population may react to changes in covariates, we use the estimated relationships between disturbance and survival, and between weather and survival/reproduction, and calculated the expected changes in colony size for specific values. The estimates for parameters in the model come directly from our analysis described above, except for juvenile survival and movement, which we did not examine here. Instead, we assume that juveniles are similar to adults as was found in Covas et al. (2004).

Results

Survival and movement

We first examined variation in survival using models that constrained movement to be a function of distance only (models 1–8; Table 1). Among these models, the AIC$_c$-selected best model was the most general model (model 1),

which allowed for interactive effects of year and colony on survival. However, model 2, including only a year effect on survival, was nearly as well supported as model 1. Because model 2 is much simpler, we used that one to examine variation in movement (below). Models assuming additive effects of year and colony (model 3), or colony effects alone (model 8) were poorly supported by the data. Of the spatiotemporal variation in survival, just 2.7 % was due to the colony main effect (ANODEV $F_{16,147} = 0.25$, $P = 0.9$, comparing models 1, 6, and 8), 27.1 % due to the year main effect (ANODEV $F_{10,153} = 5.7$, $P = <0.001$, comparing models 1, 2, and 6), and the remainder (70.2 %) due to the interaction between colony and year. Differences among colonies in survival were therefore not consistent from year to year.

The covariate models (models 4, 5, and 7) were less well supported than the fully time-dependent model 2. However, given the degree of temporal variation, this is expected. Weather explained 30.1 % of the year-to-year variation in survival (ANODEV $F_{3,7} = 1.01$, $P = 0.4$, based on models 2, 4, and 6). Survival increased with rainfall [Fig S1, Electronic Supplementary Material; partial coefficient on the logit scale: 0.0015 (95 % confidence interval 0.0004–0.0026)/mm], and minimum temperature [0.19 (0.12 to 0. 26)/ °C], but tended to decrease with maximum temperature [−0.07 (−0.16 to 0.03)/ °C].

Disturbance explained 7.1 % of the spatio-temporal variation in survival ($F_{4,159} = 2.6$, $P = 0.04$, based on models 1, 5, and 6). More frequent captures led to lower survival [Fig S2, Electronic Supplementary Material; number of capture sessions, −0.13 (−0.20 to −0.06); captures at the nest, −0.02 (−0.03 to −0.01)]. The effects of monitoring of breeding activity, and the use of metal colour rings had confidence intervals that widely overlapped zero [−0.03 (−0.20 to 0.14), and −0.15 (−0.61 to 0.31), respectively], and hence did not appear to have a significant effect on survival. Density explained <1 % of the spatio-temporal variation in survival ($F_{4,159} = 0.2$, $P = 0.9$, based on models 1, 6, and 7).

Sociable weavers were more likely to move among colonies that were closer together (Fig. 2a). Including additional covariates on movement improved the models (models 9 to 12; Table 1), except for the weather covariates (model 13). The AIC$_c$ best model by far was the one including the effects of colony size on movement (model 9), and implied that weavers were more likely to move from small to large
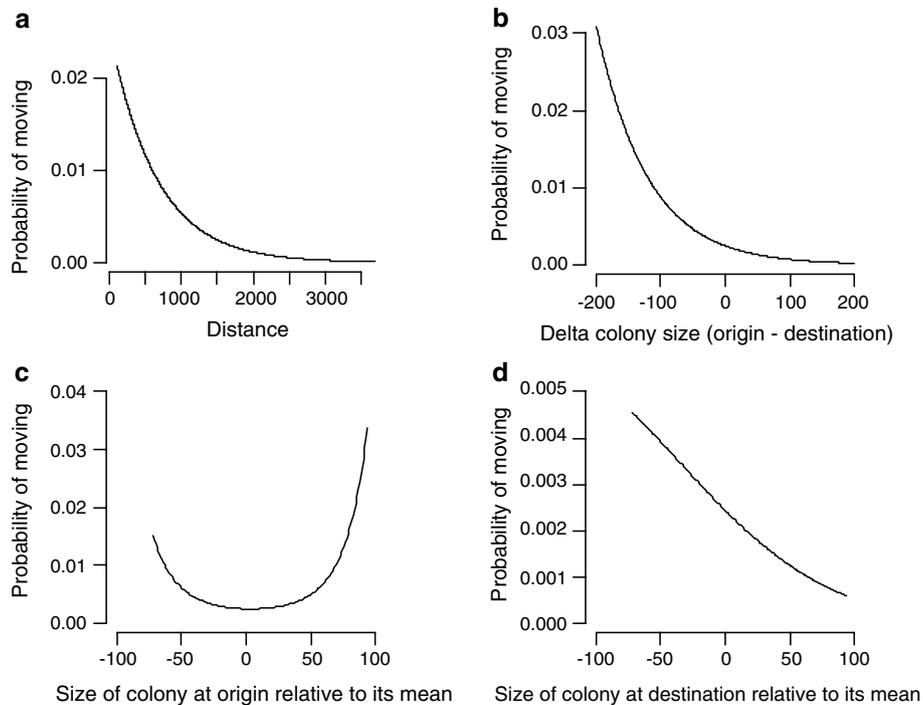

Fig. 2 Estimated effects of distance (m) and measures of colony size on movement of adult sociable weavers among 17 colonies on Benfontein Farm, South Africa. The estimated relationships are from the best-supported capture-mark-recapture model, model 9 (Table 1). They are **a** logit(movement) = −0.0016 (95 % confidence interval: −0.0019 to −0.0013) × distance, **b** logit(movement) = −0.013 (−0.018 to −0.0073) × difference in size between colony of ori-gin and colony of destination, **c** logit(movement) = −0.0021 (−0.0093 to 0.0050) × relative colony size at origin + 0.0003 (0.0002–0.0004) × (relative colony size at origin)², and **d** logit(movement) = −0.0115 (−0.0215 to −0.0014) × relative colony size at destination − 0.00004 (−0.0002 to 0.0001) × (relative colony size at destination)²

colonies than the other way round (Fig. 2b). Furthermore, they were more likely to emigrate from relatively large and relatively small colonies as opposed to those close to their long-term mean (Fig. 2c), whereas they were more likely to immigrate into colonies that were below their long-term mean (Fig. 2d).

Based on the AIC_c best-supported model, model 9 (Table 1), survival varied over the years and ranged from 0.48 (0.41–0.55) to 0.83 (0.77–0.87) with a median of 0.62. The movement probabilities ranged from 0.00002 (0.000006–0.00005) to 0.1104 (0.0543–0.2071) with a median of 0.0028, and recapture probabilities increased with field effort, ranging from 0 (in years without capture effort) to 0.998 (0.995–0.999), with a median of 0.65.

Reproduction

The mean annual number of fledglings produced per female across all years and colonies was 0.7 (minimum = 0, maximum = 2.4). However, reproduction varied strongly among years and colonies (Table 2), even though we only had 4 years of data. The majority of the total variation was among years (57.2 %), whereas less was due to variation among colonies (34.1 %), and little was due to the interaction between colonies and year (8.7 %). This suggests that year-to-year fluctuations had a similar effect on all colonies. Variation in rainfall was the most important of the weather variables we examined. It was positively related to reproductive success (Fig S3, Electronic Supplementary Material; coefficient on the log scale: 0.0030 (0.0025–0.0034), $P < 0.001$), and explained more than half of the year-to-year variation in reproduction, 53.4 %, even though this is not significant with only 4 years of data ($P > 0.2$).

Colony size, relative to its mean, explained 11 % of the total variation in reproductive success, with colonies below their long-term mean having relatively high success [linear coefficient −0.0086 (−0.0128 to −0.0046), $P < 0.001$; quadratic coefficient 0.00017 (0.00006–0.00028), $P = 0.001$]. Disturbance (models 11–12), Allee effect (model 9), and mean colony size (model 8) explained less than 2 % of the relevant variation. For the next section, we assume that half of the fledglings were females, which is a reasonable assumption given that the sex ratio in the population is approximately balanced (Doutrelant et al. 2004).

Metapopulation dynamics

We first parameterized the metapopulation model (Eqs. 1, 2, 3) using parameters that varied among colonies only, i.e. they were constant over time [CMR model 8 (Table 1); and model 2 (Table 2)]. Movement was a function of distance only. We chose this model rather than the AIC_c best model

because we wanted to examine how well colony differences in fitness explain broad differences in colony-size trends over time. We will examine how time-variable demographic rates (induced by covariates) improve the fit of the model in a next step, below. The time-invariant parameterization reproduced observed colony dynamics well for most colonies (Fig. 3). The most dramatic exception was colony 8, for which the model predicted a fast increase (grey line in Fig. 3, panel 8). However, this colony did in fact increase at about the predicted rate for the years in which we observed reproduction there (1999 and 2000). Setting reproduction to the average value across colonies resulted in a better match of the longer-term dynamics of this colony (solid black line in Fig. 3, panel 8). Across all colonies, this revised parameterization predicted a mean colony decline of −10.9 %/year. This is close to the observed decline in mean colony size of −9.4 %/year.

In this model with demographic parameters held constant over time, the final population size was generally most sensitive to changes in survival rates, less sensitive to changes in movement, and least sensitive to changes in reproduction (Figs S4 and S5, Electronic Supplementary Material). The sensitivity varied among colonies with similar patterns for survival and reproduction. The sensitivity of the final population size to changes in movement ranged from negative to positive depending on whether birds moved from more quickly declining colonies to less quickly declining ones, or the other way round. The results of the elasticity analysis revealed the same general patterns as the sensitivity analysis except that the final population size was least elastic to changes in movement.

Next, we examined whether a more realistic representation of movement could capture the observed dynamics better. For this, we used movement probabilities obtained from the best-supported CMR model (model 9; Table 1), which allowed movement to vary with local colony size in addition to distance between colonies. This parameterization captured some of the temporal changes in local colony decline (dashed lines in Fig. 3).

Keeping the more realistic movement rates, we then parameterized the model using the estimates obtained from the CMR model where survival was constrained to be a function of disturbance (model 5; Table 1; see dotted lines in Fig. 3). Across all colonies, this parameterization produced a mean colony decline of -9.3 %/year. Using the estimated relationship between disturbance and survival (from CMR model 5; Table 1) we then calculated that the expected adult survival rate would have been 0.71 (CI 0.68, 0.74), had there been no disturbance. Parameterising the metapopulation model using this survival rate led to a mean yearly colony decline of −2.3 % (CI −6.8, 1.7). This shows that the estimated effects of disturbance would have had the potential to contribute considerably to the observed
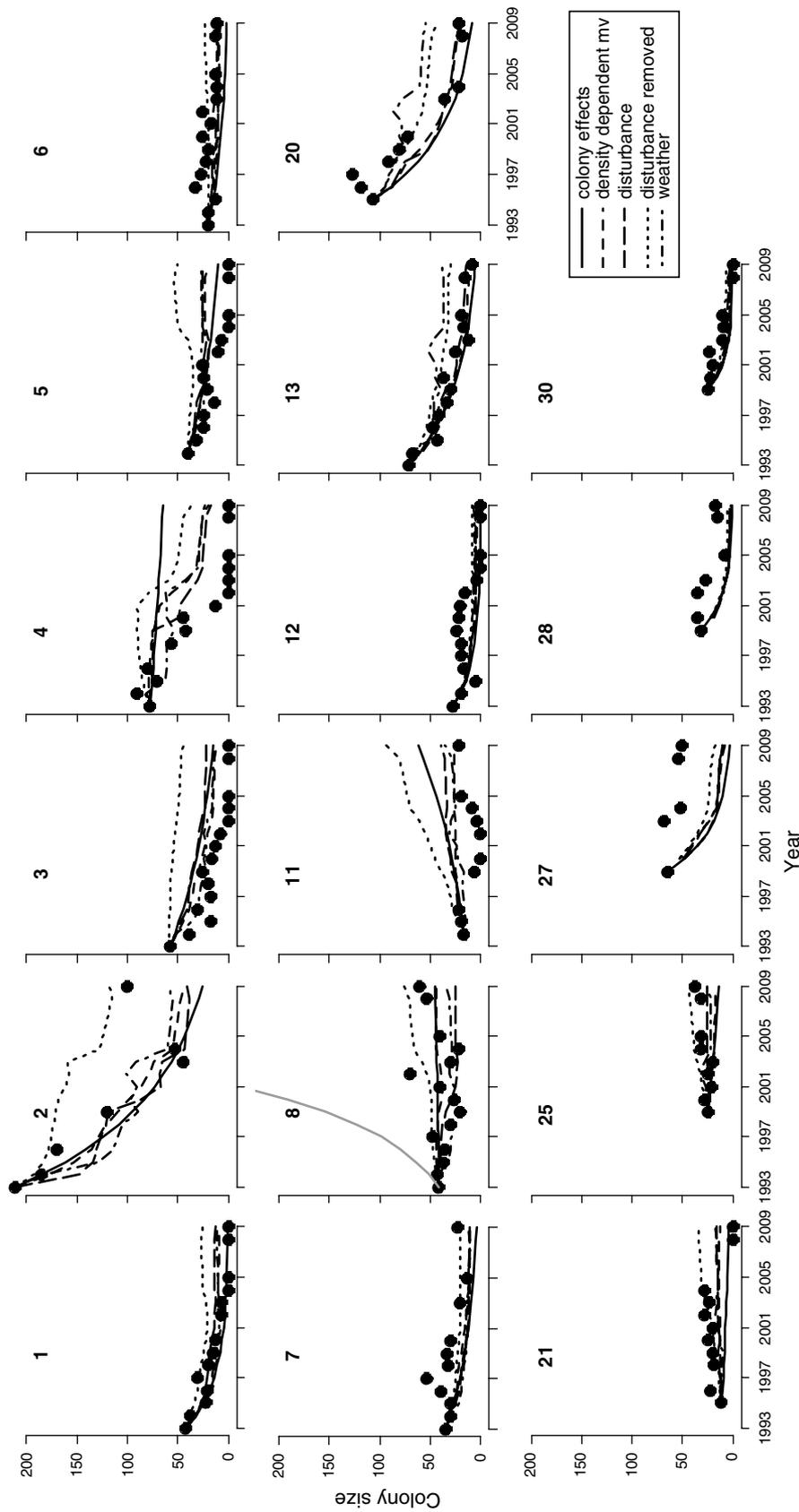
Fig. 3 Population dynamics of 17 sociable weaver colonies on Benfontein Farm, South Africa. *Filled circles* show actual colony counts. The *lines* show colony dynamics projected from the first counts, using the metapopulation model in Eqs. 1, 2, 3. The *solid lines* represent a version of the model that was parameterised with time-invariant demographic rates that differed among colonies, with distance-dependent movement. The *dashed lines* in addition allow for density effects on movement as shown in Fig. 2. The *long-dash* and *dash-dotted lines* represent the parameterisations where demographic rates were estimated as a function of disturbance, and weather, respectively. The *dotted lines* are the model predictions for the hypothetical scenario that no field work had been conducted in this population. The *panel numbers* refer to the numbered colony locations in Fig. 1

decline of this metapopulation, but they are unlikely to completely account for it.

In addition to the effects of disturbance, we were also interested in the effects that weather could have had on the dynamics of this metapopulation. We parameterized the metapopulation model using the estimates from the models where demographic rates were dependent on weather [CMR model 4 (Table 1); model 5 (Table 2); see dash-dotted lines in Fig. 3]. With this parameterization, the metapopulation model produced a mean colony decline of −7.7 %. Using the estimated relationships between demographic rates and weather, we explored how changes in weather potentially could influence this population using a scenario in which weather was more favourable for the weavers (lower maximum temperature, higher minimum temperature, and more rainfall). We calculated expected survival and reproduction under weather that was improved by 0.5 SDs compared to the observed values, i.e. an additional 50 mm of rain, the minimum temperature being 0.62 °C higher and the maximum temperature being 0.53 °C lower. This led to survival ranging from 0.60 to 0.77 over the years, and the number of fledglings produced per female to range from 0 to 2.7. With this parameterization, we predict that the colonies will increase on average by 5.5 %/year. Relatively small changes in weather can thus potentially affect colony dynamics considerably, even though it needs to be kept in mind that we estimated the effect of weather on reproduction from just 4 years of data.

Discussion

We studied the demographic mechanisms of colony decline in a metapopulation of sociable weavers in South Africa. In general, the balance of additions and losses of individuals determines population dynamics: $\Delta N = B + I - D - E$, i.e. a change in population size ΔN is made up of births (B) plus immigrants (I) minus deaths (D) minus emigrants (E). We examined all of these components, expressed as per capita rates, in a set of 17 colonies making up local populations in a metapopulation of sociable weavers ranging widely in size and rate of change, with most of them declining (see Fig. 3). We found that survival varied between years and was affected by weather, increasing with rainfall and minimum temperature, but tended to decrease with increased maximum temperature. Researcher-induced disturbance also had a negative influence on survival, with more frequent capture sessions leading to lower survival. Movement was affected by colony size and distance. Sociable weavers tended to move from small to large colonies, but there was also an effect of colony size trend, with weavers tending to move away from colonies that were larger or smaller than their long-term mean. Movement was also

more frequent among nearby colonies. Reproduction varied substantially between years and was mostly affected by rainfall and, to a lesser extent, colony size, with higher success in colonies below their long-term mean, concurring with findings from a previous study on this population (Covas et al. 2008). We used a metapopulation model to judge the effects of covariates on overall dynamics of this metapopulation and found small changes in weather and, to a lesser extent, that disturbance can affect colony dynamics considerably.

We started by examining the spatio-temporal variation in survival and reproduction. If a large proportion of this variation was attributable to the temporal component alone, this would suggest important external drivers affecting the population as a whole. A predominant spatial component would indicate that mostly local factors are governing the dynamics of this population. A large interaction component would indicate that large-scale external drivers are modified by local conditions. Of course, longer-term dynamics of this population may also be subject to external forcing that does not vary much over the time scale (17 years) we considered here.

We found that the spatial (colony) and temporal (year) effects and their interaction made different relative contributions to variation in survival and reproduction. The interaction term explained most of the variation in survival, suggesting that large-scale external effects on survival are modified by local conditions. The colony main effect explained little of the spatio-temporal variation in survival. On the other hand, the year effect was the largest component of variation over the 4 years in which we studied reproduction. The smallest component of variation in reproduction came from the interaction between colony and year, showing that temporal variation in reproduction was fairly synchronized among colonies over the 4 years for which we had such data. We next looked at covariates that may partially explain these patterns of spatio-temporal variation in demographic rates.

We found a negative effect of field-work intensity on survival, even though it only explained a small proportion of the spatiotemporal variation (7 %). Nevertheless, the matrix model suggested that the decrease in survival induced by field-work-related disturbance could have considerably contributed to the observed population decline. We can see at least three possible explanations for these results:

(a) Field work did actually harm the birds, in contrast to the finding that mist netting is generally safe for passerine birds (Spotswood et al. 2011).
(b) Since this is an observational study, we may have happened to study colonies intensely that were declining for other reasons.

(c) Numerous captures caused individuals to move away from the studied colonies. In response to the results presented here, we have decreased the handling time by working in larger teams and are now only capturing each colony once per year.

Colony size and relative density varied across space and time and these covariates could thus potentially explain variation among colonies, years, and the interaction effect. However, these variables appeared to be almost completely unrelated to survival, and only relative density explained a relatively low and non-significant proportion of the spatio-temporal variation in reproduction (11 %).

Our study was not long enough to find conclusive evidence about the effect of temporal covariates. However, we found indications that rainfall was positively related to both survival and reproduction and, in conjunction with temperature in the case of survival, explained a considerable proportion of the temporal variation in both demographic rates during our study period (about 30 % of the variation in survival and 50 % of the variation in reproduction). Earlier studies on sociable weavers found a positive effect of rainfall on breeding (Covas et al. 2008), but not survival (Covas et al. 2004). Breeding and survival of birds in semi-arid regions are often related to rainfall (Maclean 1970; Lloyd 1999; Altwegg and Anderson 2009), which is an important driver of dynamics in semi-arid and arid regions. It triggers a spike in plant growth, then insect abundance, and then seed availability (Noy-Meir 1973).

Movement among colonies was strongly related to colony size as birds were more likely to move from small to large colonies. Higher per capita movement rates from small to large sub-populations is a prediction of the balanced dispersal hypothesis (McPeek and Holt 1992) and has been found in other bird meta-populations (Doncaster et al. 1997; Serrano et al. 2005). In the case of the sociable weaver colonies we studied, however, colonies not only differ in mean size but also in predation and parasite load, which are related to colony size (Spottiswoode 2007). Brown et al. (2003), when considering broad size classes only, found that individuals in a subset of our metapopulation preferentially moved among similar-sized colonies. We found that sociable weavers in our study area were more likely to emigrate from colonies that were either far below or above their long-term mean size, and thus there was evidence for both positive and negative density dependence in emigration. This can be explained by conspecific attraction and competition processes acting simultaneously. For example, smaller colonies may be less attractive than larger ones, but individuals might also leave in response to overcrowding (Kim et al. 2009) and the increased nestling parasite load and predation associated with large colony size (Spottiswoode 2007). Among birds, positive density dependence in emigration, i.e. higher emigration rates as density increases, is found more often than negative density dependence, i.e. lower emigration rates as density increases (Matthysen 2005). Positively density-dependent emigration increases the stability of metapopulations because this type of movement leads to higher colonisation rates (Sæther et al. 1999). Increased emigration at low colony sizes is a type of Allee effect (Courchamp et al. 2008) and can lead to sudden extinction of colonies that drop below a certain size. However, the fact that we found no evidence of an Allee effect on survival or reproduction suggests that birds mostly moved to other colonies when colonies became very small. This type of Allee effect would have less of an impact on the dynamics of the metapopulation than it may appear from studying individual colonies (Fowler 2009), even though it may lead to an extinction threshold at low habitat occupancy (Amarasekare 1998). In theory, negative density-dependent movement leads to lower proportions of occupied patches and less stable metapopulation dynamics (Sæther et al. 1999). In our study population, this effect would be compounded by the tendency of birds to be attracted to larger colonies, and away from smaller ones. On the other hand, sociable weavers in our study population were more likely to immigrate into colonies that were below their long-term average colony size. The occurrence of both behaviours in this population may thus lead to a rescue effect in declining colonies and more stable dynamics of the metapopulation.

Using a multi-site matrix projection model, we found that the estimated demographic rates (survival, dispersal, and reproduction) reproduced the observed dynamics of this metapopulation well. Given the good overall agreement between model and observations, we further used it to gauge the effects of different scenarios on the dynamics of the metapopulation. We found that the estimated effects of field-work disturbance on survival had the potential to considerably decrease overall population growth. However, even in the absence of field work, the best estimate for overall population growth remained negative. This agrees with the qualitative observation that colonies not subject to intense study in our area also declined during the study period and suggests that other drivers contributed to population decline. Of six colonies for which we had occasional counts, four went extinct and only one increased over the course of our study. The marked effects of rainfall and temperature detected here suggest that weather could be such a driver. The metapopulation model showed that even modest changes in climate would have a large effect on population growth, given the estimated relationships between weather and demographic rates. With the predicted increased climate variability for this region (DEA 2011), extreme temperatures with negative effects on sociable weavers may become more common in the future.

To conclude, by integrating the three central demographic parameters (survival, movement and reproduction) and investigating a set of environmental and intrinsic factors likely to affect them, we were able to obtain an understanding of (1) what the main drivers of these parameters are, and (2) how they contribute to influence population dynamics. This shed light on the mechanisms of decline in this metapopulation and provided important information on the mechanisms regulating a wild bird population in a relatively poorly studied ecosystem. Some of the mechanisms unveiled here are likely to be particularly important in these arid regions (e.g. rainfall), while others might be ubiquitous (e.g. relative density). We encourage other researchers to follow a similar integrative approach to broaden our understanding of the specificity and generality of factors affecting population dynamics.

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