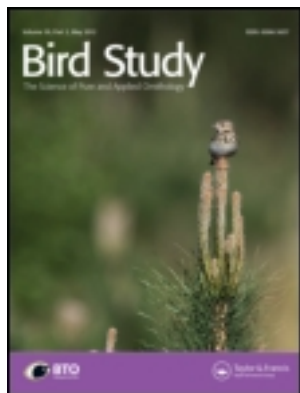


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# Effects of summer weather on reproductive success of the Red-backed Shrike (*Lanius collurio*)

PETER SØGAARD JØRGENSEN<sup>1\*</sup>, ANDERS P. TØTTRUP<sup>1</sup>, CARSTEN RAHBEEK<sup>1</sup> and MARTEN GEERTSMA<sup>2</sup>

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**Capsule** Summer weather affects reproductive success in the Red-backed Shrike (*Lanius collurio*).

**Aims** To investigate the relationship between reproductive success and weather conditions in the European breeding areas.

**Methods** Using a Principal Component Analysis, we investigate how summer (July) weather affects reproductive success in two populations in northwestern Europe. Further, we assess the general relationship between reproductive success and weather in a review of published results.

**Results** Weather is correlated with reproductive success in five out of six European populations, including the two populations at the northwestern range edge as well as three out of the four reviewed populations, all in central Europe. In general, sunny, warm and dry weather increases reproductive success, while rainy and cold weather has the opposite effect.

**Conclusion** Our findings suggest that the warmer summers predicted under a future climate could increase the reproductive success of the Red-backed Shrike. Yet the effect of more extreme weather is yet to be examined. Future investigation of the relationship between weather and the population dynamics across a large spatial scale could help us estimate for which species we should expect general effects of climate change.

Passerines exhibit some of the most well documented responses to climate change (Parmesan & Yohe 2003). In particular, pole-ward range shifts (Huntley *et al.* 2007), shifts to earlier spring arrival at the breeding area (Lehikoinen *et al.* 2004, Tøttrup *et al.* 2006) and initiation of breeding (Dunn 2004) have been documented repeatedly in Europe and North America (Parmesan & Yohe 2003). As a vital demographic rate known to depend on environmental conditions (Newton 2004), reproductive success is likely to be involved in these climate-change responses whether as a consequence of phenological response (Both *et al.* 2006) or as a contributing cause leading to climate-induced range shifts (Huntley *et al.* 2007). Understanding the relationship between reproductive success and local weather conditions is important to assessing how individual bird populations will respond to changes in climate (e.g. Both *et al.* 2006). Yet,

studies looking at this relationship across multiple populations on the scale of continental regions are rare.

In long-distance migrants, the question of how reproductive success will change as a result of climate change is complicated by the fact that populations spend periods of the year on different continents and moving between them (Newton 2007). Thus, change in reproductive success can be the result of varying environmental conditions in disparate locations (Runge & Marra 2005). Conditions in the breeding area and wintering area up to the onset of spring migration have most often been suggested to influence reproductive success (Newton 2004), but carry-over effects (Marra *et al.* 1998) from the previous breeding seasons or the staging areas during autumn migration have recently been raised as other influential factors (Passinelli *et al.* 2010, Schaub *et al.* 2011).

The Red-backed Shrike (*Lanius collurio*) has been subject to several multi-year studies of reproductive success (e.g. Müller *et al.* 2005, Golawski 2006, 2008, Husek & Adamik 2008, Schaub *et al.* 2011) and given

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the species reliance on an insect diet, weather conditions are often discussed in connection with fluctuation in demographic parameters (Ash 1970, Bibby 1973, Passinelli *et al.* 2010, Pedersen *et al.* 2011, 2012, Schaub *et al.* 2011). Most notable was the discussion of causality for the large decline in the now nearly extinct British breeding population (Ash 1970, Bibby 1973, UK Biodiversity Group 1998, Araujo & Rahbek 2006, Tryjanowski *et al.* 2006). The decline occurred over several decades (Bibby 1973) with no clear pressure from the British spring and summer climate (Jenkins *et al.* 2009). In fact, the decrease in breeding range between 1970 and 1990 contradicted predictions based on climate envelope modelling (Araujo & Rahbek 2006). Furthermore, Tryjanowski *et al.* (2006) compared parameters of reproductive success in one of the final strongholds of the British population with parameters in an apparently stable Central European population and found them comparable. Thus, there is still uncertainty about the causes that led to the British decline.

The Red-backed Shrike has been in decline in several Western European countries throughout the 20th century. The decline is especially attributed to change in land-use patterns such as agricultural intensification (Tucker & Heath 1994). At the same time the Red-backed Shrike has expanded its European range to the north (Tucker & Heath 1994; Hagemeyer & Blair 1997; BirdLife International 2004). This latter trend is in line with predictions from species distribution modelling (Huntley *et al.* 2007). The Red-backed Shrike therefore constitutes an example of where regional population trends within Europe might be governed by different global change processes.

In this study we synthesize current knowledge on the association between weather conditions and reproductive success in the Red-backed Shrike. First, we examine two populations in Western Europe (Bargerveen, The Netherlands and Hulsig Hede, Denmark) at the species' northwestern range edge. Secondly, to assess the degree to which effects are similar between European populations, we review published studies looking at the weather–reproductive success relationship.

Local summer conditions are expected to influence reproductive success by the following processes: sunny, warm and dry weather is believed to increase survival of nestlings due to good insect foraging opportunities and a general high abundance of food sources, and by providing a benign nest microclimate for the young (Cramp & Perrins 1993, Glutz von Blotzheim & Bauer

1993). Precipitation is expected to have a negative effect on the survival of offspring through lack of food, and a higher predation pressure due to the adults needing to spend more time searching for food (e.g. Cramp & Perrins 1993, Glutz von Blotzheim & Bauer 1993, Husek & Adamík 2008).

## METHODS

### Study sites and populations

The Dutch population of Red-backed Shrike declined from several thousand to a few hundred pairs in the 20th century and now has only a few strongholds, the main one being in the Bargerveen reserve (Geertsma *et al.* 2000). The decline is thought mainly to be caused by loss of suitable habitat linked to eutrophication processes and agricultural intensification (Esselink *et al.* 1995). The Danish population has gone through a historical decline since the middle of the 20th century (Grell 1998), and some sites with large historical populations have now been totally abandoned (Frølich 2007). The national population appears to have stabilized and mainly thrives in the western part of the country, with only one large population in the eastern part (Grell 1998, DOFbasen 2010, Pedersen *et al.* 2011, 2012).

Bargerveen (52°40'40"N, 07°02'08"E) is a 22-km<sup>2</sup> isolated remnant of a large former peat bog in the easternmost part of the Netherlands, near to the border of Germany. It is surrounded by cultivated and urban land (Geertsma *et al.* 2000). The data from Bargerveen cover the period 1993–2007. Hulsig Hede (57°41'00"N, 10°28'00"E) is a 35-km<sup>2</sup> dune heath area in the northernmost part of Jutland, Denmark. The westernmost part of the area is dominated by drifting sand dunes. Further inland the vegetation changes along a west–east gradient. The heath is bordered by coniferous plantations. The data from Hulsig Hede cover the period 2003–2007. Both the Dutch and Danish areas are part of the EU NATURA-2000 network.

### Field methods

Data on reproductive success were collected from Bargerveen between the beginning of May to late August and from early June to early August at Hulsig Hede due to difference in arrival and onset of reproduction. All resident pairs and territorial solitary males were mapped. For a large proportion of all pairs,

the nest was found, either through behavioural observations or by searching in suitable bushes or trees. Clutch size was noted and each nest visited on one to three occasions to keep track of brood size. The lowest observed number of nestlings is defined here as the number of potential fledglings. Usually this number was noted when nestlings were at an age of 7–10 days. In many nests the number of potential fledglings was confirmed later, just before fledging.

A pair is defined according to three possible criteria: (1) finding of a nest in use; (2) a resident pair noted on several dates; (3) the detection of young fledglings (i.e. not able to make flights over longer distances). A successful pair is defined as a pair with at least one chick surviving to the age of fledging. *Pairs checked for fledglings* is the number of pairs for which the number of fledglings is known (observations of unsuccessful pairs included).

The following population-level reproductive success parameters were estimated.:

- (1) *Number of fledglings per successful pair.*
- (2) *Number of fledglings per pair*, which is calculated as the total number of fledglings divided by *pairs checked for fledglings*.
- (3) *Nestling mortality*, which is the difference between clutch size and number of fledglings for pairs checked for fledglings (therefore including unfertilized and unhatched fertilized eggs).
- (4) *Proportion of successful pairs*, which is the number of successful pairs divided by *pairs checked for fledglings*.

We analyse only the data from the western part of Hulsig Hede, which was covered in all years (eastern part not covered in 2003), as there is some difference in the overall habitat type between the two parts and this might add non-random noise to the data set.

### Meteorological data

The local weather data used for Hulsig Hede and Bargerveen were gathered from the website of the Meteorological Institute of Denmark (DMI, [www.dmi.dk](http://www.dmi.dk)) and The Royal Meteorological Institute of the Netherlands (KNMI, [www.knmi.nl](http://www.knmi.nl)), respectively. Monthly weather variables from July (the month with most nests containing nestlings at both sites) were extracted or calculated based on the freely available data from the above websites. These are number of monthly sunshine hours, the mean monthly day temperature (°C), the number of days with

**Table 1.** Key statistics for climate variables used in the populations in the Netherlands (NL) and Denmark (DK).

July climate variable	Site	Min	Max	Mean	sd
Average day temperature (°C)	NL	19.2	28.3	22.5	2.6
	DK	18.7	24.3	21.0	2.3
Sunshine hours (h)	NL	97.2	318.6	201.7	65.1
	DK	159	312	228.6	58.2
Rainfall (mm)	NL	34.3	154.6	87.1	35.6
	DK	29	127	85.6	35.9
Rainy days (days)	NL	4	19	12.1	4.5
	DK	6	18	12.0	4.6

precipitation above 0.1 mm (DMI standard measure) and the monthly amount of precipitation (mm). For Hulsig Hede, regional data (from Nordjylland, DMI) on amount of precipitation and sunshine duration were used as complete data were not available from the local station in Skagen. For Bargerveen all monthly variables were based on daily data from the nearest public weather station (60 km away) in Groningen (Eelde) (Table 1).

### Data analysis

Because weather variables often are intercorrelated we used a Principal Component Analysis (PCA; Pearson 1901) to summarize the variation in the four weather variables for July separately for each population. PCA decreases the risk of committing a type I error, a potential problem when conducting multiple tests with intercorrelated explanatory variables. Next we performed a regression with the first principal component as explanatory variable, to investigate the effect of local summer weather on each of the four reproductive success parameters in a Generalized Linear Model. The slope of the regression can be interpreted as the general association between weather conditions and a given component of reproductive success. The underlying distribution was assumed to be binomial (*proportion of successful pairs*), analogous to a logistic regression or Gaussian with a 'log' link-function (all other reproductive success components). Accordingly we used F-tests (Gaussian models) and Chi-square tests (binomial models) to test the significance of the correlations.

We first investigated the generality of weather effects using data from both populations in a model including the interaction between site and the first principal component for weather. The full model was tested against a model with shared slope but site-dependent intercept (test of interaction between principal

component and site), which in turn was tested against a model with one slope and one intercept (test of additive effect of site), which finally was tested against a model including only an intercept term (test of a general weather effect). Secondly, because the analysis of the overall data does not necessarily reflect our ability to detect within-population effects of weather, we performed the regressions on the site-specific data set (using the first principal component as the only explanatory variable).

Model assumptions were checked using residual plots (variance homogeneity) and Box–Cox plots (normality). A Box–Cox transformation was used to achieve Gaussian distribution for reproductive success parameters that deviated from this assumption. R 2.10.0 (R Development Core Team 2008) was used for all statistical analyses.

## Review

We searched ISI Web of Knowledge for the term combination '(Red-backed AND Shrike) OR (Lanius AND collurio)' in the title or topic field and first scanned the title of all resulting 883 resulting publications to determine relevance. Of these, five publications used statistical tests to analyse the effect of weather on one or more components of reproductive success. For each these five studies we

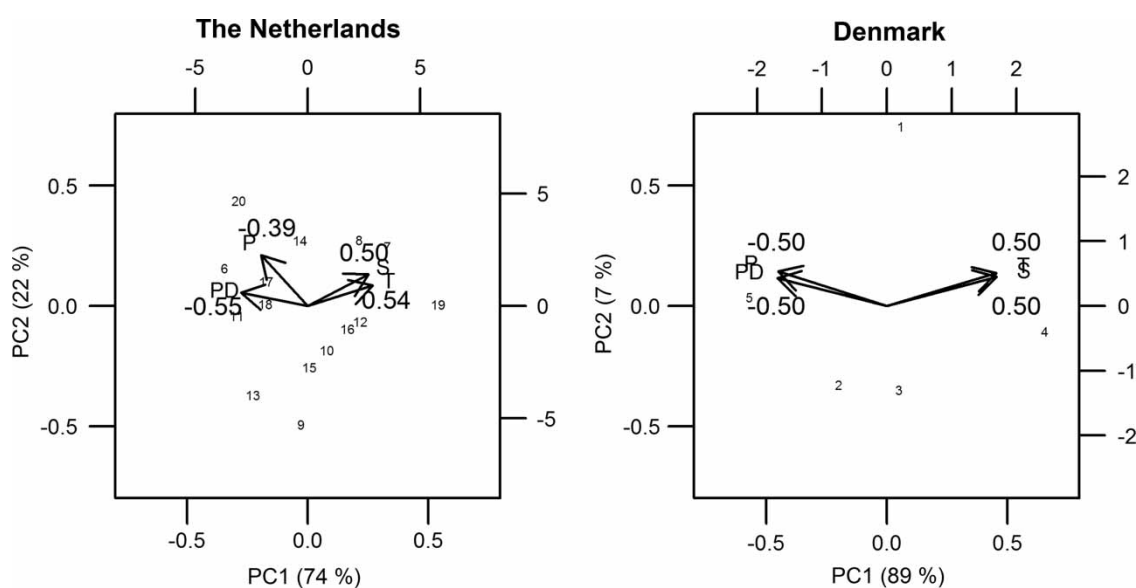
obtained the following characteristics: location of the study; study length; whether monthly meteorological means or weather conditions specific for each breeding pair were used as explanatory variables; the investigated components of reproductive success; investigated weather variables; statistical methods; and results relating to other environmental conditions.

## RESULTS

### Reproductive success in the Dutch and Danish populations

The first principal component of the PCA explained 74 and 89% of variation in the main weather variables in the Netherlands and Denmark. High values of the principal component were positively correlated with temperature and sunshine, and negatively correlated with the two precipitation variables (Fig. 1). The principal component therefore summarizes local summer weather along a 'cold and wet'–'hot and sunny' continuum. Summary statistics of weather variables from the two populations are presented in Table 1.

Weather had a significant (fledglings per pair, fledglings per successful pair and nestling mortality) or marginally significant effect (proportion of successful pairs) on all four parameters of reproductive success (Table 2), in all cases in the expected direction.



**Figure 1.** Biplot of the Principal Component Analysis showing the data points for each year (numbered 1 to study length). The vector of each weather variable and its correlation with the first principal component (PC1) is shown as arrows and a number next to the arrow, respectively. Percentages in the axis label indicate the amount of variation in the weather data explained by the respective principal component. Weather variables: P, precipitation; PD, precipitation days; T, temperature; S, sunshine hours.



**Table 2.** Weather effects on reproductive success assessed from joint and separate analysis of the two populations. All joint analyses have  $n = 20$  and separate analyses  $n = 15$  (NL) or  $n = 5$  (DK). *Model* indicates the degree to which the full model could be simplified (*Interaction* – no simplification, *Additive* – shared weather and different intercepts, *General* – shared weather effect and intercept) or the data set which was analysed (NL – Netherlands, DK – Denmark). *Intercept* and *slope* give model parameter estimates. The difference in null and residual deviance indicates the amount of variation explained by the model. *P* values indicate the significance of a model parameter and the model simplification tests (models simplified to the first significant or marginally significant value). \* indicates  $0.01 < P < 0.05$ , \*\* indicates  $0.05 < P < 0.10$ ; \*\*\* indicates analysis on Box–Cox transformed data.

	Reproductive success parameter	Model	Intercept	Slope	Null deviance	Residual deviance	<i>P</i> value slope	<i>P</i> value intercept site	<i>P</i> value interaction (weather × site)
Joint analysis	Proportion of successful pairs	Interaction	NL: 0.79 DK: 0.75	0.004 0.23	30.0	25.0	0.10 < 0.085**	–	0.08**
	Fledglings per pair	General	2.65	0.15	4.89	3.65	0.03*	0.10 <	0.10 <
	Fledglings per successful pair	Additive	NL: 4.01 DK: 4.50	0.089	3.04	1.65	0.045*	0.008**	0.10 <
	Nestling mortality	General	2.02	–0.067	0.968	0.720	0.02*	0.10 <	0.10 <
Separate analysis	Proportion of successful pairs	NL	0.79	0.003	21.9	21.8	0.10 <	–	–
	Fledglings per pair	DK	0.76	0.233	6.79	3.10	0.05*	–	–
		NL***	2.66	0.106	3.48	2.77	0.09**	–	–
	Fledglings per successful pair	DK***	2.74	0.078	1.25	0.55	0.10 <	–	–
		NL	4.01	0.021	1.04	0.75	0.045*	–	–
	Nestling mortality	DK	4.51	0.022	1.05	0.90	0.10 <	–	–
		NL	2.00	–0.054	2.76	2.30	0.10 <	–	–
		DK	2.20	–0.043	0.030	0.004	0.02*	–	–

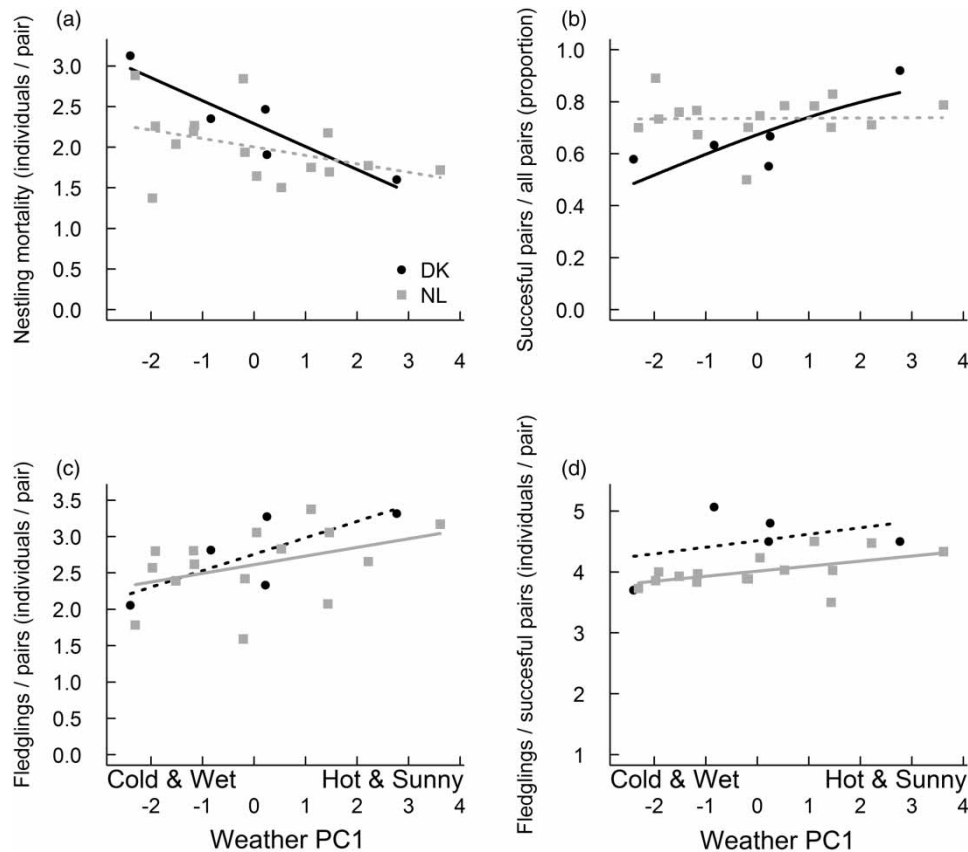
Reproductive success components increased with warm and sunny weather and decreased with colder and wet conditions. The effect of weather on proportion of successful pairs tended to differ between the populations in the Netherlands and Denmark ( $P = 0.07$ ), with a general positive effect in Denmark (slope = 0.23,  $R^2 = 0.97$ ,  $P = 0.045$ ) and no evident effect in the Netherlands (slope = 0.003,  $R^2 = 0.001$ ,  $P > 0.10$ ). The effect on fledglings per successful pair did not differ between populations ( $P = 0.81$ ), and generally had a positive effect (slope = 0.089,  $P = 0.045$ ). However, the Danish population had a higher general level of fledglings per successful pair ( $P = 0.008$ , Hulsig-intercept = 4.50, Bargerveen-intercept = 4.01). For fledglings per pair and nestling mortality there was a general significant effect of weather ( $0.01 < P < 0.05$ , slope<sub>FP</sub> = 0.15, slope<sub>NM</sub> = –0.07) and no interaction with site. When analysed separately for the Dutch and Danish population, four of the eight regressions of reproductive success components on weather PC1 were either significant or marginally significant ( $0.05 < P < 0.10$ , Table 2). Again, all significant and non-significant effects of weather were in the direction as expected (Fig. 2).

## Review

The relationship between reproductive success and weather variables has previously been statistically

examined and published from four other populations (Fig. 3). All of the populations were in areas dominated by open agricultural land. When including the Danish and Dutch populations weather variables were correlated with reproductive success in five of the six populations (Table 3). In all cases the correlation was in the expected direction. One analysis applied at a larger spatial scale of the whole Czech Republic did not find any effects of weather on brood size (Husek & Adamík 2008).

In a five-year study of a Polish population looking at clutch size, clutch loss (number of unhatched eggs) (Golawski 2008) and nestling mortality (Golawski 2006), nestling mortality was positively correlated with precipitation (Golawski 2006). In contrast, clutch size, and clutch loss were uncorrelated with temperature and precipitation (Golawski 2008). In an analysis using 36 years of ringing data on brood size in the Trutnov-Jicin area (Czech Republic), brood size at the time of ringing decreased with an increasing number of precipitation days in June (Husek & Adamík 2008). In a 24-year study of the breeding population near Göppingen in Germany (Schaub *et al.* 2011), temperature and precipitation days were positively and negatively associated with the probability of a pair to raise young in a given year, respectively. Temperature and precipitation days had a relatively weak association with fledglings per pair and fledglings per successful pair. Despite these correlations, vegetation



**Figure 2.** Scatter plots of reproductive success components and the first principal component from the Principal Component Analysis. (a) Nestling mortality, (b) proportion of successful pairs, (c) fledglings per pair and (d) fledglings per successful pair. Lines shown are regressions fitted separately to each data set. Solid lines are significant ( $P < 0.05$ ) or marginally significant ( $0.05 < P < 0.10$  – fledglings per pair in NL), stippled lines have  $P > 0.10$ . Danish data are given in black and the Dutch in grey.

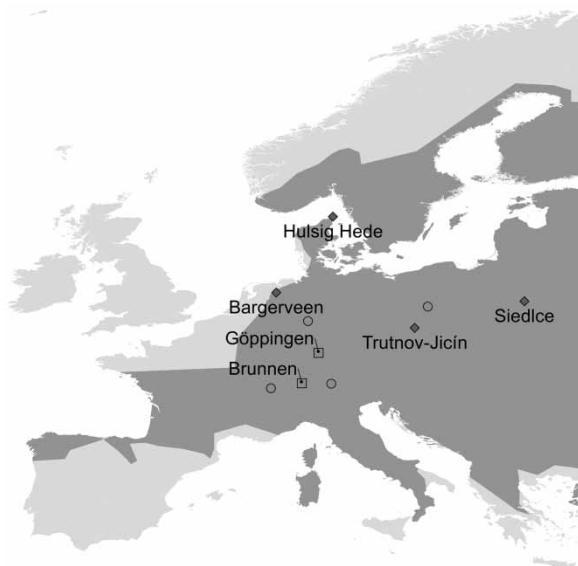
greenness (NDVI) during autumn in the Sahelian staging area explained two (proportion of successful pairs), four (fledglings per successful pair) and eight (fledglings per pair) times the amount of variation explained by either temperature or precipitation days in the breeding area. Finally, no effects of investigated weather variables on proportion of successful pairs nor fledglings per successful pair was found in a detailed but short-term (5-year) study of the population in Brunnen, Switzerland (Müller *et al.* 2005). Instead, characteristics of the particular nesting site such as nest concealment explained a larger amount of the variation in reproductive success (Müller *et al.* 2005).

## DISCUSSION

We report effects of local weather conditions on reproductive success in the Red-backed Shrike. In line with expectations based on the species' breeding

biology, shrikes had higher reproductive success during warm, dry and sunny summers. These results hold for populations at the northwestern range edge and are further supported when based on all statistical evaluations of this relationship. If future European summers become warmer and drier as result of climate change, the reproductive success of the Red-backed Shrike in central and northwestern Europe could increase. However, the specific outcome will probably depend on the details of an altered meteorology. In particular, the effects of the increased frequency of extreme weather events on population-level reproductive success are poorly studied, but are expected to increase variation in reproductive success between pairs in a given year.

Dependent on the population, different components of reproductive success were correlated with weather. This might reflect that breeding conditions are differentially influenced by weather. In the Dutch



**Figure 3.** Location of populations where reproductive success (diamonds), population abundance (circles) or both (squares) have been analyzed in relation to weather conditions. The populations where population abundance was investigated were all included in Pasinelli *et al.* (2011). The European range extent is sketched in darker colouration (Cramp & Perrins 1993).

population, the fact that two out of four components of reproductive success did not show a significant or marginally significant relation to weather could possibly be explained by the effect of management to increase the water level on habitat quality. The management has resulted in an increase in observed predation (Bargerveen Foundation, unpubl.). This underlines the need to take other environmental conditions into account, especially when habitats change due to management practices during the survey period. In the Danish population we suggest low statistical power to be the main reason significant correlations were not found for two out of four components of reproductive success.

### Reproductive success and breeding site weather across Europe

Most of the six studied populations differed in the set of reproductive success parameters that were investigated. If some stage of the breeding cycle is more or less sensitive to weather this difference in methodology could affect the comparison of results between populations. For example, Golawski (2008) suggested that the Red-backed Shrike was less vulnerable to variation in weather during the incubation period, where the male can supply the

female with extra food, contrasting with the period after hatching of the eggs where nestlings need to be fed and both sexes will forage if needed (Cramp & Perrins 1993). This might explain why no measurable effect of weather was found on variation in clutch size and clutch loss in the Polish population. Furthermore, differences in vegetation type and openness of the landscape are likely to be important site-level variables.

Although weather conditions seem to have a general effect on the Red-backed Shrike, the relative importance should depend on the degree to which other environmental factors are limiting reproductive success. If, for example, a population is subject to a relatively high density of predators, the spatial variation (within-years) and temporal variation (between-years) in predator density will probably be more important in determining individual and mean reproductive success of the population, respectively. This might explain why variables related to nest concealment and density of predators outperform models including weather variables in the Swiss population (Müller *et al.* 2005). Similarly, in the British population there has been speculation that predators (human egg collectors or other mammals) had a role in limiting the reproductive success of the British population before it was down to only a few breeding sites (Bibby 1973, Tryjanowski *et al.* 2006).

The reviewed studies differed in their use of observational unit in the analyses. In the Polish and Swiss populations, analyses of reproductive success were carried out on the level of individual pairs and related to weather conditions during the reproductive period of that particular pair. This is in contrast to analysis of the Dutch, Danish and Czech populations, where mean reproductive success was related to monthly mean weather conditions. The former analysis is geared towards detecting specific conditions that provide the basis for success or failure of a pair, whereas the latter analysis can only describe the effect of general but local weather conditions in a given year. Detail might be gained into the causes determining success of individual pairs in the former analysis. However, because there are many observations from each year, i.e. under the same general conditions, the analysis is dependent on accounting for variables with more fine scaled spatial variability like territory quality and nest site characteristics. On the other hand, studies carried out at the population level implicitly assume that variables at the individual level contribute randomly to variation in reproductive success between years. The consistency of results, despite different



**Table 3.** The table summarizes analyses of reproductive success in relation to weather conditions. Location of the study, start and end year and length of study are shown, as well as the studied components of reproductive success, the investigated weather variables, any weather effects and characteristics of the statistical methods. Reproductive success components: PPS, proportion of successful pairs; FP, fledglings per pair; FPS, fledglings per successful pair; NM, nestling mortality; BS, brood size; CS, clutch size. Weather variables: P, precipitation; PD, precipitation days; T, temperature; S, sunshine hours; NAO, North Atlantic Oscillation Index; NDVI, Normalized Difference Vegetation Index.

Reference	Location	Start year	End year	Study length (years)	Reproductive success component	Weather variables	Weather measurement period	Weather effects	Statistical methods
Golawski 2006, Golawski 2008	Siedlce, Poland	1999	2003	5	NM, CS, clutch loss (CS - hatched eggs)	T, P, PD	Mortality and clutch loss: May, June; Clutch size, per pair: 4 days before onset of laying + during incubation	NM: P positive. CS: Non	Multiple regression Mortality and loss: Stepwise selection Clutch size: No model reduction
Hušek & Adamik 2008	Czech Republic	1964	2004	41	BS (at time of ringing)	NAO, T, P, PD	Spring (NAO), May (T), June (P)	No effects	Multiple regression (including all significant univariate, no reduction)
Hušek & Adamik 2008	Trutnov-Jicín, Czech Republic	1964	2004	36	BS (at time of ringing)	NAO, T, P, PD	Spring (NAO), May (T), June (P)	BS: June PD negative	Multiple regression (including all significant univariate, no reduction)
Müller <i>et al.</i> 2005	Brunnen, Switzerland	1988	1992	5	PPS, FPS	T, P (PCA)	Per pair: 15 days after start of incubation	No effects. Other nest site level variables important.	Model selection (stepwise)
Schaub <i>et al.</i> 2011	Göppingen, Germany	1982	2006	25	PPS, FP, FPS	T, PD, NDVI	T, PD: June-July, NDVI: September-October (Sahel)	PPS: T, NDVI positive & PD negative. FP & FPS: NDVI positive.	Model selection (candidate set)
This study	Hulsig Hede, Denmark	2003	2007	5	NM, PPS, FP, FPS	T, S, P, PD (PCA)	July	NM: PCA negative. PPS: PCA positive	Univariate PCA regression
This study	Bargerveen, Netherlands	1993	2007	15	NM, PPS, FP, FPS	T, S, P, PD (PCA)	July	FP & FPS: PCA positive	Univariate PCA regression

observational units, suggests that the effects of weather are general both in terms of variation within the breeding season and between years.

Although shrikes have some ability to change their diet in response to inclement weather (Tryjanowski *et al.* 2003), it has been shown elsewhere that heavy or long-lasting rain lowers the food availability for Red-backed Shrikes, increases parasite load (Votypka *et al.* 2003), damages nests and causes increased nestling mortality due to chilling and starvation (Husek & Adamik 2008). We further hypothesize that temperature and amount of sunshine have a positive effect on insect abundance. As a consequence of this relationship, in cold and wet summers the parent shrikes need to spend more time searching for food, which in turn weakens the ability to protect the nest against predators. Still the question of how much this weather-driven variation in reproductive success contributes to the overall population growth rate remains to be addressed.

### Carry-over effects and regulation of population size

Although we show that populations' reproductive success are correlated with weather conditions in the breeding area, a recent meta-analysis found that fluctuations in population size were positively correlated with environmental conditions outside the breeding areas (Pasinelli *et al.* 2011). This result supports the 'tub-hypothesis' stating that population size is mainly limited by survival in the non-breeding season (Saether *et al.* 2004). Furthermore, the only study in our review to investigate potential carry-over effects from the wintering and migratory staging areas on reproductive success found stronger effects of autumn conditions in the Sahel compared to breeding site conditions (Schaub *et al.* 2011). Overall, this illustrates a plausible scenario for the limiting effects of environmental conditions in long-distance migrants: Environmental conditions in the breeding, staging and wintering areas all have a regulating influence on population size, with carry-over effects on reproductive success sometimes surpassing effects of local conditions in the breeding area.

By tracking long-distance migrants throughout the year, studies taking advantage of new technologies provide more detailed information on the specific whereabouts of migrants (Stutchbury *et al.* 2009, Bachler *et al.* 2010, Tøttrup *et al.* 2012). In the future this will allow studies of migrant population dynamics to assess, with higher certainty, the degree to which variation in demographic parameters can be attributed

to environmental conditions along the migratory route and to disentangle causes and effects between correlation such as arrival time and reproductive success. This will be an important improvement in furthering our understanding of the dynamics of long-distance migrants under future climate change.

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