

Impact of density and environmental factors on population fluctuations in a migratory passerine

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Summary

1. Populations of plants and animals typically fluctuate because of the combined effects of density-dependent and density-independent processes. The study of these processes is complicated by the fact that population sizes are typically not known exactly, because population counts are subject to sampling variance. Although the existence of sampling variance is broadly acknowledged, relatively few studies on time-series data have accounted for it, which can result in wrong inferences about population processes.

2. To increase our understanding of population dynamics, we analysed time series from six Central European populations of the migratory red-backed shrike *Lanius collurio* by simultaneously assessing the strength of density dependence, process and sampling variance. In addition, we evaluated hypotheses predicting effects of factors presumed to operate on the breeding grounds, at stop-over sites in eastern Africa during fall and spring migration and in the wintering grounds in southern Africa. We used both simple and state-space formulations of the Gompertz equation to model population size.

3. Across populations and modelling approaches, we found consistent evidence for negative density-dependent population regulation. Further, process variance contributed substantially to variation in population size, while sampling variance did not. Environmental conditions in eastern and southern Africa appear to influence breeding population size, as rainfall in the Sahel during fall migration and in the south African wintering areas were positively related to population size in the following spring in four of six populations. In contrast, environmental conditions in the breeding grounds were not related to population size.

4. Our findings suggest negative density-dependent regulation of red-backed shrike breeding populations and are consistent with the long-standing hypothesis that conditions in the African staging and wintering areas influence population numbers of species breeding in Europe.

5. This study highlights the importance of jointly investigating density-dependent and density-independent processes to improve our understanding of factors influencing population fluctuations in space and time.

Key-words: birds, density dependence, population regulation, state-space model, stochastic non-linear population model

Introduction

Explaining variation in population size over time remains a great challenge in ecology (May 1999). Populations typically fluctuate through the combined effects of density-dependent

and density-independent processes, although the relative role of these processes is debated (White 2008). Density-dependent processes refer to the influence of population density on vital rates and the subsequent effects of changes in vital rates on population growth rate. Density-independent processes include environmental and demographic stochasticity, which arise from environmental influences such as weather or food

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availability and from random deviations of vital rates, respectively (Lande, Engen & Saether 2003). Both types of stochasticity are usually subsumed as 'process noise' or 'process variance' (e.g. Dennis *et al.* 2006). The separation of density-dependent and density-independent processes in empirical data is usually complicated by the fact that counts of wild animals, and even of plants (Kéry & Gregg 2003), hardly ever reflect the true population size (Freckleton *et al.* 2006). This measurement or observation error is referred to as sampling variance (Dennis *et al.* 2006). Often it is unknown how strongly fluctuations of observed population size are affected by sampling variance. Even worse, sampling variance may confound the quantification of density-dependent and density-independent processes from time-series data (Shenk, White & Burnham 1998; Freckleton *et al.* 2006; Lebreton 2009). Thus, insights into the dynamics of populations require that density dependence, process variance and sampling variance be jointly modelled (Williams, Ives & Applegate 2003).

The challenge of explaining variation in population size is amplified in migratory species where individuals spend parts of the year in different areas. In such species, process variance and density dependence may include factors acting on the breeding grounds as well as during migration and in wintering areas. While the importance of factors on the breeding grounds to changes in population size has long been recognized (Newton 2004), there is growing evidence that conditions experienced during migration and in winter play an important role in population processes year-round (Norris & Marra 2007 and references cited therein).

Here, we present analyses of long-term population counts of the red-backed shrike *Lanius collurio* Linnaeus, 1758 from six regions in Central Europe, the centre of the species' geographic breeding range, to increase our understanding of the processes potentially influencing population dynamics in a migratory species. First, we assessed the strength of density dependence and estimated process and sampling variance by means of state-space models, which have been successfully applied in previous analyses of similar time-series data (e.g. Williams, Ives & Applegate 2003; Dennis *et al.* 2006; Knappe 2008). A state-space model consists of two stochastic models, one for an unobserved variable (e.g. true population size) and one for an observed variable (e.g. observed population size or count); the latter is usually formulated as a function of the unobserved variable and the sampling variance (Dennis *et al.* 2006). The occurrence of density-dependent population regulation has been demonstrated in many taxa (e.g. Sibly *et al.* 2005; Brook & Bradshaw 2006). In the red-backed shrike, a negative relationship between density and nest success has been found (Müller *et al.* 2005). We therefore expected to find evidence for negative density dependence in the six study populations.

Second, we tested hypotheses to evaluate environmental factors that may explain temporal variation in red-backed shrike population size, while accounting for density dependence and sampling variance. Numerous studies have shown how environmental stochasticity affects population size (e.g.

Dennis & Otten 2000). Weather conditions during or shortly after settlement can influence breeding population size of several bird species in the same year through increased post-arrival mortality (Newton 2007). We hence expected variation in population size of the red-backed shrike to be positively related to temperature and negatively related to rainfall during settlement in May (hereafter referred to as settlement hypothesis).

According to the tap hypothesis (Saether, Sutherland & Engen 2004), environmental conditions during the breeding season affect population size in the next breeding season. We assessed environmental conditions via weather variables because they are closely linked with the occurrence and availability of the shrike's main prey (large insects, Glutz von Blotzheim & Bauer 1993). Specifically, we predicted positive relations of temperature and negative relations of rainfall, respectively, in one breeding season and population size in the next.

The tub hypothesis, on the other hand, states that conditions during the non-breeding season affect survival and so population size in the following breeding season (Saether, Sutherland & Engen 2004). For migratory species, conditions during fall migration, in the winter quarters and/or during spring migration may be important (Newton 2004). Based on ringing recoveries, red-backed shrikes are known to migrate through eastern Africa and to winter in southern Africa. Because the species is largely insectivorous year-round (Glutz von Blotzheim & Bauer 1993), we examined the influence of factors known to be correlates of invertebrate food supply in dry environments, such as the amount of rainfall and the normalized difference vegetation index (NDVI), on population size in the following breeding season. We predicted that population size would be positively related to rainfall and/or to NDVI values either in eastern Africa during fall and spring migration, respectively, or in the southern African wintering sites.

Red-backed shrikes have suffered population declines in many European countries and belong to the Annex I of the Birds directive of the European Union listing threatened species in need of conservation measures. An additional aim of this study was therefore to improve knowledge about factors potentially influencing red-backed shrike populations to aid in recovery of the species.

Materials and methods

STUDY SPECIES AND POPULATIONS

The red-backed shrike is a trans-Saharan migratory species that returns to the breeding grounds from late April to early June (depending on altitude). Males fiercely defend all-purpose territories. The nesting period extends from late May to early August, during which one brood typically consisting of five or six eggs is produced (and a replacement clutch in case of nest loss); true second broods are rare (Glutz von Blotzheim & Bauer 1993).

For this paper, we made use of own census data and published data from long-term population studies in Central Europe. Study populations were located in Switzerland (3), Germany (2) and Poland (1).

All populations inhabited agricultural landscapes structured to varying extents by hedges, groups of bushes and trees, extensively used meadows, pastures, etc. The Swiss populations at Brunnen (46°19'N/07°39'E, 850–1090 m asl, 0.73 km²), Canton Valais (south-western Switzerland), and at Ramosch (46°50'N/10°23'E, 1090–1680 m asl, 2.21 km²), Canton Grisons (eastern Switzerland), had been annually censused by experienced bird researchers of the Swiss Ornithological Institute since 1988 until 2006 and 2007, respectively, on six occasions from May to early July. Data for the third Swiss population were obtained from Zollinger (2006) (and supplemented by surveys from 2006 and 2007), who studied the ecology of the species close to Cossonay (46°38'N/06°28'E, 420–980 m asl, 30 km²), Canton Vaud (western Switzerland), since 1993 until present. On average, six surveys were annually conducted from May to August and population size assessed by the number of territories present on June 15 (Zollinger 2006). The two German populations at Göppingen (48°39'N/09°47'E, 370–580 m asl, 18 km²) and Edertal (51°10'N/09°07'E, 190–440 m asl, 33 km²) had been studied since 1969 and 1984, respectively. For the Göppingen population, data up to 2003 were taken from Jakober & Stauber (2004) and supplemented by surveys from 2004 to 2007. Population size was again assessed by the number of territories on June 15 (Jakober & Stauber 1987). For the Edertal population, data were taken from Lübcke (2007). All potential habitats within the study area were visited up to three times per year from May 20 to July 31. Each registration of single males and/or females, territorial pairs and adults with juveniles was considered to represent one territory (Lübcke 2007). The Polish population near Leszno (51°51'N/16°35'E, 80 m asl, 10 km²) in south-western Poland has been intensively studied since 1971 (Kuzniak 1991; Tryjanowski & Sparks 2001; Tryjanowski *et al.* 2003). Number of territories was based on regular surveys supplemented by nest searching on at least one weekly visit to the study area.

ESTIMATING DENSITY DEPENDENCE, PROCESS VARIANCE AND SAMPLING VARIANCE

We used a discrete-time, stochastic model for analysing time series of population size of single populations as described by Dennis *et al.* (2006). The approach allows to jointly estimate density dependence, process variance ('environmental-type process noise') and sampling variance ('observation error'). Following Dennis *et al.* (2006), we used the Gompertz model

$$N_t = N_{t-1} \exp(a + b \ln N_{t-1} + E_t) \quad \text{eqn 1}$$

where N_t is true population size at time t (assumed unknown), a and b are constants, and E_t (the process noise) is normally distributed with mean 0 and variance σ^2 . Note that N_1 is true population size at time $t = 1$ (i.e. the first year of study), a measures population growth rate at size $N = 1$, and b estimates the strength of density dependence, with a value of 0 indicating density independence. This nonlinear Gompertz model has long been used in density-dependent modelling and described density dependence in many taxa well (Sibly *et al.* 2005; Brook & Bradshaw 2006; Dennis *et al.* 2006). Equation 1 can be expressed on the logarithmic scale as

$$X_t = X_{t-1} + a + bX_{t-1} + E_t = a + cX_{t-1} + E_t \quad \text{eqn 2}$$

where $X_t = \ln N_t$, $X_{t-1} = \ln N_{t-1}$, $c = b + 1$, and X_1 is a random normal variable (c.f. Dennis *et al.* 2006). This form of the Gompertz model is a linear, first-order autoregressive [AR(1)] time-series model (Dennis *et al.* 2006). Because population counts based on surveys hardly ever represent the true population size, the

assumption is made that the surveys yield an estimate Y_t of the true logarithmic population size X_t , such that

$$Y_t = X_t + F_t \quad \text{eqn 3}$$

where F_t is the sampling noise ('observation error') assumed to be normally distributed with mean 0 and variance τ^2 . Equations 2 and 3 together represent the Gompertz state-space (hereafter GSS) model. Combining Eqns 2 and 3 by substituting X_t in Eqn 2 by $Y_t - F_t$ from Eqn 3, and letting $X_{t-1} = Y_{t-1} - F_{t-1}$ (Dennis *et al.* 2006), results in

$$Y_t = a + cY_{t-1} + E_t + F_t - cF_{t-1}. \quad \text{eqn 4}$$

Estimates for the unknown parameters (a , c , σ^2 , τ^2) of the GSS model were obtained through maximum likelihood (ML) estimation using PROC MIXED IN SAS 9.1.3 based on the SAS code provided by Dennis *et al.* (2006) in their Appendix B.

Complications in the ML estimation in GSS models can arise because mixed effects likelihood functions tend to have multiple local maxima (Dennis *et al.* 2006), in which case the ML estimates found by PROC MIXED, and hence the parameter estimates, may not necessarily be the correct ones. To account for this possibility, we calculated likelihood functions for a grid of user-specified starting values of the parameters a , c , σ^2 and τ^2 , respectively (using the PARMs option in PROC MIXED). Evaluation of graphs plotting the log-likelihoods vs. the different values of a , c , σ^2 and τ^2 (see Dennis *et al.* 2006, p. 330) did not however indicate evidence for the existence of alternative local maxima in any of the six populations, hence we report original parameter estimates reported by PROC MIXED.

ENVIRONMENTAL FACTORS

Data on temperature and rainfall in the breeding grounds were obtained from weather stations located in proximity to the study populations (Table S1, Supporting information). We calculated mean temperature and mean rainfall for May alone (referred to as May temperature and May rain) and for June and July combined (June/July temperature and June/July rain) from daily mean temperature values and from daily amounts of rainfall, respectively. May rain and temperature were used to evaluate the settlement hypothesis, the combined June/July rain and temperature for evaluation of the tap hypothesis.

NDVI values for the fall staging areas in the Sahel zone (hereafter NDVI_Sahel), the wintering grounds in southern Africa (NDVI_southern Africa) and the spring staging areas in eastern Africa (NDVI_Ethiopia) were taken from <http://igskmncnw.b015.cr.usgs.gov/adds>. Spatial resolution was 8 km. NDVI is a ratio based on the reflectance of near-infrared (NIR) and red light (RED) measured from AVHRR sensors on NOAA satellites and is expressed as $(\text{NIR} - \text{RED})/(\text{NIR} + \text{RED})$. NDVI provides information about the 'greenness' and vegetation density and closely correlates with above-ground net primary productivity (Pettorelli *et al.* 2005). NDVI_Sahel data were calculated for each year from the mean NDVI of September and October from an area covering the southern parts of Sudan (south of Khartoum) as well as small areas of Uganda, Congo and Ethiopia bordering Sudan. Yearly NDVI_southern Africa data were calculated based on the mean NDVI from the months December to March from entire Botswana and Zimbabwe as well as from small parts of adjoining Mozambique, Zambia, Namibia and South Africa, respectively (matching the distribution of the red-backed shrike during this period according to Bruderer & Bruderer 2008). NDVI_Ethiopia data were annually

calculated from the mean NDVI from 21 March through April from Ethiopia.

Rainfall data were taken from <http://www.ncdc.noaa.gov/cgi-bin/res40.pl?page=gsod.html> and covered the same areas in fall (13 weather stations), winter (40) and spring (17) as the NDVI just mentioned. For each time period (e.g. fall 1999), daily precipitation was averaged across all weather stations within the respective area, and mean rainfall per period was then expressed as the average of these daily means over the period of interest. The spring period included rainfall in March and April, the fall and winter periods covered the same months as the NDVI.

NDVI and rainfall were not significantly correlated within periods [Spearman rank correlations, $n = 20$ in each case, NDVI_Sahel vs. rain_Sahel (fall): $r_s = 0.13$, $P = 0.591$, NDVI_southern Africa vs. rain_southern Africa (winter): $r_s = 0.01$, $P = 0.954$, NDVI_Ethiopia vs. rain_Ethiopia (spring): $r_s = 0.37$, $P = 0.104$].

EVALUATION OF HYPOTHESES

Based on Akaike's information criterion corrected for small sample sizes (AICc, Burnham & Anderson 2002), we first evaluated whether or not the populations showed evidence for density-dependent regulation. The density-independent GSS model is represented by $c = 1$ ($b = 0$) in Eqn 2 (Dennis *et al.* 2006), which can be achieved by fixing c at 1 in PROC MIXED with the PARMS option. Note that both the density-independent and density-dependent models are based on the same stochastic noise structure and take into account potential sampling variance. Depending on the outcome of this first evaluation, we used the density-dependent or density-independent GSS model as our null model to which we added environmental variables as covariates to represent the hypotheses to be examined. In this way, it was possible to investigate whether or not environmental variables explained variation in population size, while simultaneously accounting for density dependence effects and sampling variance. For each population, we constructed models by adding to the null model the respective variables of each hypothesis separately and in combination. For example, to model environmental effects possibly acting in the fall staging areas at time $t - 1$ on population size at time t in the density-dependent GSS model, we used

$$X_t = a + cX_{t-1} + dZ_{t-1} + E_t \quad \text{eqn 5}$$

where X_t , X_{t-1} , a , c and E_t as in Eqn 2, d = regression coefficient and Z_{t-1} = covariate at $t - 1$.

Our time series ranged in length from 15 to 20 years and were too short to evaluate models with interactions among the covariates of a given hypothesis or models containing covariates from different hypotheses. A complete list of the 21 models examined per population is available in Table S2 (Supporting information). We then evaluated the relative performance of each model in the candidate model set (including the null model) by means of AICc values. The model with the lowest AICc value was considered to be the best one, representing the best compromise between overfitting because of too many parameters and bias because of too few parameters (Burnham & Anderson 2002). Based on AICc values, we calculated Akaike weights, which indicate how well each model in the set of candidate models is supported by the data, and evidence ratios, which indicate the likelihood of one particular model being better supported by the data than another model (Burnham & Anderson 2002). Finally, to account for model selection uncertainty (Burnham & Anderson 2002), regression coefficients and associated standard errors (SE) were averaged based on Akaike weights of those models from the 21

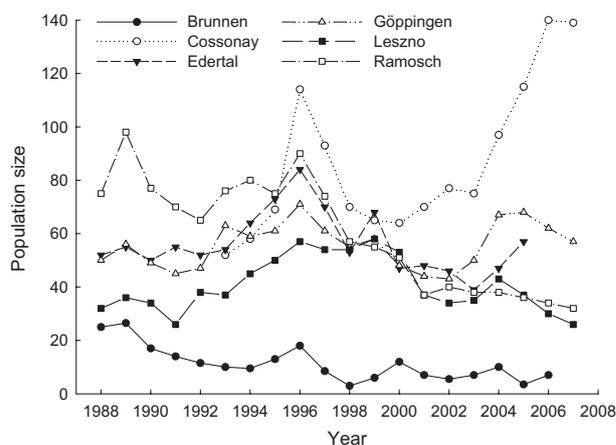


Fig. 1. Observed population sizes of the red-backed shrike in the study areas of Switzerland (Brunnen, Cossonay, Ramosch), Germany (Edertal, Göppingen) and Poland (Leszno). Data for the population Edertal taken from Lübecke (2007).

candidate models per population that contained the covariate of interest.

State-space models of the form presented previously are complex and data-hungry (Dennis *et al.* 2006). The time series available were comparatively short (Fig. 1), which may have rendered σ^2 and τ^2 not separately estimable (Knappe 2008). The use of a model too complex for the data may thus impair our ability to detect effects of the environmental covariates. Therefore, we additionally evaluated the hypotheses on the basis of the simple Gompertz model (Eqn 2, hereafter sG model), which does not account for sampling variance (see Dennis & Otten 2000 for a similar application of the Ricker model). Parameters (a , c , σ^2 and those of the environmental covariates) were obtained through ML estimation (PROC MIXED). Model selection was conducted as described for the GSS model, with the null model now being the sG model, to which environmental covariates were added.

Similarly, because of the relatively limited data at hand, we did not investigate joint density dependence across populations (Dennis, Kemp & Taper 1998), which would have required additional parameters to be estimated.

Approximate 95% confidence intervals for the parameters a , c , σ^2 and τ^2 of the GSS model and the parameters a , c and σ^2 of the sG model were computed from likelihood profiles (Lindén & Knappe 2009). These were obtained by calculating the log-likelihoods for a sequence of user-specified values of each parameter while fixing the values of the remaining parameters to their respective ML estimate. The 95% confidence interval then consists of the parameter values for which the log-likelihood \geq maximum log-likelihood $- 3.84/2 =$ maximum log-likelihood $- 1.92$ (Stryhn & Christensen 2003). Profile likelihood computations were performed in R (R Development Core Team 2008).

Results

DENSITY DEPENDENCE, SAMPLING VARIANCE AND PROCESS VARIANCE

The evidence for density-dependent population regulation was much better than for density-independent regulation (Fig. 2). In all six populations, AICc values were lowest for the density-dependent model. Evidence ratios (density-

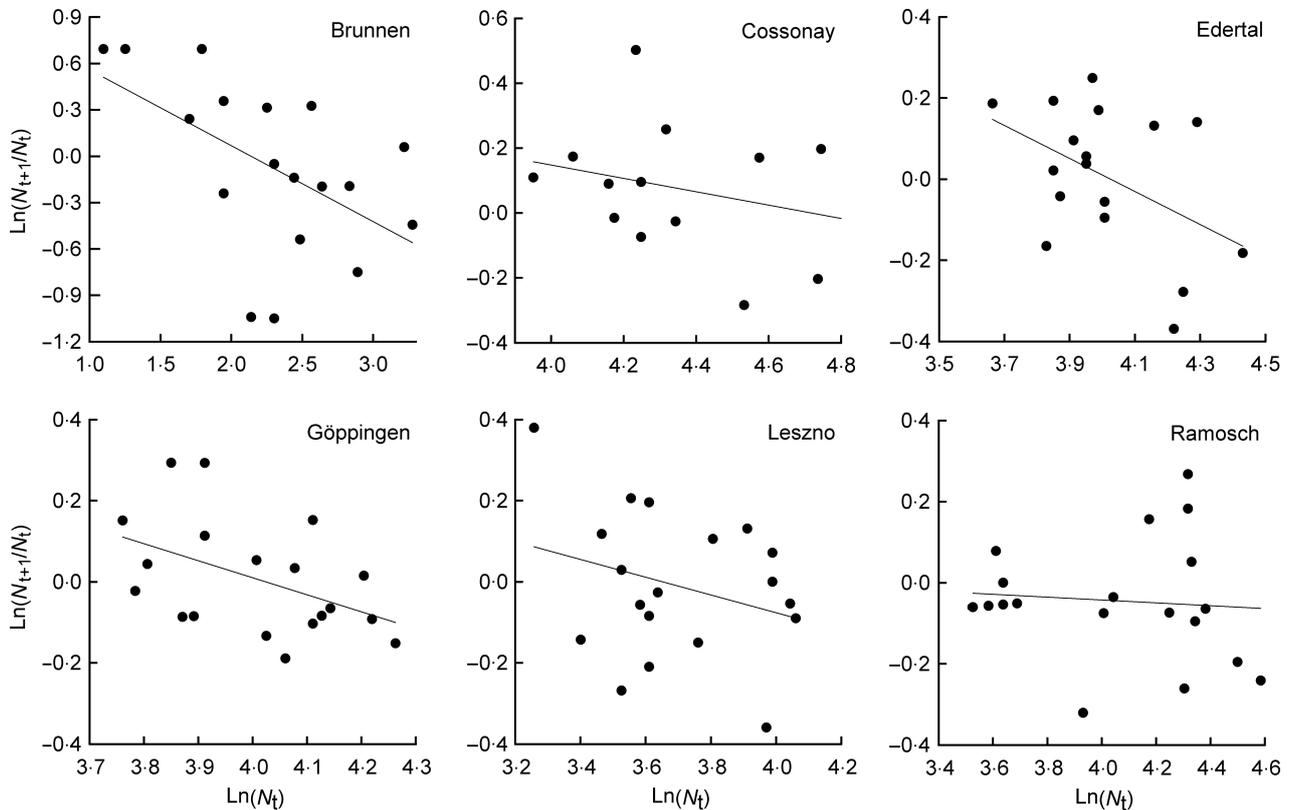


Fig. 2. Patterns of density dependence in six red-backed shrike populations. Data points are ln-transformed observed population size N . Regression lines based on b -values of the Gompertz state-space model given in Table 1.

dependent vs. density-independent model) varied between 2.3 (Ramosch) and 47.7 (Göppingen). For all populations, we thus used the density-dependent GSS model as our null model in all further analyses.

Sampling variance τ^2 was very small in all populations (Table 1). That is, observed fluctuations in population counts (Fig. 1) were not generally because of observation error and thus largely reflected true fluctuations in population size. In turn, aside from density dependence, process variance, i.e. environmental-type process noise, strongly contributed to variation in population size (Table 1, column ϕ).

Estimates of density dependence b and process variance σ^2 from the sG model, which did not account for sampling variance τ^2 , mirrored those obtained from the GSS model (Table 1). More specifically, the ratio of the process variances (σ^2) from the GSS model (σ_{GSS}^2) and sG model (σ_{sG}^2) gave values ranging from 0.843–0.996 (Table 1, column $\sigma_{\text{GSS}}^2/\sigma_{\text{sG}}^2$). This indicates that accounting for sampling variance τ^2 reduced estimates of environmental variability only slightly in most populations (i.e. by maximally 15.7%, considering that the ratio of $\sigma_{\text{GSS}}^2/\sigma_{\text{sG}}^2$ at Edertal was 0.843, Table 1).

VARIATION IN POPULATION SIZE

GSS model

In four of the six populations, best-supported GSS models included covariates referring to the tub hypothesis.

In each of these four populations, the second ranking model had $\Delta\text{AICc} > 2.3$ to the highest ranking model. Based on Akaike weights, highest ranking models had more than three times better support than the respective second-best models (Table S2, Supporting information). In contrast, the best-supported model in the remaining two populations was the null model (i.e. the GSS model without environmental covariate). Neither the settlement nor the tap hypothesis was supported in any population.

Model selection thus revealed that breeding population sizes at Cossonay, Edertal and Göppingen were positively related to Sahel rainfall in the previous fall, while population size at Brunnen was positively related to rainfall in southern Africa in the previous winter (Fig. 3). Model-averaged estimates for both covariates (rain_Sahel and rain_southern Africa, respectively) were larger than the associate SEs (Table 2).

sG model

Results for the sG model are presented in Appendix S1 (Supporting Information). Briefly, the sG model supported the tub hypothesis as well, whereas none of the other hypotheses received support.

In summary, according to both the GSS model and the sG model, rainfall in the Sahel during fall migration appeared to be important for breeding population size in the following

Table 1. Results of Gompertz state-space (GSS) and simple Gompertz (sG) models per population

Population	<i>n</i>	GSS model					sG model				
		<i>a</i>	<i>b</i>	σ^2	τ^2	ϕ	<i>a</i>	<i>b</i>	σ^2	$\sigma_{\text{GSS}}^2/\sigma_{\text{sG}}^2$	
Brunnen	19	1.014 (0.811;1.217)	-0.440 (-0.53; -0.355)	0.2301 (0.13;0.469)	0.0000 (0;0.179)	1	1.051 (0.842;1.259)	-0.491 (-0.58; -0.403)	0.2357 (0.113;0.424)	0.976	
Cossonay	15	0.748 (0.671;0.826)	-0.169 (-0.187; -0.152)	0.0389 (0.021;0.088)	0.0000 (0;0.021)	1	0.972 (0.877;1.067)	-0.206 (-0.228; -0.184)	0.0393 (0.017;0.076)	0.990	
Edertal	18	1.740 (1.676;1.805)	-0.434 (-0.45; -0.418)	0.0210 (0.012;0.047)	0.0010 (0;0.018)	0.954	1.636 (1.566;1.711)	-0.407 (-0.425; -0.389)	0.0249 (0.013;0.05)	0.843	
Göppingen	20	1.743 (1.693;1.792)	-0.435 (-0.447; -0.423)	0.0144 (0.008;0.029)	0.0000 (0;0.009)	1	1.688 (1.634;1.743)	-0.420 (-0.433; -0.406)	0.0156 (0.008;0.03)	0.923	
Leszno	20	0.835 (0.772;0.897)	-0.232 (-0.249; -0.215)	0.0271 (0.016;0.054)	0.0000 (0;0.015)	1	0.800 (0.724;0.875)	-0.219 (-0.239; -0.199)	0.0296 (0.016;0.057)	0.916	
Ramosch	20	0.306 (0.262;0.351)	-0.077 (-0.089; -0.067)	0.0226 (0.013;0.023)	0.0000 (0;0.012)	1	0.098 (0.032;0.163)	-0.035 (-0.051; -0.019)	0.0227 (0.012;0.043)	0.996	

In parentheses: 95% confidence intervals.

n = number of years; *a* = intercept; *b* = *c* - 1 and gives the magnitude of density dependence, with *b* = 0 indicating density independence; σ^2 = process variance (environmental-type process noise); τ^2 = sampling variance (observation error); ϕ = proportion of variability in population size because of process variability [i.e. $\sigma^2/(\sigma^2 + \tau^2)$]; σ_{GSS}^2 = process variance σ^2 of GSS model; σ_{sG}^2 = σ^2 of sG model; the ratio $\sigma_{\text{GSS}}^2/\sigma_{\text{sG}}^2$ gives magnitude of reduction of process (i.e. environmentally-induced) variability estimated by accounting for sampling variance (σ_{GSS}^2) relative to process variability estimated when not accounting for sampling variance (σ_{sG}^2). Note that σ^2 in the sG model is calculated as sum of squared model residuals (i.e. error sum of squares) divided by *n* - 1 (Dennis & Otten 2000).

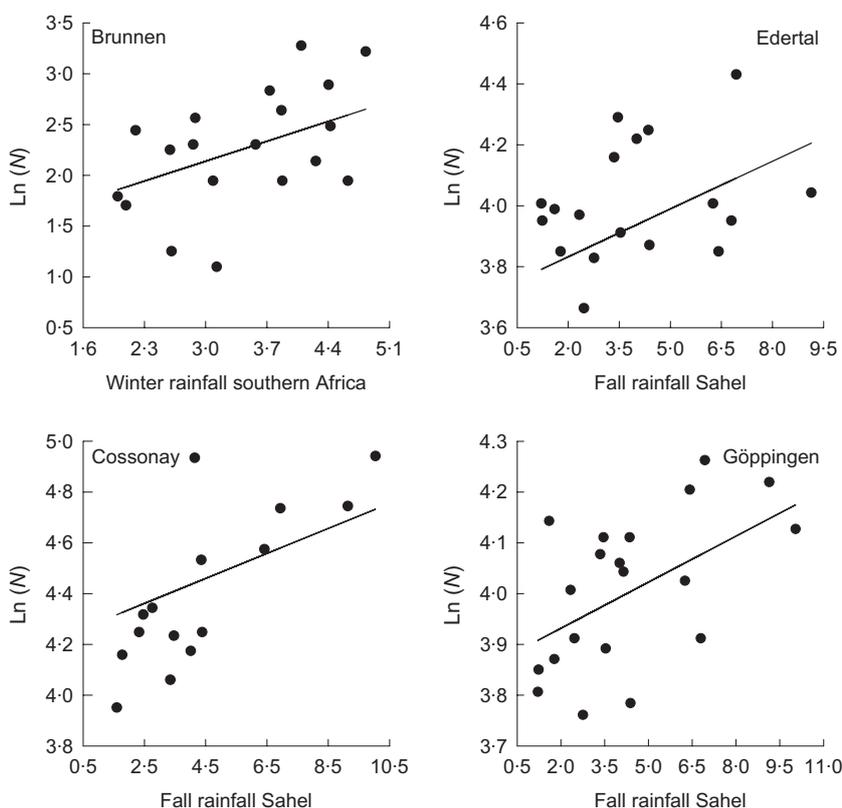


Fig. 3. Relations between average rainfall (mm) in the fall staging areas and on the wintering grounds, respectively, and ln-transformed observed population size *N* in the following spring. Regression lines based on predicted values of best-supported Gompertz state-space models given in Table S2 (Supporting information).

spring, as was, to a lesser extent, also rainfall in southern Africa (wintering areas).

Discussion

Time-series data of population size in the form presented in this study are widespread in ecology. Yet, application of ade-

quate statistical models to explain temporal variation in population size, while simultaneously estimating sampling variance (observation error), process variance (environmental-type process noise) and the strength of density dependence is still uncommon (Freckleton *et al.* 2006; Lebreton 2009). This is surprising because it is well known that count data, often collected to estimate population size, hardly ever

Table 2. Model-averaged estimates (and unconditional SE) per variable and population

Model	Hypothesis	Variables	Brunnen ($n = 19$)	Cossonay ($n = 15$)	Edertal ($n = 18$)	Göppingen ($n = 20$)	Leszno ($n = 20$)	Ramosch ($n = 20$)	
GSS	Settlement	May rain	0 (0.002)	0.001 (0.001)	0 (0.001)	0.002 (0.003)	0.001 (0.003)	0.003 (0.007)	
		May temperature	-0.001 (0.003)	-0.003 (0.005)	-0.001 (0.002)	0 (0.001)	0.001 (0.002)	0.001 (0.002)	-0.001 (0.002)
		June/July rain	-0.004 (0.011)	-0.001 (0.003)	-0.003 (0.005)	0 (0.001)	0 (0.001)	0 (0.001)	-0.005 (0.010)
	Tap	June/July temperature	0.030 (0.054)	0 (0.001)	0 (0.001)	0.001 (0.001)	0.001 (0.001)	0 (0.001)	0 (0.002)
		NDVI_Ethiopia	0 (0)	0 (0)	0 (0.001)	0 (0)	0 (0.001)	0 (0)	0 (0)
		NDVI_Sahel	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
	sG	Settlement	NDVI_southern Africa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)
			Rain_Ethiopia	0.021 (0.041)	0.004 (0.009)	0.006 (0.011)	0.004 (0.008)	-0.002 (0.005)	0.004 (0.009)
			Rain_Sahel	0.001 (0.006)	0.029 (0.027)	0.043 (0.021)	0.020 (0.017)	0.002 (0.004)	0.002 (0.004)
Tap		Rain_southern Africa	0.165 (0.152)	0.003 (0.007)	-0.008 (0.014)	-0.001 (0.004)	-0.001 (0.004)	0.001 (0.004)	
		May rain	0.002 (0.006)	0 (0)	0.003 (0.006)	0.002 (0.004)	0.002 (0.003)	0.007 (0.014)	
		May temperature	-0.002 (0.006)	-0.001 (0.002)	-0.004 (0.008)	-0.001 (0.003)	0.001 (0.002)	-0.001 (0.002)	
Tub	June/July rain	-0.021 (0.045)	-0.024 (0.040)	-0.002 (0.004)	0.003 (0.007)	0.009 (0.014)	0.009 (0.014)	-0.003 (0.006)	
	June/July temperature	0.012 (0.025)	0 (0.001)	0 (0)	0.011 (0.019)	0.010 (0.019)	0.001 (0.002)		
	NDVI_Ethiopia	0 (0)	0 (0)	0 (0.001)	0 (0)	0 (0.001)	0 (0)		
GSS	Settlement	NDVI_Sahel	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
		NDVI_southern Africa	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
		Rain_Ethiopia	0.096 (0.122)	0.013 (0.022)	0.045 (0.041)	0.005 (0.01)	0.001 (0.003)	0.029 (0.038)	
	Tap	Rain_Sahel	-0.002 (0.006)	0.047 (0.025)	0.029 (0.021)	0.010 (0.014)	0 (0.001)	0.001 (0.002)	
		Rain_southern Africa	0.033 (0.062)	0.001 (0.003)	-0.044 (0.052)	-0.003 (0.008)	-0.005 (0.010)	-0.004 (0.009)	

Model-averaging was performed over the 21 candidate models examined per population (see Table S2, Supporting information for a complete list of models). 0 denotes estimates (SE), which were equal to zero to three digits.

GSS, Gompertz state-space model; sG, simple Gompertz model; NDVI, normalized difference vegetation index.

reflect true population size (Freckleton *et al.* 2006). The magnitude of this sampling variance should be estimated, as it may have important implications for the detection of density dependence (Shenk, White & Burnham 1998) and hence for the projection of population fluctuations, for example in the context of population viability analysis (Morris & Doak 2002). The possibilities to apply adequate statistical approaches to time-series data have recently been facilitated for example because of freely available code for widely used statistical software (e.g. SAS, R, Dennis *et al.* 2006) as well as because of recent developments in the application of Bayesian methodologies (Knappe 2008). Broad application of these approaches is encouraged to improve our understanding of the processes that determine population dynamics.

In this study, one such approach based on the GSS model has been applied. Sampling variance turned out to be negligible, suggesting that the population counts of the red-backed shrike were precise. This was expected for two of the six study populations (Göppingen and Leszno), which had been the subjects of extensive research including colour banding and nest searches. That population counts were also quite precise in the other four populations, which had been studied less intensively, may be explained by the conspicuousness of the brightly coloured males in the breeding season, which often perch on exposed parts of hedges and bushes in their territories (Glutz von Blotzheim & Bauer 1993), making the monitoring of the population size of the species relatively easy. This is corroborated by Kéry & Schmidt (2008), who estimated detection probability of red-backed shrikes in 1-km quadrats to be fairly high, with 2.7 surveys per season yielding a 95% probability of detecting the species, if present.

Density dependence appeared to be important in the regulation of red-backed shrike population size. In all six populations, density-dependent models were better supported by the data than density-independent models, with negative relations between the population sizes in successive years. Adding environmental covariates to the models did not alter the pattern of density dependence in principle: estimates of density dependence were on average reduced by 19% (range 0–58%) compared to the models without environmental covariates. How could negative density dependence operate in this species? Nest success has been shown to decrease with increasing intraspecific density (Müller *et al.* 2005), suggesting density-dependent regulation on the breeding grounds. Whether density dependence also acts via other pathways on the breeding grounds or in the non-breeding season, as suggested for several bird species (Newton 2004), cannot currently be assessed. Whatever the mechanism, our study adds to the substantial evidence that intraspecific density is an important factor in the regulation of populations (e.g. Sibly *et al.* 2005; Brook & Bradshaw 2006).

Aside from density dependence, most of the variation in population size among years was attributed to process variance. However, most of the environmental covariates considered were only weakly related, if at all, to population size. We only found support for the tub hypothesis, suggesting environmental conditions in the staging areas during fall migra-

tion and in the wintering sites to be of some importance for explaining variation in population size of the red-backed shrike in the following spring. Population size was positively related to mean rainfall in the Sahel during fall migration (three populations) and to mean rainfall in southern Africa in the wintering grounds (one population). In each of these four populations, model-averaged estimates of the respective covariates were larger than their associated, unconditional SEs (Table 2). Diversity and abundance of insects are known to be positively related to rainfall in many parts of Africa (Todd *et al.* 2002). Because red-backed shrikes primarily feed on insects year-round, individuals may benefit from increased food availability in relatively wet years in areas of fall migration and in the wintering areas, resulting in increased breeding population size the following spring. Interestingly, however, apparent annual survival of red-backed shrikes from the population Göppingen was not related to rainfall (or NDVI) in the Sahel and in southern Africa, respectively, whereas reproductive output increased with NDVI in the Sahel during the previous fall migration, that is, with vegetation development and hence food supply (M. Schaub, H. Jakober & W. Stauber, unpublished). Thus, although findings from both Schaub *et al.* (unpublished) and our study suggest effects of environmental conditions in the Sahel in fall for red-backed shrike populations next spring, the mechanism behind the apparent carry-over effects found in both studies is currently unclear. Nevertheless, our findings are consistent with the long-standing hypothesis that conditions in the African staging and wintering areas may affect population numbers of (some) species breeding in Europe (Newton 2004).

It is noteworthy that the relations between rainfall in Africa during fall/winter and breeding population size in the following breeding season were found with the GSS model and with the sG model, although results from the latter were generally less clear (Table S2, Appendix S1, Supporting information). It thus seems that random variation in population size owing to the unaccounted for sampling variance in the sG model was sufficient to mask the weak relations between population size and rainfall in Africa, even when the sampling variance reported in this study was small. Failing to account for sampling variance may therefore lead to erroneous conclusions with respect to the effects of environmental factors on population fluctuations (Lindén & Knappe 2009).

The settlement hypothesis was not supported. Effect sizes were generally small, suggesting that conditions during settlement did not influence subsequent population size. Studies reporting adverse effects of weather conditions upon arrival of migrants on population size generally implicated severe events such as snowstorms or freezing conditions (Newton 2007). Such conditions did probably not occur in the populations studied here, because red-backed shrikes settle in May, when prolonged cold spells are uncommon. Alternatively, the birds may have delayed arrival on the breeding grounds as a consequence of prevailing severe weather conditions (e.g. Ahola *et al.* 2004).

The tap hypothesis, stating that breeding population size is affected by environmental conditions during the previous

breeding season (Saether, Sutherland & Engen 2004), has received support in studies on some passerines and non-passerines, but not in others (summarized in Newton 2004; Saether, Sutherland & Engen 2004). We found no support for the tap hypothesis, because models with covariates referring to the tap hypothesis did not explain variation in population size of the red-backed shrike better than models without covariates (i.e. the null model). In addition, effect sizes were always smaller than the associated SEs, indicating weak relations to population size at best. A negative influence of local weather, in particular of rainfall, on different aspects of red-backed shrike's breeding ecology has been suggested (e.g. Husek & Adamik 2008), but was not always found (Müller *et al.* 2005). Local negative effects at the nest level need not necessarily translate into a reduction in population size 1 year later, because (i) the red-backed shrike may partly compensate for complete nest losses by re-nesting, (ii) local recruitment in the red-backed shrike appears to be low anyway (Müller *et al.* 2005), and (iii) adult losses (through increased mortality because of high parental effort during periods of inclement weather) may be offset by immigrants.

In conclusion, we found evidence for negative density-dependent regulation of the breeding population size in this migratory bird species. In addition, conditions in the African fall staging and wintering areas appeared to affect population size in the following spring, thus lending support to the tub hypothesis. Environmental factors on the breeding grounds did not seem to influence breeding population size; that is, neither the settlement nor the tap hypotheses were supported. However, environmental factors such as predator composition or density have been shown to affect breeding population size in many bird species (Newton 1998). Therefore, fluctuations in population size of most migratory species are expected to result from the many factors acting during different parts of the annual cycle. To further our understanding of population dynamics, future studies need to focus on the mechanisms affecting vital rates and dispersal behaviour rather than on time-series analyses.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Results of the sG model.

Table S1. Overview on the study populations.

Table S2. List of the candidate models examined.

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