

# The influence of climatic conditions in breeding grounds and migratory flyways on a subalpine Norwegian Willow Warbler (*Phylloscopus trochilus*) population

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Many European-breeding bird species wintering south of the Sahel region in Africa have been reported to be in decline since the 1970s. However, most studies focus on conditions local to the breeding sites as determinants of population change, despite the potential influence on populations during migration and over-wintering. To investigate the relative importance of climate at the breeding site and during migration and overwintering periods, we studied a Fennoscandian Willow Warbler (*Phylloscopus trochilus*) population that has been monitored in its subalpine breeding grounds in Norway over the last 45 years (1967–2011). The long-term trend for our population follows a quadratic trend, showing a marked period of decline after the late 1960s, followed by some increase during the last two decades. The most parsimonious model of the annual change in the Willow Warbler population is obtained by combining the mean June temperature and the Sahel spring index. The annual rate of change in the Willow Warbler population was positively related to summer temperatures on the breeding grounds and positively related to Sahel precipitation, although the statistical support is not very strong. Our study shows that climatic conditions at different stages of the annual cycle have influence on the population change. However, the on-going habitat changes in tropical Africa most likely have negatively affected on the overall population size of the Willow Warbler. This habitat loss may prevent many long-distance migratory bird species from returning to their former population peaks, even though the impact from the recent Sahelian drought may have culminated.



## 1. Introduction

Around one quarter of the European-breeding bird species migrate to sub-Saharan Africa to over-winter. However, the population size of many of these species shows strong temporal variation; during the period 1970–2005 almost 60% of these species have been reported in decline (Sanderson *et al.* 2006, Zwarts *et al.* 2009, Thaxter *et al.*

2010). Their population dynamics may be controlled by factors such as food and nest site availability, competitors, predators, disease and harsh weather. The key factors that limit the population size, and the mechanisms that are driving the population dynamics, are, however, often poorly understood (Murdoch 1994, Rodenhouse *et al.* 2003, Newton 2004). Many studies of migratory bird species still seem only to focus on events associ-

ated with the breeding grounds, or how climate change correlates with phenology, and only a few have been devoted to the interaction between large-scale climatic patterns and population dynamics (Jonzén *et al.* 2002). However, in addition to conditions at the breeding grounds, long-distance migratory species, such as the Willow Warbler (*Phylloscopus trochilus*) in Fennoscandia, may also be affected by the weather conditions during their migration and/or at their wintering grounds, e.g., drought in their African winter quarters (Peach *et al.* 1991, Payevsky 2006), or abundant winter rainfall in North Africa which trigger an earlier start of the northward migration of sub-Saharan wintering species (Saino *et al.* 2007). Occasionally birds can also suffer substantial mortality due to severe storm events during their migrations, or have great mortality losses due to “winter-like” conditions just after their arrival to their breeding grounds (Newton 2006). Marra *et al.* (1998) in their Seasonal Interaction Hypothesis, point out the importance of seasonal interactions on the population dynamics of migratory bird species. According to their hypothesis, the key is to determine which events produce the strong carry-over effects by examining the seasonal interactions. This may also reveal the cause of the population decline reported for so many European-breeding bird species.

Climate clearly plays an important role in determining bird population trends, as it affects the timing of migration, the condition of birds during migration, and the food resources available during their breeding-, migrating- and wintering phases (Silllett *et al.* 2000, Jonzén *et al.* 2002). In addition to local weather conditions at the breeding grounds, where long-distance migrants in northern Europe only stay for about four months, the birds have to cope with conditions in their tropical wintering areas where they may stay for about half the year, as well as those to which they are exposed during their spring and autumn migrations, e.g. storm events (Newton 2006). Just a single serious event during one of these phases in their annual cycle may have a substantial effect on the population size; for example Webster & Marra (2005) have shown that winter habitats may be a limiting factor for long-distance migrants because poor condition during that part of the life cycle affects the breeding strategies of individual birds.

The African Sahel is an important transition zone for bird species migrating to and from Europe over the arid Sahara, between their wintering areas in more humid tropical habitats further south and their breeding grounds to the north. In the 1970s and 1980s the Sahel region suffered a severe dry period, causing a slow, continuous desertification (Thiollay 2006, Wilson & Cresswell 2006). The rainfall recently seems to have returned to levels slightly below the 1898–1993 average, but with high annual variability (Dai *et al.* 2004). The recovery from this great Sahelian drought has also been monitored by analyses of satellite images which show an increase in greenness over large parts of the Sahel since the early- and mid-1980s, when the peak of this Sahelian desiccation was seen (Herrmann *et al.* 2005). Some significant reductions in long-distance migrant species from the 1960s towards the 1990s were found to be correlated with changes in rainfall in their African winter quarters (Winstanley *et al.* 1974, Peach *et al.* 1991, Boehning-Gaese & Bauer 1996), and lately more stable situations, and even some recoveries, after the termination of this long dry spell are observed for some of the same African migrants (e.g., Clark *et al.* 2002, Thingstad *et al.* 2006, Karlsson 2007, Balmer *et al.* 2013).

The relative importance of conditions in breeding grounds, migration routes and wintering quarters in determining population trends needs further research (Sanderson *et al.* 2006, Newton 2010). Our contribution here originates from a study lasting 45 years, in which we have monitored the breeding bird community in a subalpine woodland area in central Norway. The predominant species in this low-productive and species-poor bird community is the insectivorous Willow Warbler. Willow Warblers breed for the first time at an age of one year, and have a longevity generally of 1–4 years (Bairlein 2006). However, the reported maximum longevity achieved by a wild Willow Warbler can be as high as 11.8 years (Fransson 2010). A study from Britain found that youngsters had a 24% change of surviving to return to breed, and adults had a survival rate of 32% (Siriwardena *et al.* 1998).

Our breeding population belongs to the subspecies *P. t. acredula*. These warblers mainly leave Fennoscandia in August, and migrate southwest to their wintering grounds in Africa south of the

Sahel, from Cameroon and DR Congo throughout East and South Africa (Bairlein 2006); Norwegian birds seem mainly to occur north of the Gulf of Guinea during the winter seasons (Bakken *et al.* 2006). Thus they have to cross the vast Sahara desert on a non-stop flight before they enter better conditions in the Sahel belt. After 5–6 months in their African winter quarters, the Willow Warblers start their northward migration in late February or March. The birds again cross the Sahara before reaching their Fennoscandian breeding grounds mainly in May or early June.

This study explores some of the climatic factors that may drive the dynamic pattern of the breeding Willow Warbler population we have monitored back to the 1960s focussing on both local conditions in the breeding grounds, and in the Sahel. Such knowledge may be of considerable importance when we try to interpret possible effects of local and global climate patterns, or more long-term climatic changes, on migratory birds.

## 2. Material and methods

### 2.1. Study area

The study area is located in a subalpine birch (*Betula pubescens* ssp. *czerepanovii*) woodland in Budalen (62°45' N, 10°30' E), central Norway. The breeding population has been monitored in a study plot of 24 ha located 800–880 m a.s.l. in the “upland downy birch woodland subzone” (Moen 1999) with a scattered shrub layer dominated by juniper (*Juniperus communis*).

### 2.2. Field data sampling

The study plot was a fixed transect of 2.4 km × 100 m which has been surveyed in June 1967–2011 (by Olav Hogstad 1967–2004, Per Gustav Thingstad 2005–2011) in accordance with the international recommendations for the standardized mapping method (~10 censuses, chiefly in early morning dispersed over 3–4 survey periods, cf. Bibby *et al.* 1992), thus given us annual territory numbers of all the local breeding bird populations; amongst these the Willow Warbler is the dominant species. The number of territories within the transect were

recorded during the most active territory display period (in June in this subalpine habitat) and used as a proxy of population size. Since territories (a cluster consisting of at least 3 records from a least two different survey periods) may be large in relation to the transect width, territories that were not completely within the transect were recorded as the fraction of the whole territory that fell within the transect. Note that data from 1998 and 1999 are missing.

### 2.3. Climatic parameters

The impact of annual variations in the weather conditions during the breeding season in Budalen was determined from measurements of temperature, precipitation and snow cover at nearby meteorological stations. We used the mean June temperature, and total June precipitation as hypothesised explanatory variables, since June covers the period when the birds arrive and nest at the local breeding ground. Further we added the mean temperature and precipitation in July, since that month cover the last part of the breeding cycle including the period the birds stay in the vicinity of their nesting area. However, those July variables showed no relation to the varying annual territory numbers. We also included a snow melt variable in the candidate models to account for inter-annual differences in vernal phenology. This variable is defined as the first day of the spring with snow cover below 50%. In our study area, the data from nearby meteorological stations have not revealed significant changes in the mean temperature and precipitation neither in June nor in July, although the timing of snow melt has been weakly delayed (linear regression: slope = -0.22, SE = 0.11,  $R^2 = 0.07$ ,  $F_{1,41} = 4.16$ ,  $p = 0.048$ ), during the 45 years study period.

During the other phases of their annual life-cycle, the Willow Warblers are under the influence of climatic conditions on their migrating route and in their wintering areas. Even though trans-Saharan songbirds move on rapidly, they are dependent on finding stops to feed during their migrations (Newton 2010). The feeding conditions may be explained by global climatic indexes, e.g., the Sahel rainfall index, indicates relative precipitation in the Sahel region. Therefore, this index was

Table 1. Summary of the local-scale (breeding season) and large-scale variables (migration and wintering) used in candidate models of willow warbler population size.

	Variable	Unit
<i>Local-scale</i>		
Summer	June mean temperature	°C
	July mean temperature	°C
	June precipitation	mm
	July precipitation	mm
	Snow melt	Date
<i>Large-scale</i>		
Spring	Sahel spring (same year)	Index
Winter	Sahel winter (November–February)	Index
Annual	Sahel annual (previous calendar year)	Index

used as the biannual migratory passages over the Sahel region are assumed to be the most climatically-severe stages of the annual cycle of the Willow Warbler, exclusive the breeding season (e.g., Zwarts *et al.* 2010). The Sahel precipitation anomalies for 1966–2011, and the indices for spring (March–April) and autumn (September–October), as well as for the wintering period (November–February), were extracted from the Joint Institute for the Study of the Atmosphere and Ocean (<http://jisao.washington.edu/data/sahel/>), were used as hypothesised independent variables. The Sahel index is estimated as the mean monthly precipitation deviation in cm with respect to the average over the period 1950–79; positive values denote a higher precipitation than “normal”. However, the index for the autumn was highly correlated with the annual index ( $r = 0.794$ ), and therefore skipped. Accordingly, the annual index from the previous calendar year were used as hypothesised an independent variable, and the spring and winter indices from the current year, to reflect the conditions encountered by the breeding population during their migrations (and wintering) in the given year.

**2.4. Statistical analyses**

Due to the low survival rate of the Willow Warbler (reported to be 0.32 for adult and 0.24 for first-year for birds breeding in British farmlands (Siriwar-

dena *et al.* 1998)) the individual survival and reproduction can also be considered to operate on an annual scale. The rate of change in the Willow Warbler population size (number of territories) from one year to the next was analysed using Gaussian family generalised linear models (in R 2.15.2; R Core Team 2012), of the form shown in equation 1. Gaussian family models were used in place of Poisson family models since the response variable was not integer.

$$\ln(N_{t+1} / N_t) = \ln(N_t) + \text{climatic variables} + \text{intercept} + \text{error} \tag{1}$$

The dependent variable was the annual rate of change  $[\ln(N_{t+1} / N_t)]$ , and candidate models were developed using the independent variables listed in Table 1. The most parsimonious model was selected on the basis of minimum Akaike’s Information Criterion (AIC), from a model set ranging from the full model including all candidate variables (but not interactions), to the null (intercept-only) model. Model averaging was performed across all models to estimate the relative importance of the different independent variables, using the R package glmulti (Calcagno 2013). Temporal autocorrelation functions were also computed for

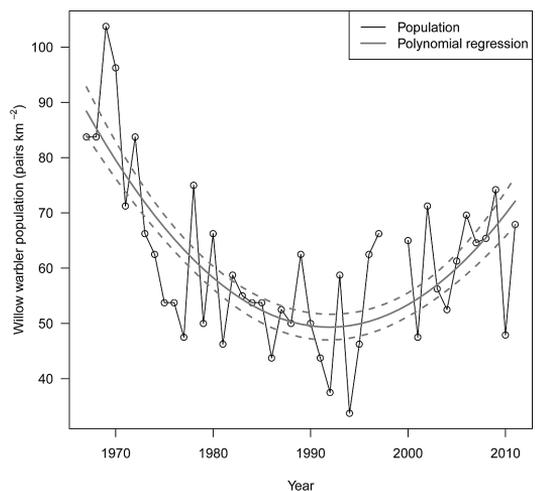


Fig. 1. Population of Willow Warblers recorded at Budalen. The observations are shown by points joined with black line, as the population estimate in the study area. The solid grey line shows the fitted quadratic regression, and dashed grey lines show the standard error of the fit.

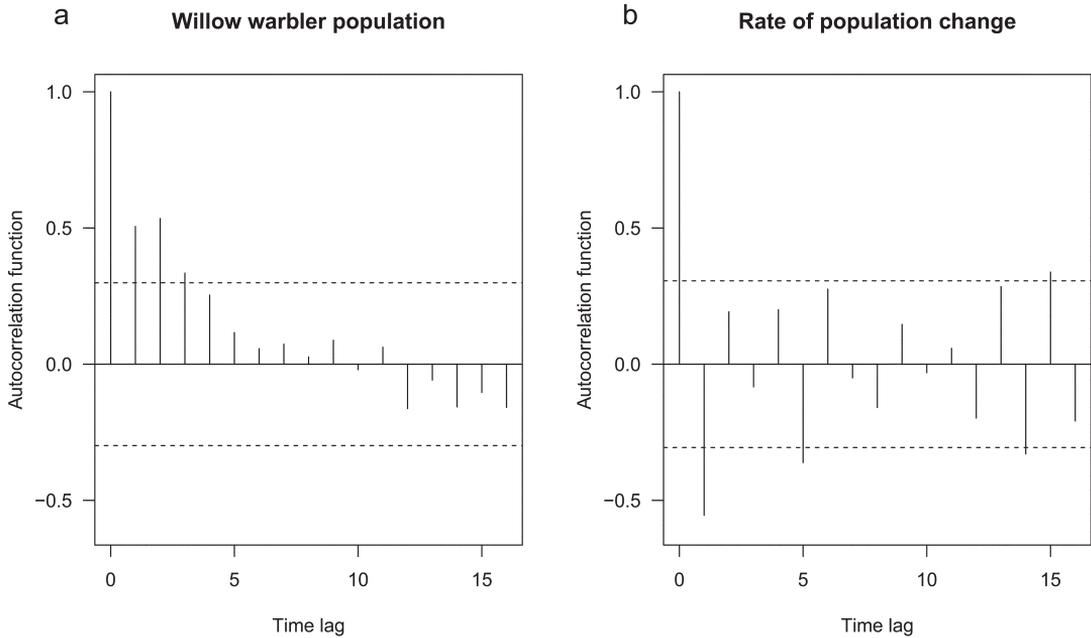


Fig. 2. Autocorrelation functions for the Willow Warbler population density (a), and the rate of change in the population density (b). The vertical lines show the correlation coefficient (y value) of the population with itself lagged by x years. The dotted horizontal lines are 95% confidence bands for zero autocorrelation.

both the Willow Warbler population and the rate of change of the population to assess the link between years in determining the population dynamics.

### 3. Results

#### 3.1. The population pattern of the Willow Warbler

The Willow Warbler population at Budalen decreased from between 20 and 25 territories in the late 1960s to around 10 and 15 during the 1990s, before recovering to about 15–16 in 2005–2011 (Fig. 1). This population trend showed a strong fit to a quadratic regression ( $R^2 = 0.52$ ,  $F_{1,40} = 8.9$ ,  $p = 0.005$ ), with a minimum in the early 1990s.

The Willow Warbler population size showed a positive autocorrelation with one, two and three year time lags (Fig. 2a), indicating that the population size was linked to the size in the three previous years. The rate of change in the Willow Warbler population showed a negative correlation at the one year time lag (Fig. 2b), indicating that a population increase in one year tended to be associated with a decrease in the following year.

#### 3.2. Influence of climatic variables on the Willow Warbler population

The most parsimonious model of the annual change in the Willow Warbler population included local mean June temperature, and the Sahel spring index. The June temperature was included in the two most parsimonious models (Table 2), whilst the annual Sahel index was included in the second most parsimonious model. However, the model including only the natural logarithm of the previous year's population size also had relatively high support (Table 2). 57% of the evidence base supported the inclusion of June temperature and 49% of the evidence base supported the inclusion of the Sahel spring index as predictors of the Budalen Willow Warbler population (Table 3). The additive effects of local June temperature and Sahel wetness in the most supported model are shown in Fig. 3. Assuming a population of 59 pairs (the median over the study period at the Budalen study site), for the average June temperature of 10.3°C, an increase in the Willow Warbler population can be expected when the Sahel index is positive (wet), and a decrease in the Willow Warbler population when the Sahel index is negative (dry).

Table 2. AIC model selection table for the change in the willow warbler population. The representation of a parameter in that candidate model is shown by 1 in the respective column. The model complexity ( $K$ ) is shown along with the AIC value and the difference between the model AIC value and the most parsimonious model's AIC value. Models are ordered with the most parsimonious at the top and only the 20 models with the most support are presented. The log initial population size and intercept were included in all candidate models.

June temp.	June prec.	Snow thaw	Sahel spring index	Sahel autumn index	Sahel annual index	$K$	AIC	$\Delta$ AIC
1	–	–	1	–	–	5	–7.27	0
1	–	–	–	–	1	4	–7.21	0.06
1	–	–	–	–	–	5	–6.49	0.78
–	–	–	–	–	–	3	–6.31	0.96
1	–	–	1	–	1	6	–6.23	1.04
1	1	–	1	–	–	6	–6.16	1.11
–	–	–	1	–	–	4	–6.13	1.13
1	1	–	–	–	–	5	–6.02	1.24
–	–	–	–	–	1	4	–6.02	1.25
1	–	–	–	–	1	5	–6.02	1.25
–	1	–	–	–	–	4	–5.85	1.42
–	1	–	1	–	–	5	–5.80	1.47
1	1	–	–	–	–	6	–5.68	1.59
1	–	–	–	–	1	5	–5.65	1.62
–	1	–	1	–	1	6	–5.59	1.68
–	–	–	1	–	1	5	–5.51	1.76
1	–	–	1	1	–	6	–5.48	1.79
–	1	–	–	1	–	5	–5.45	1.82
1	1	–	1	–	1	7	–5.44	1.83
1	1	1	–	–	–	6	–5.42	1.85

Table 3. Model-averaged effects shown in order of importance.

	Estimate	Unconditional variance	No. models	Importance	$\pm$ (95% CI)
Intercept	2.431	0.348	64	1	1.196
$\ln(N_t)$	–0.632	0.022	64	1	0.298
June temperature	0.019	0.001	32	0.571	0.047
Sahel spring index	0.073	0.011	28	0.494	0.210
June precipitation	–0.001	0	32	0.456	0.002
Snow melt	0	0	32	0.326	0.003
Sahel autumn index	0.004	0	20	0.246	0.019
Sahel annual index	0.007	0	13	0.221	0.028

## 4. Discussion

### 4.1. Willow Warbler dynamics and seasonal interactions

The trend for our Willow Warbler population, recorded over a 45 year study period, demonstrated a strong quadratic trend, with a steep declining phase from the late-1960s to the late-1980s fol-

lowed by a phase with some increase starting during the 1990s. In Sweden there are two subspecies breeding, *trochilus* in the southernmost provinces and *acredula* in the boreal central and northern parts. These two subspecies show different trends; *trochilus* is still declining while *acredula* is not (Svensson 2004), and the Willow Warbler population at Ammarnäs in Swedish Lapland shows the same recently more stable pattern (www.luvre.

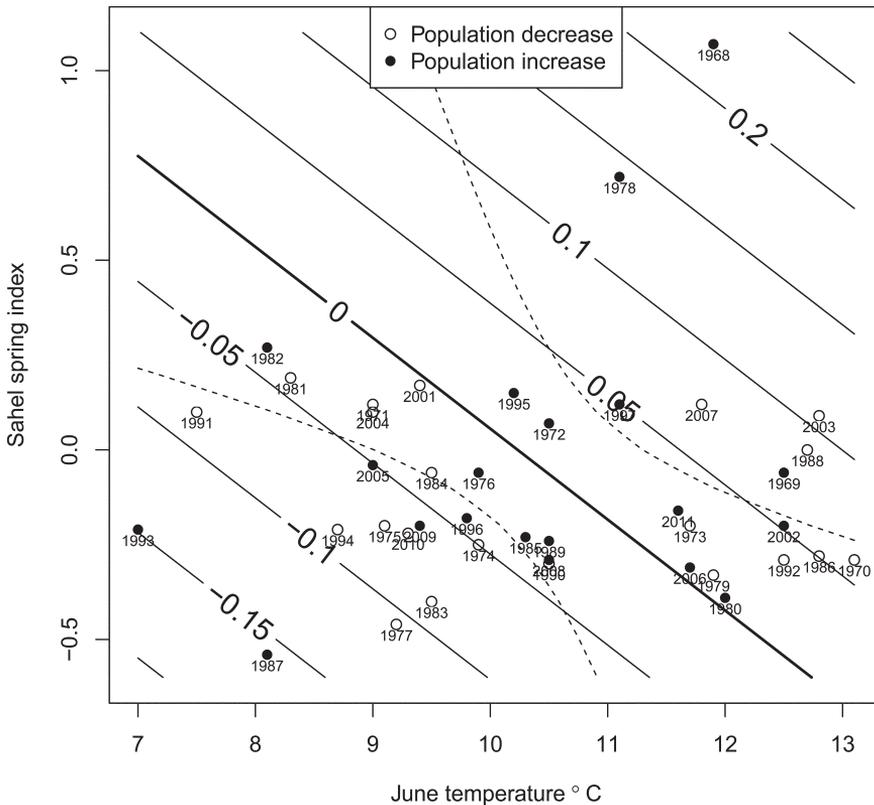


Fig. 3. Contour plot showing the predicted rate of change (back transformed) in the Willow Warbler population (labelled contours) for a given mean June temperature at the breeding ground (x axis) and a given Sahel spring index (y axis). Predictions are estimated for the median previous-year's population size over the study period (59 pairs). The contour line of 0.1 indicates the conditions at which the population can be expected to increase by 10% and the contour of  $-0.1$  a decrease of 10%. The dashed lines show the standard error around the contour of stable population size. Annual variation in June temperatures and Sahel spring indices are shown, labelled by year. Solid points show years for which the population increased (or remained stable), and open points years for which the population decreased.

org/bjorkfaglar.htm), indicating that most of the Fennoscandian Willow Warbler populations (at least of *acredula*) are undergoing recovery from the great Sahelian drought. The same pattern is reported from UK, where the Willow Warbler population still show significant declines in south and east England, while there is slight increase within the populations in north and west England, as well as in Scotland and Ireland (Morrison *et al.* 2010), which suggest that variation in the quality of their breeding habitat has a significant contribution on the recent population changes (Morrison *et al.* 2013), while difference in migration routes and wintering areas might be responsible for some of

the distinction between the two subspecies in Sweden (Svensson 2004), environmental changes in Africa on the region scale can also create such pattern (Morrison *et al.* 2010). However, the situation even for these “recovered” populations is still far below the former levels recorded in the 1960s and early 1970s.

Many studies provide indications for population changes to a large degree being associated with variations in survival (cf. Siriwardena 1998). This is also reported to be the case for the Willow Warbler (Peach *et al.* 1995). Still it might be likely that other aspect such as demography and breeding success are at least equally important as drivers for

the population sizes. Success in one period affects success in the next, as seen in the year-to-year changes in the numbers of breeding pied flycatchers which were associated with the previous year's nesting success (Virolainen 1984, Thingstad *et al.* 2006). However, these topics are outside the scope for this paper, and are only indirectly measured as the varying numbers of annually breeding warblers in our study transect.

Our data show that both local conditions (the mean temperature during June) and climatic conditions during the spring migration across the Sahel (Sahel spring index) contribute to determining the annual rate of change in this Willow Warbler population. Surprisingly the annual Sahel index did not feature in the most supported models. The wet season in the Sahel coincides with the breeding period for the Willow Warbler, thus the Sahel is at its driest for the spring migration. This may explain the support for the spring precipitation in the Sahel being a key determinant of the Willow Warbler population change: any increase in precipitation for the northward migration should increase the survival and condition of migration birds. The additive effect of the Sahel precipitation index and the local summer temperature suggest that good weather conditions at the Fennoscandian breeding grounds potentially can offset at least some of the negative impact of drier Sahel conditions to maintain the population size. However, our data should be interpreted with caution, since the support for the local June temperatures and Sahel spring precipitation as predictors of the breeding population was not high at 57% and 49% respectively.

Our data support the hypothesis that long-distance migratory species populations, such as the Willow Warbler in Fennoscandia, are affected by the weather conditions during their migration and at their wintering grounds, e.g., drought in their African winter quarters (Peach *et al.* 1991, Payevsky 2006), or abundant winter rainfall in North Africa which trigger an earlier start of the northward migration of sub-Saharan wintering species (Saino *et al.* 2007). Many studies of migratory bird species still seem only to focus on events associated with the breeding grounds, or how climate change correlates with phenology, and only a few have been devoted to the interaction between large-scale climatic patterns and population dy-

namics (Jonzén *et al.* 2002). Marra *et al.* (1998) in their Seasonal Interaction hypotheses, pointed out the importance of seasonal interactions on the population dynamics of migratory bird species. According to their hypothesis, the key is to determine which events produce the strong carry-over effects by examining the seasonal interactions. By combining climatic parameters from the breeding ground and global climatic indexes (the Sahel rainfall index) in our study, we achieved to disclose some of this interaction for our Fennoscandian Willow Warbler population. However, also other weather conditions might cause irregular high mortality losses during the birds' migration, in particularly severe storm activities (Butler 2000, Newton 2006).

#### 4.2. Habitat degradation

Some of the reasons for many bird species decline, such as our migratory species, are not only related to climatic events. An on-going serious threat is connected to changes in land use, e.g., drainage of wet grassland and reduced livestock grazing, which have given a continuous decline in insect production in many European countries (e.g., Pettersson *et al.* 1995, Newton 2010). The Willow Warbler is one of the species which has declined rapidly since the 1980s in most of Britain, in particularly in the southern parts (Morrison *et al.* 2010). However, for some of the declining trans-Saharan migratory bird species, particularly habitat generalists like the Willow Warbler, it is hard to imagine that the main causes of their negative trends should be found within the Fennoscandian breeding habitats. As Fuller *et al.* (2005) claimed pressure on migration and during winter, due to land-use changes and/or increase hunting, might be responsible for their reduction as well as reduced habitat quality at their breeding grounds. In fact, near the equator in Africa more than 30% of the forest was lost between 1970 and 2000, and cultivated land increased by 21%, resulting in increased use of irrigation, loss of wetlands and more use of pesticides (UNEP 2002). Although we can see some recent increase in the size of our breeding Willow Warbler population, the influence of various encroachments on some essential habitats in recent decades, not least in Africa

(Zwarts et al. 2010, Morrison et al. 2010, 2013), makes it hard to see a situation in the foreseeable future which can allow the total population size to return to the levels of the 1960s and early-1970s. Nonetheless, the Willow Warbler seems to be not as severely affected as many other bird species, e.g., some raptors, waterbirds and more specialist passerines (Payevsky 2006, Sanderson et al. 2006, Thiollay 2006, Zwarts et al. 2010, Newton 2010).

### 4.3. Concluding remarks

In their Seasonal Interaction Hypothesis (SIH), Marra et al. (1998) pointed out the importance of seasonal interactions on the population dynamics of migratory bird species. According to SIH, the key is to determine which events produce strong carry-over effects by examining the seasonal interactions. Our study shows that the strongest carry-over effects for the Willow Warbler are related to the local mean temperature in June at their breeding grounds, and in addition the Sahel drought conditions that confront the birds during their spring migration to Europe. Apart from long-term changes in the rainfall in the Sahel, we have no evidence of a more long-lasting change in our Willow Warbler population that can be related to climate change at the breeding grounds where no warming has been observed during the last 45 years. However, relatively warm summers in the typically cool Fennoscandian subalpine breeding grounds, could to some degree compensate for drier conditions during the spring migration in maintaining the short term population size. On the other hand, the on-going habitat alternations due to large human population growth, not at least in equatorial parts of Africa, may make it hard for many long-distance migratory bird species, including the Willow Warbler, to return to their pre-Sahelian drought population levels in the 1960s, even given a cessation of the worst dry spell period.

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### Klimatets inverkan på en subalpin lövsångarpopulation i Norge

Många europeiska häckfågelarter som övervintrar söder om Sahelregionen i Afrika har uppvisat minskande bestånd sedan 1970-talet. Trots att förhållanden under flyttning och övervintring potentiellt har en stor inverkan på populationers dynamik, har de flesta studier koncentrerat sig på lokala förhållanden i häckningshabitatet. Vi har i 45 års tid (1967–2011) följt med en subalpin lövsångarpopulation (*Phylloscopus trochilus*) i mellersta Norge. Utgående från de observerade fluktuationerna i data har vi försökt klarlägga klimatets relativa betydelse under häckning, flyttning och övervintring.

Populationen uppvisade en kvadratisk trend, med en skarp minskning från 1960-talet, med botten i början av 1990-talet och sedan en ökning fram till 2011. Den bästa modellen för populationens tillväxt kombinerade medeltemperaturen i Juni på häckningsområdet med nederbördsindexet i Sahel samma vår, men de statistiska sambanden med klimatet var svaga. För båda klimatvariablerna var sambandet med den årliga populationstillväxten positivt, d.v.s. varm sommar på häckningsområdena och relativt mycket nederbörd i Sahel gagnade lövsångarna.

Vår studie stöder tanken att klimatet påverkar denna migrerande arts populationstillväxt under olika skeden av årscykeln. Det är troligt att de pågående habitatförändringarna i tropiska Afrika dessutom har haft en negativ inverkan på lövsångarens populationsstorlek under vår studieperiod. Minskningen av lämpligt habitat kan förhindra långdistansflyttare från att nå samma populationstätheter som på 1960-talet, även om inverkan av senaste torrperiod i Sahel kan tänkas vara över.

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