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Research Paper

**Effects of spring weather on laying dates, clutch size, and nest survival of ground-nesting passerines in abandoned fields**

Viktoria Grudinskaya1,2, Stanislav Samsonov3, Elena Galkina1, Alexander Grabovsky1, Tatiana Makarova1, Tatiana Vaytina1, Svetlana Fedotova1 and Dmitry Shitikov1

1Moscow Pedagogical State University, 2Zoological Museum of Moscow State University, 3A. N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Science

**ABSTRACT.** Weather conditions have a significant impact on the life-history strategies of birds. The mechanisms by which weather variability drives demographic processes in boreal passerines have been investigated insufficiently. We examined the effects of spring weather on first egg-laying dates, clutch size, and nest survival of Booted Warbler (*Iduna caligata*) and Whinchat (*Saxicola rubetra*) breeding in abandoned agricultural fields in the north of European Russia in 2005–2019. We used general linear models to express first egg-laying dates and clutch size and program MARK to model nest survival as a function of weather variables. Our results demonstrated that variability of May precipitation and averaged daily temperature are important drivers of first egg dates, clutch size, and nest survival in both species. The first egg dates of Booted Warblers and Whinchats were determined primarily by the May temperature: the warmer the weather in May, the earlier the laying dates. Taking into account the effect of the first egg date, the clutch size of Booted Warblers strongly depended on the May averaged daily temperatures, whereas the clutch size of Whinchats was weakly affected by May precipitation. The spring weather had a strong impact on Booted Warbler and Whinchat nest survival, potentially by influencing the activity of nest predators. We suggest that years with a coincidence of low spring precipitation and temperature are the “bad” years for reproduction of boreal grassland birds.

Les effets du climat printanier sur les dates de ponte, la taille des couvées et la survie des nids de passereaux nichant au sol dans des champs abandonnés

**RÉSUMÉ.** Les conditions météorologiques ont un impact majeur sur les stratégies de reproduction des oiseaux. Les mécanismes par lesquels la variabilité météorologique détermine les processus démographiques des passereaux des régions boréales ont été insuffisamment examinés. Nous avons examiné les effets du climat printanier sur les dates de première ponte, la taille des couvées et la survie des nids d’hypolaïs bottées (*Iduna caligata*) et de tariers des prés (*Saxicola rubetra*) qui se reproduisaient dans des champs agricoles abandonnés au nord de la Russie européenne de 2005 à 2019. Nous avons utilisé des modèles linéaires généraux pour exprimer les dates de première ponte et la taille des couvées et le programme MARK pour modéliser la survie des nids comme une fonction des variables météorologiques. Nos résultats indiquent que la variabilité des précipitations en mai et les températures moyennes quotidiennes sont des éléments déterminants pour les dates de première ponte, la taille des couvées et la survie des nids dans les deux espèces. Les dates de première ponte d’hypolaïs bottées et des tariers des prés étaient principalement déterminées par la température en mai : plus le temps était chaud, plus la ponte était précoce. En tenant compte de l’effet de la date de première ponte, la taille des couvées d’hypolaïs bottées dépendait fortement des températures quotidiennes moyennes en mai, alors que la taille des couvées de tariers des prés n’était que peu affectée par les précipitations de mai. Le climat printanier impactait fortement la survie des nids d’hypolaïs bottées et de tariers des prés, potentiellement en raison de son influence sur l’activité des prédateurs des nids. Nous suggérons que les années lors desquelles les précipitations et les températures printanières sont faibles devraient être considérées comme des “mauvaises” années pour la reproduction des oiseaux des prairies boréales.

**Key Words:** abandoned fields, Booted Warbler, clutch size, first egg laying date, nest survival, spring weather, Whinchat

**INTRODUCTION**

Weather conditions have a significant impact on the life-history strategies of birds (Dunn and Winkler 2010, Andreason et al. 2020). In the response to the effects of global climate change, the influence of climatic variation on breeding productivity has recently attracted increasing attention (Winkler et al. 2002, Ockendon et al. 2013, Imlay et al. 2018). Both long-term and stochastic changes in temperature and precipitation may have fundamental consequences for avian reproduction. Many studies have demonstrated that stochastic weather variability can strongly influence different components of bird productivity such as the first egg date (Bowers et al. 2016, Duursma et al. 2018, Shave et al. 2019), clutch size (Rotenberry and Wiens 1991, Skagen and Yackel Adams 2012), and nest survival (Skagen and Yackel Adams 2012, Conrey et al. 2016).

Avian breeding productivity and its components may depend on daily or seasonal weather parameters. In the latter case, both average weather characteristics over a given season and discrete
weather events can influence avian breeding success (Skagen and Yackel Adams 2012). Local weather conditions preceding the onset of egg laying (spring weather) often have a decisive influence on avian breeding productivity and its components (Sokolov 2000, Weatherhead 2005, Martin et al. 2017, Zuckerberge et al. 2018, Londe et al. 2020). One of the well-documented effects of warmer spring temperatures is a change in the first egg dates which may shift in response to earlier springs (Dunn and Winkler 2010, Imlay et al. 2018, Shave et al. 2019). Additionally, clutch size could be related to average temperature or precipitation at the onset of egg formation (Skagen and Yackel Adams 2012, Conrey et al. 2016). Extremely cold or hot conditions during the early breeding season as well as heavy rainfall or prolonged droughts during this period could also be associated with lower rates of nesting success (Zuckerberg et al. 2018). Spring weather variability can directly affect nest survival through mortality of clutches during spring cold snaps or storm events (Skagen and Yackel Adams 2012, Martin et al. 2017), as well as indirectly through changes in the number or behavior of predators (Morrison and Bolger 2002), or shifting in nesting microhabitats (Martin 2001). Moreover, spring weather data may provide a means of obtaining information about the character of the future breeding season, which may help birds to maximize their lifetime production of young (Järvinen and Väisänen 1984).

Spring weather can be of particular importance to breeding productivity in regions with highly variable climate (Järvinen 1989, Mahony et al. 2006, Collister and Wilson 2007, Artemyev 2013). In this case, significantly deviating from the average weather parameters can be reflected in “bad” or “good” breeding seasons (Järvinen and Väisänen 1984). Components of bird productivity can decrease to almost zero values in “bad” years, and they can be many times higher than the average for a number of years in “good” years (Morrison and Bolger 2002). For example, populations of Pied Flycatcher (Ficedula hypoleuca) breeding at the northern edge of their range, where annual temperature variation was high, showed greater interannual variation in clutch size, hatching success, and fledging success compared to southern populations where temperatures were more predictable (Järvinen 1989, Artemyev 2008, 2013). This mechanism of regulation of annual productivity is well known for northern latitudes (Järvinen 1989, Mahony et al. 2006, Martin et al. 2017) and arid regions (Morrison and Bolger 2002, Conrey et al. 2016, Ruth and Skagen 2018).

Birds of open grasslands are more susceptible to extreme weather compared to forest species (Zuckerberg et al. 2018). Grassland birds in western and central Europe are experiencing population declines primarily driven by agricultural intensification and changes in land use (Bowler et al. 2019). In European Russia the differentiation of habitats takes place, which consists of the alternation of extensive abandoned lands with increasingly intensively cultivated fields. The numbers of meadow and shrub meadow passerines such as Sylvia warblers, Booted Warblers (Hippolais caligata), and Whinchats (Saxicola rubetra) are stable in abandoned lands and strongly decreased in regions with intensively cultivated fields (Sviridova et al. 2020). Climate change poses additional threats of unknown magnitude for the grassland birds (Bowler et al. 2019). To evaluate the efficacy of bird conservation in a changing climate, it is critical to understand the effects of weather on bird demography. The responses of grassland species to annual weather variability may yield insights into how birds might respond to future changes in climate (Skagen and Yackel Adams 2012).

Here, we used a 15–year dataset to determine the impact of spring weather variability on breeding productivity of Booted Warbler and Whinchat inhabiting abandoned agricultural fields in Russky Sever National Park (north of European Russia). Whinchat have undergone a massive decline in Europe over the last decades and are currently still decreasing (Henderson et al. 2014, Fay et al. 2021). In European Russia, the density of Whinchats remains stable in most localities (Sviridova et al. 2020). Booted Warblers are a common widespread passerine species of steppe and forest-steppe regions of European Russia East, West Siberia, and Kazakhstan. By the end of 20th century, the species range has expanded through the North-West regions of Russia (Shitikov et al. 2012, 2014). Previously, we found that Booted Warbler and Whinchat nest survival in the abandoned fields of Russky Sever National Park varied annually and decreased to less than 5% in “bad” years (Shitikov et al. 2012, 2015). The main reason for low nest survival was predation by the common adder (Vipera berus) and Hooded Crow (Corvus cornix), which allowed us to assume that changes in nest predators’ activity and species composition had a major impact on annual variability of nest survival of Booted Warblers and Whinchats (Shitikov et al. 2012, 2015, Samsonov et al. 2018). We found significant inter-year variation in the clutch size of Whinchats (Shitikov et al. 2015) and no variation in Booted Warbler clutch size (Shitikov et al. 2012).

The goal of this study was to examine the effect of spring weather on reproductive parameters of Booted Warblers and Whinchats. We quantified the first egg-laying dates, clutch sizes, and nest survival of both species and modeled the relative effect of temperature and precipitation variables in spring on different breeding parameters. Given the high annual variability of spring weather in the north of European Russia, we hypothesized that it may have a direct or indirect effect on most reproductive parameters of ground-nesting passerines in abandoned fields.

**METHODS**

**Study site and study species**

The study was carried out during 2005-2019 in abandoned fields in the southern part of the Russky Sever National Park near the Topornya village (59°46′N, 38°22′E). The study site was located in a large patch (> 700 ha) of open habitats including abandoned fields, meadows, small woods, and villages. Ruderal vegetation such as corn sow thistle (Sonchus arvensis), mugwort (Artemisia vulgaris), field thistle (Cirsium setosum), cow parsley (Anthriscus sylvestris), musk thistle (Carduus nutans), and couch grass (Elytrigia repens) occupied more than 90% of the study site. Plant cover height was 10–15 cm at the beginning of the breeding season (late May–early June) and reached 50–70 cm by the time of fledging (the first half of July). During the 15 years of our study, May temperature and precipitation varied widely (Fig. 1a). The 15-year averages were as follows (± SE): precipitation 59.0 ± 7 mm (range 15–101 mm); averaged daily mean temperature 11.5 ± 0.5°C (range 6.0–14.4°C). Total year precipitation varied from 465 mm in 2013 to 967 mm in 2009. There were not any statistically significant temporal trends in May temperature (LM, β= -0.01 ±0.12, 95% CI-0.26, 0.27) and precipitation (LM, β= -1.83±1.71,
Fig. 1. Annual variations in May weather parameters (a, the whiskers indicated 95% CI), first egg-laying dates (b, median ± 25–75 percentile), clutch size (c, mean ± SE), and nest-survival rates (d, annual overall nest survival ± SE) of Booted Warbler and Whinchat in abandoned fields of Russky Sever National Park, 2005–2019.

95% CI -5.53, 1.87). Precipitation and temperature values were obtained from the nearest weather station, located in Belozersk (60°02′N 37°47′E) 43 km away from our study site.

The Booted Warbler and Whinchat are widespread in open habitats in the north of European Russia. Booted Warblers spend the non-breeding period in India and arrive at breeding grounds in late May (Shitikov et al. 2014), while Whinchats winter in sub-Saharan Africa and arrive at breeding grounds in early May (Taylor 2018). Whinchats are an obligate ground-nesting species, whereas Booted Warblers nest both on the ground and at a height of 1–40 cm on plant shoots (sagebrush *Artemisia* spp., knapweed *Centaurea* spp.). Both species are typically socially monogamous and single-brooded.

Field methods
Fieldwork started each year between 15–25 May and lasted until 20–21 July. Nests of both species were located by observing behavior of adult birds and systematically searching all suitable breeding habitats. The total size of the nest-searching area within the study site varied from 250 ha in 2005 to 450 ha after 2012. Geographic coordinates of all nests found were obtained using Garmin GPS navigators. All nests were checked every 2–3 days except near the expected fledge date when they were visited on alternate days. During each nest check, we recorded the presence or absence of adults, the number of eggs or nestlings, and the nestling age. When hatching date was not known, the age of nestlings was estimated by comparing the degree of feather development with that of nestlings of known age. At the age of approximately 7 to 9 days old, nestlings were banded with an aluminum ring on one tarsus and a plastic color ring on both tarsi. Adults were captured using mist nets or spring traps and were ringed with an aluminum ring and individual combinations of colored plastic rings. Monitoring of individually marked fledglings and adult birds was used to determine the nest fates. We back-calculated the first egg dates from estimates of nestling age or hatching date (13 days of incubation starting with the penultimate egg). We excluded nests found on the day of fledging from the nest survival analysis since we had only one consecutive visit to these nests. Clutch size was calculated only for nesting attempts found before hatching because partial predation or mortality of nestlings can occur in both species. We excluded renesting attempts from laying date and clutch-size analyses.

A nest was considered successful if it produced at least one fledgling. If a nest was found empty around the expected time of fledging, we confirmed breeding success by locating marked fledglings and observing parents carrying food and being engaged...
in defensive behavior. On the contrary, a nest was considered unsuccessful if it was found empty or adult birds did not appear near the nest for two or more consecutive visits in a row. For such nests, we visually identified a probable cause of the failure. Unsuccessful nests included those that were depredated, abandoned with eggs, or failed as a result of some other cause, such as the death of nestlings for other reasons. Depredation was inferred from strong indicators such as the disappearance of eggs or nestlings from active, monitored nests before the expected date of fledging. Since 2016 we have used automatic motion sensor cameras (trail cameras) to fix predator species identity (see Samsonov et al. 2022 for detailed description of the camera study). The cameras were placed 0.4–1.2 m from the nest and camouflaged with vegetation. The cameras were placed > 1.5 m from the nests at the incubation stage and were moved closer after hatching to avoid nest abandonment. In total, cameras were installed at 80 Booted Warbler and 118 Whinchat nests. We used camera data to clarify the fate of the nests (depredation, abandoned by adults, starvation of nestlings, etc.).

Data analysis
We modeled daily nest-survival rates of focal species using robust nest-survival models in program MARK (Dinsmore et al. 2002). To limit the number of evaluated models, we applied a hierarchical model-selection procedure (Conroy et al. 2016). We started the analysis by creating a constant-survival model. Further, we continued with the time-dependent models including time of season and nest-age effects, since variation in daily nest-survival rates with nest age and time of season is common in grassland birds (Grant et al. 2005), including Booted Warblers and Whinchats (Shitikov et al. 2012, 2015). Time of season is the number of days after the day when the first nest was found (Dinsmore et al. 2002). Time-dependent effects with linear and quadratic terms were included in the analysis. A linear model assumes an increase or decrease in daily nest-survival rates with the advance of the breeding season or nest age, while a quadratic model assumes daily nest-survival rates are highest or lowest mid-season or near the hatching date (Grant et al. 2005). The linear terms were included along with the quadratic terms in the quadratic models. We created only univariate models (5 candidate models, Appendix 1) to choose the best supported base model because the age of the nest and the date can be correlated. We assumed that the May temperature and precipitation were the indicators of spring weather conditions (the pre-breeding and the beginning of breeding season). To evaluate the influence of spring weather on daily nest-survival rates we added variables containing May averaged daily mean temperature and May precipitation covariates to the best baseline models for each species. We tested for correlation among these variables and found no significant correlations ($r = 0.29, p = 0.45$).

To calculate annual overall nest-success rates, we constructed a separate set of nest-survival models containing a constant-survival model and a model with year effect. Annual overall nest-survival probabilities were then evaluated by raising the estimated daily nest-survival rates obtained from the year-effect models to survival probabilities were then evaluated by raising the estimated

To determine the relationship among first egg date, clutch size, and their respective explanatory variables we used general linear models. We constructed all the models in R 3.6.2 (R Core Team 2019) and used the dredge function in the MuMIn package (Bartoń 2020) for model selection. We used the log-transformed first egg date (the number of days after 1 May) as a dependent variable for laying-date analysis. Since laying date has a strong impact on clutch size in passerines (Winkler et al. 2014), we used the residuals from a regression of clutch size on egg-laying date as the dependent variable. We did not use a generalized linear model with Poisson distribution for the response variable because, as is typical for avian clutch-size data (Kerry and Royle 2016; Dillon and Conway 2018), our data were highly under dispersed, and a linear model proved to be more appropriate. We used May precipitation and May averaged daily mean temperature as fixed effects. We did not use the female identification number as a random factor in modeling, since most of females had only one record in the dataset. Only 10 females of Booted Warbler and 9 females of Whinchat had multiple years of data. We assumed multiple years for these 19 birds were independent observations. We used the dredge function in the MuMIn package (Bartoń 2020) to model selection.

We based our interpretations of the relative influence of all variables on (1) the $AIC_c$ values for models with and without a variable were compared, and (2) whether or not the confidence intervals (CI) spanned zero (Burnham and Anderson 2002). The best supported model was defined as that with the lowest $AIC_c$ with models separated by $AIC_c < 2$ deemed similarly well supported. The best model for each variable was used to compute the CI. Effects were considered strong if the 95% CI did not span zero, weak if the 90% CI did not span zero, and as having no relationship with the predictor variable if the 90% CI spanned zero (Skagen and Yackel Adams 2012).

RESULTS

Demographic parameters
During fifteen breeding seasons of the study, we located 624 Booted Warbler nests (24, 47, 40, 45, 39, 27, 38, 26, 47, 56, 57, 64, 35, 37, 42 from 2005 to 2019, respectively) and 634 Whinchat nests (20, 14, 30, 16, 15, 23, 53, 42, 72, 66, 55, 65, 76, 46, 41 from 2005 to 2019, respectively). The first egg dates were defined for 588 Booted Warbler and 578 Whinchat nests. Adequate information existed to determine the clutch size for 333 Booted Warbler and 345 Whinchat nests. Nest survival analyses were based on the sample of 500 nests monitored over 7244 exposure days for Booted Warblers and on the sample of 539 nests monitored over 6215 exposure days for Whinchats. The earliest first egg date in Booted Warblers varied from 29 May in 2019 to 8 June in 2008, and median first egg date varied from 3 June in 2016 to 13 June in 2008 (Fig. 1b). The median first egg date across all years (2005–2019) is 8 June. The median first egg-laying date of Booted Warblers significantly decreased across the 15-year study period ($\beta = -0.21 \pm 0.06, 95\% CI -0.32, -0.09$). The earliest first egg date in Whinchats varied from 13 May (2013, 2016, 2018, 2019) to 24 May in 2008, and median first egg date...
Breeding was successful in 316 nests (55.8% of the nests with known fate) of Booted Warbler and in 380 nests (62.9% of the nests with known fate) of Whinchat. A total of 250 nests of Booted Warbler and 224 nests of Whinchat failed during the study period. The fate was unknown for 58 Booted Warbler nests and 29 Whinchat nests. Predation was the major cause of nest failure, as 194 Booted Warbler and 159 Whinchat nests were depredated. The direct impact of weather conditions (a clutch was flooded, nests were overturned by the wind, or juveniles died of starvation during severe cooling) led to the failure of 7 Booted Warbler nests and 1 Whinchat nest. Another 29 Booted Warbler nests and 18 Whinchat nests were abandoned by adults for no apparent reasons, which also do not exclude the influence of weather conditions. Several nests (18 of Booted Warbler, 24 of Whinchat) were abandoned by adults after research manipulations (catching adults, installing cameras) and were excluded from the subsequent nest survival analysis. Since agricultural land cultivation in the research area has almost completely ceased, the impact of this factor was also low: only 2 nests of Booted Warbler and 3 nests of Whinchat failed due to plowing. The year-effect models were the top ranked for both species, while constant nest-survival models had $\Delta AIC_c = 61.67$ for Booted Warbler and $\Delta AIC_c = 21.31$ for Whinchat. Booted Warbler annual overall nest-success rates varied from 0.03±0.02 in 2008 to 0.82±0.09 in 2018, while Whinchat annual overall nest-success rates varied from 0.01±0.01 in 2008 to 0.86±0.09 in 2018 (Fig. 1d). There were non-significant temporal trends in daily nest-survival rates of both species across the 15-year study period (Booted Warbler $\beta = -0.01±0.01$, 95% CI -0.04, 0.02; Whinchat $\beta = -0.01±0.02$, 95% CI -0.03, 0.05).

### Impact of spring weather on first egg-laying date

The most parsimonious laying-date models for Booted Warblers included the May averaged daily temperature and a combination of May precipitation and averaged daily mean temperature (Table 1). May averaged daily mean temperature had a strong negative effect and May precipitation had no effect on Booted Warbler first egg date (Table 2). The most parsimonious laying-date models for Whinchats included both weather covariates also (Table 1). May averaged daily mean temperature had a strong negative effect and May precipitation had no effect on Whinchat first egg dates (Table 2).

| Model | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ Weight | $K$ |
|-------|---------|----------------|----------------|-----|
| **First egg-laying date**<br>Booted Warbler (n = 588 nests) | 678.85 | 0.00 | 0.70 | 3 |
| TempMay | 680.52 | 1.67 | 0.30 | 4 |
| TempMay+PrecMay | 4119.99 | 0.00 | 0.72 | 3 |
| Whinchat (n = 578 nests) | 4121.91 | 1.91 | 0.28 | 4 |
| TempMay | 4121.91 | 1.91 | 0.28 | 4 |
| TempMay+PrecMay | 4121.91 | 1.91 | 0.28 | 4 |

### Impact of spring weather on clutch size

Laying dates had a strong negative effect on clutch size of both species (Booted Warbler: $\beta = -0.007±0.001$, 95% CI -0.009, 0.005; Whinchat $\beta = -0.005±0.001$, 95% CI -0.006, 0.004) so we used residuals from a regression of clutch size on egg-laying date as the dependent variable for clutch-size analysis. Three top-ranked ($\Delta AIC_c < 2$) Booted Warbler clutch-size models included both weather covariates separately and in combination (Table 1). May averaged daily mean temperature had a strong positive effect on Booted Warbler clutch size and May precipitation had no effect on Booted Warbler clutch size (Table 2). The top-ranked clutch-size models for Whinchats included May precipitation and both covariates combination (Table 1). According to these models, the May precipitation had a weak positive effect on the clutch size of Whinchat (Table 2).

| Model | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$ Weight | $K$ |
|-------|---------|----------------|----------------|-----|
| **Clutch size**<br>Booted Warbler (n = 333 nests) | 491.92 | 0.00 | 0.41 | 4 |
| TempMay+PrecMay | 491.56 | 0.36 | 0.34 | 3 |
| PrecMay | 490.48 | 1.44 | 0.20 | 3 |
| Whinchat (n = 345 nests) | -651.30 | 0.00 | 0.42 | 3 |
| PrecMay | -651.23 | 0.07 | 0.41 | 4 |
| PrecMay+TempMay | 1589.55 | 0.00 | 0.72 | 4 |
| **Nest survival**<br>Booted Warbler (n = 500 nests) | 1591.41 | 1.87 | 0.28 | 5 |
| Age$^2$ + PrecMay | 1372.23 | 0.00 | 0.45 | 3 |
| Age$^2$ + PrecMay + TempMay | 1372.51 | 0.28 | 0.39 | 2 |

### Impact of spring weather on daily nest-survival rate

The most parsimonious baseline Booted Warbler nest-survival models incorporated the quadratic age of the nest (Appendix 2). The final most parsimonious models for Booted Warblers included quadratic age of nest and May precipitation; quadratic age of nest, May precipitation, and May averaged daily mean temperature (Table 1). May precipitation had a strong positive impact on nest-survival rate of Booted Warblers (Table 2). The most parsimonious Whinchat baseline model was an intercept-
Table 2. Influence of spring weather on reproductive parameters of Booted Warbler (*Iduna caligata*) and Whinchat (*Saxicola rubetra*) in Russky Sever National Park, 2005–2019.

| Covariate               | β ± SE | 95% CI | Effect          |
|-------------------------|-------|--------|-----------------|
| First egg-laying date   |       |        |                 |
| Booted Warbler (n = 585 nests) |      |        |                 |
| TempMay                 | -1.27 ± 0.12 | -1.51, -1.04 | strong negative |
| PrecMay                 | -0.005 ± 0.008 | -0.022, 0.012 | no effect       |
| Whinchat (n = 578 nests) |      |        |                 |
| TempMay                 | -1.34±0.16 | -1.65, -1.03 | strong negative |
| PrecMay                 | -0.005 ± 0.014 | -0.033, 0.023 | no effect       |
| Clutch size             |       |        |                 |
| Booted Warbler (n = 335 nests) |      |        |                 |
| TempMay                 | 0.0007±0.0004 | 0.0001, 0.001 | strong positive |
| PrecMay                 | 0.0004±0.0002 | -0.0002, 0.0007 | no effect       |
| Whinchat (n = 345 nests) |      |        |                 |
| PrecMay                 | 0.0005±0.0001 | 0.0001, 0.0009 | weak positive   |
| Nest survival           |       |        |                 |
| Booted Warbler (n = 500 nests) |      |        |                 |
| PrecMay                 | 0.014 ± 0.003 | 0.01, 0.02 | strong positive |
| TempMay                 | 0.01 ± 0.03 | -0.05, 0.07 | no effect       |
| Whinchat (n = 539 nests) |      |        |                 |
| PrecMay                 | 0.005 ± 0.003 | 0.001, 0.012 | strong positive |
| TempMay                 | 0.07 ± 0.03 | 0.003, 0.13 | strong positive |

95% CI are indicated.

Effect sizes (regression coefficient β with SE, and confidence limits, CI) are taken from the best-approximating models (Table 1) containing the parameter. TempMay - May averaged daily mean temperature, PrecMay - May precipitation.

only model. Two top-ranked weather models included the combination of both covariates and May precipitation separately (Table 1). Both weather covariates had a strong positive impact on the Whinchat daily nest-survival rate (Table 2).

**DISCUSSION**

Here we investigated the effect of spring weather conditions on the first egg dates, clutch size, and daily nest-survival rates of Booted Warblers and Whinchats in abandoned fields in the north of European Russia. Our results demonstrated that variability in May precipitation and average daily mean temperature is an important driver of breeding phenology, clutch size, and nest survival in both species. We suggest that the weather during pre-breeding and early breeding periods has a strong impact on life-history traits of the two focal species.

At our study site, the first egg date of Booted Warblers and Whinchats varied significantly from year to year (Fig. 1b): the differences between earliest and latest median first egg dates were 10 days for Booted Warblers and 14 days for Whinchats. These variations were determined primarily by the May averaged daily mean temperature. Therefore, our findings support numerous long-term studies suggesting the birds lay their first egg earlier in years with higher spring temperatures (Dunn and Winkler 2010, Charmantier and Gienapp 2014, Duursma et al. 2018, Shave et al. 2019).

The clutch size in both species expectedly depended on the first egg date: the earlier the birds started egg laying, the larger the full clutch size. The relationship between the first egg date and clutch size is well known for many passerine species and is usually explained by seasonal patterns of food supply, predation pressure, or physiological constraints (Christians et al. 2001, Cooper et al. 2005, Winkler et al. 2014). This allows us to assume the indirect effect of May temperatures on the breeding productivity of focal species: Booted Warblers and Whinchats begin to nest earlier in years with warm spring, which is reflected in larger clutch size.

Spring weather conditions at our study site had a direct impact on both species' clutch size even after regression against laying date. Several studies reported the direct effect of weather conditions on clutch size (Skagen and Yackel Adams 2012, Conrey et al. 2016). For example, clutch size in the Lark Bunting (*Calamospiza melanocorys*) in the shortgrass prairie of northeastern Colorado was positively related to daily rainfall at the onset of egg formation (Skagen and Yackel Adams 2012). Woodlarks (*Lullula arborea*) in eastern England laid larger clutches when rainfall was low and temperature high during the pre-laying period (Wright et al. 2009). We assumed that spring weather could affect clutch size through impact on nest predation pressure. Birds may reduce clutch size in years with high predation pressure (Doligez and Clobert 2003, Dillon and Conway 2017). In our study, the minimum clutch size in Booted Warblers was recorded in 2008 and in 2017, and in Whinchats - in 2017 (Fig. 1c). Namely, these two years were characterized by the driest and coldest springs (Fig. 1a), as well as the highest predation pressure (Fig. 1d). We speculate that Booted Warblers and Whinchats laid fewer eggs in the coldest and driest years (2008 and 2017) to reduce the risk of predation. Additional studies are needed to confirm or disprove this assumption.

The weather conditions in May had a strong effect on Booted Warbler and Whinchat nest survival. For both species, the influence of the precipitation in May had a significant impact; moreover, the average daily temperature in May affected the breeding success of Whinchats (Table 2). The minimum nest-survival values in both species were obtained in 2008 and 2017 (Fig. 1d). The significant decrease in breeding success in years with cold and dry springs can be attributed to several factors. Primarily, many researchers have described the direct effect of weather conditions on reproductive success through excessive mortality of clutches during spring cold snaps or storms (Skagen and Yackel Adams 2012, Martin et al. 2017). At our study site, predation was the main reason for nest destruction of both species. We registered only a few cases of the mortality of Booted Warbler or Whinchat nests caused by a sharp deterioration in weather conditions, which cannot explain the revealed statistical regularities.

Weather conditions often affect the activity of nest predators of ground-nesting birds, especially snakes (Cox et al. 2013). Morrison and Bolger (2002) proposed that early-season rainfall governed Rufous-Crowned Sparrow (*Amphipola ruficeps*) reproduction by suppressing nest predation by snakes. At our study site, the common adder is one of the most numerous nest predators of Booted Warbler and Whinchat (Samsonov et al. 2022), thus we suggested an indirect impact of May temperature and precipitation on focal species through a change in the activity of the poikilothermic predator. The results obtained did not confirm this assumption. Breeding success of both species was influenced by weather conditions during the pre-breeding and
early breeding periods while all depredation attempts by the common adder occurred in the second half of the breeding season (Samsonov et al. 2022). Moreover, Booted Warblers start breeding in the first half of June, and therefore the weather in May could not have a direct effect on the activity of nest predators of this species.

Spring weather conditions can determine the vegetation development rate, which in turn affects the nest concealment from predators (Chase et al. 2005, Ringelman and Skaggs 2019, Laidlaw et al. 2020). According to the trap-camera study carried out at our study site during 2016–2020, the common adder attacks the nests annually; in turn, most of the attacks of Hooded Crow and Magpie (Pica pica) were recorded in 2017, while in other years corvids did not depredate nests of focal species at all (Samsonov et al. 2022). Artificial nest studies revealed that corvids were the main cause of nest mortality at our study site in 2008 as well (Shitikov et al. 2012). In our study plot, nest depredation by corvids was confined mainly to the second half of May to the first half of June (Samsonov et al. 2018). We speculate that spring nest depredation by corvids in abandoned fields might be determined by the vegetation cover height. Visually hunting corvids took mainly the poorly concealed nests (Weidinger 2002). The peaks of corvid predation at our study site were revealed in 2008 and 2017; the years with a cold and dry May (Fig. 1a). In these years, the grass cover developed slowly, and open-cup nests of Booted Warbler and Whinchat turned out to be easily depredated by corvids.

For 15 years of our observations, there were 2 years (2008 and 2017) in which the coincidence of the minimum precipitation and the minimum average temperature in May was revealed (Fig. 1a). In both years, anomalous values of first egg-laying dates, clutch size, and nest-survival rates were recorded for Booted Warblers (Fig. 1b–d). For Whinchats, deviations in all three parameters were observed only in 2017; values of breeding success were the lowest of all years in 2008 (Fig. 1d). We suggest that years with a coincidence of minimum precipitation and average temperature in May are “bad” years for reproduction of grassland birds. In such years, birds begin reproduction later and lay smaller clutches. Due to the high activity of predators and low nest concealment in “bad” years, breeding success can drop to very low values.

In passerines, birds fledging earlier in the breeding season usually have greater first-year apparent survival than later-fledging birds (Maness and Anderson 2013, McKim-Louder et al. 2013, Perlut and Strong 2016). At our study site, later fledge dates negatively affected first-year apparent survival in both species (Shitikov et al. 2020). Since in single-brooded species the first egg and fledging dates are correlated, a late start of a breeding season could lead to a significant decrease in the apparent survival rate of the first-year birds. Thus, spring weather can have an indirect effect on the first-year apparent survival by shifting the first egg-laying dates. Adult apparent survival of Booted Warblers and Whinchats at our study site depended on the previous year’s reproductive success. Booted Warbler adult apparent survival after successful breeding was twice as high as after unsuccessful breeding (0.33 against 0.16), for Whinchats these rates were 0.32 and 0.1 respectively (Shitikov et al. 2017). The effect of breeding success on Booted Warbler and Whinchat adult apparent survival is usually explained by the reduced breeding dispersal of successful breeders (Shitikov et al. 2015, 2017, Fay et al. 2021). So, a decrease in breeding success in “bad” years could be the reason for the subsequent emigration of a significant part of adults. Similar results were obtained in the taiga of Karelia, where Pied Flycatcher nest-site fidelity of adults and yearlings, and immigration rate were related to May temperature patterns (Artemyev 2008).

Our study showed that coincidence of the minimum precipitation and average temperature in May has direct or indirect effects on Booted Warbler and Whinchat life-history traits. We assume that similar effects may be valid for all grassland passerine species in the boreal zone regardless of their conservation status, as previously suggested for Pied Flycatcher in the taiga of Karelia (Artemyev 2008, 2013). The observed climate change in European Russia is manifested in an increase in average annual temperatures and an increase in spring precipitation (Zamolodchikov and Kraev 2016). Based on this, we can predict a decrease in the frequency of “bad” years in the coming years. Our study showed that increases in temperature and spring precipitation can partially offset potential negative trends in grassland bird population dynamics associated with land use changes.

Responses to this article can be read online at: https://www.ace-eco.org/issues/responses.php/2215

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LITERATURE CITED

Andreason, F., J.-A. Nilsson, and A. Nord. 2020. Avian reproduction in a warming world. Frontiers in Ecology and Evolution 8:337. https://doi.org/10.3389/fevo.2020.576331

Artemyev, A. V. 2008. Factors responsible for the long-term dynamics of the Pied Flycatcher (Ficedula hypoleuca) populations in the taiga of Karelia, Russia. Acta Ornithologica 43:10-16. https://doi.org/10.3161/000164508X345284

Artemyev, A. V. 2013. The influence of climate change on the ecology of the Pied Flycatcher (Ficedula hypoleuca) in Southern Karelia. Russian Journal of Ecology 44:239-246. https://doi.org/10.1134/S1067413613030041

Bartoň, K. 2020. MuMIn: Multi-Model Inference. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Bowers, E. K., J. L. Grindstaff, S. S. Soukup, N. E. Drilling, K. P. Eckerle, S. K. Sakaluk, and C. F. Thompson. 2016. Spring temperatures influence selection on breeding date and the
Interactions of climate extremes influence nesting success. The reproduction for sympatric songbirds in an alpine environment: Martin, K., S. Wilson, E. C. MacDonald, A. F. Camfield, M. Martin, and S. A. Trefry. 2017. Effects of severe weather on Martin, K., S. Wilson, E. C. MacDonald, A. F. Camfield, M. Martin, and S. A. Trefry. 2017. Effects of severe weather on

Morrison, S. A., and D. Bolger. 2002. Variation in a sparrow's reproductive success with rainfall: food and predator-mediated processes. Oecologia 133:315-324. https://doi.org/10.1007/s00442-005-0009-4

Ockendon, N., D. Leech, and J. W. Pearce-Higgins. 2013. Climatic effects on breeding grounds are more important drivers of breeding phenology in migrant birds than carry-over effects from wintering grounds. Biology Letters 9(6):20130669 https://doi.org/10.1098/rsbl.2013.0669

Perlut, N. G., and A. M. Strong. 2016. Comparative analysis of factors associated with first-year survival in two species of migratory songbirds. Journal of Avian Biology 47:858-864. https://doi.org/10.1080/00063657.2014.988120.

Pokhodenko, S. K., and A. A. Yackel Adams. 2012. Weather effects on avian breeding performance and implications of climate change. Ecological Applications 22:1131-1145. https://doi.org/10.1890/11-0291.1

Sokolov, L. V. 2000. Spring ambient temperature as an important factor controlling timing of arrival, breeding, post-fledging dispersal and breeding success of Pied Flycatchers (Ficedula hypoleuca) in Eastern Baltic. Avian Ecology and Behaviour 5:79-104.

Sviridova, T. V., L. V Malovichko, G. V Grishanov, and P. D. Vengerov. 2020. Breeding conditions for birds in the nowaday farmlands of European Russia: the impact of agriculture intensification and polarization, Part II: Birds. Biology Bulletin 47:1425-1436. https://doi.org/10.1134/S1062359020100246

Taylor, B. 2018. Old World Flycatchers and Chats (Muscicapidae). In Handbook of the Birds of the World Alive (J. del Hoyo, A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana, editors). Lynx Edicions, Barcelona, Spain. https://www.hbw.com.

Weatherhead, P. 2005. Effects of climate variation on timing of nesting, reproductive success, and offspring sex ratios of red-winged blackbirds. Oecologia 144:168-175. https://doi.org/10.1007/s00442-005-0009-4

Weidinger, K. 2002. Interactive effects of concealment, parental behaviour and predators on the survival of open passerine nests. Journal of Animal Ecology 71:424-437. https://doi.org/10.1046/j.1365-2656.2002.00611.x
Winkler, D. W., P. O. Dunn, and C. E. McCulloch. 2002. Predicting the effects of climate change on avian life-history traits. Proceedings of the National Academy of Sciences of the United States of America 99:13595-13599. https://doi.org/10.1073/pnas.212251999

Winkler, D. W., K. M. Ringelman, P. O. Dunn, L. Whittingham, D. J. T. Russell, R. G. Clark, R. D. Dawson, L. S. Johnson, A. Rose, S. H. Austin, W. D. Robinson, M. P. Lombardo, P. A. Thorpe, D. Shutler, R. J. Robertson, M. Stager, M. Leonard, A. G. Horn, J. Dickinson, V. Ferretti, V. Massoni, F. Bulit, J. C. Reboreda, M. Lilesthrom, M. Quiroga, E. Rakimberdiev, and D. R. Ardia. 2014. Latitudinal variation in clutch size-lay date regressions in Tachycineta swallows: effects of food supply or demography? Ecography 37:670-678. https://doi.org/10.1111/j.1600-0587.2013.00458.x

Wright, L. J., R. A. Hoblyn, R. E. Green, C. G. R. Bowden, J. W. Mallord, W. J. Sutherland, and P. M. Dolman. 2009. Importance of climatic and environmental change in the demography of a multi-brooded passerine, the woodlark Lullula arborea. Journal of Animal Ecology 78:1191-1202. https://doi.org/10.1111/j.1365-2656.2009.01582.x

Zamolodchikov, D. and G. Kraev. 2016. Influence of climate change on Russian forests: recorded impacts and forecast estimates. Sustainable forest management 4:23-31 https://wwf.ru/upload/iblock/a57/4.pdf [in Russian].

Zuckerberg, B., C. A. Ribic, and L. A. McCauley. 2018. Effects of temperature and precipitation on grassland bird nesting success as mediated by patch size. Conservation Biology 32:872-882. https://doi.org/10.1111/cobi.13089
Appendix 1.

Table A1.1. Summary of model selection results for baseline nest survival models for Booted Warbler and Whinchat in abandoned fields of “Rusky Sever” National Park, 2005-2019

| Model  | AICc   | Δ AICc | AICc Weights | K  |
|--------|--------|--------|--------------|----|
|        | Booted Warbler |        |              |    |
| Age²   | 1617.95 | 0.00   | 0.48         | 3  |
| T      | 1618.77 | 0.81   | 0.32         | 2  |
| T²     | 1620.76 | 2.81   | 0.12         | 3  |
| Age    | 1621.53 | 3.57   | 0.08         | 2  |
| (.)    | 1636.34 | 18.39  | 0.00         | 1  |
|        | Whinchat |        |              |    |
| (.)    | 1379.15 | 0.00   | 0.34         | 1  |
| Age    | 1379.42 | 0.27   | 0.30         | 2  |
| T      | 1380.91 | 1.76   | 0.14         | 2  |
| Age²   | 1381.24 | 2.10   | 0.12         | 3  |
| T²     | 1381.80 | 2.65   | 0.09         | 3  |

Age - linear effect of nest age, Age² quadratic effect of nest age, T linear effect of the time of season (the number of days after the day when the first nest was found), T² quadratic effect of the time of season, (.) – null model
APPENDIX 2. Relationship between the daily nest survival rate of Booted Warbler and nest age according to the best model without weather covariates (Age²) for the 26 June (the median hatching date). The dotted lines indicated 95% CI.