Nest survival, predators and breeding performance of Booted Warblers *Iduna caligata* in the abandoned fields of the North of European Russia

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Abstract. We examined breeding performance and the nest survival of Booted Warbler *Iduna caligata* on abandoned fields in Vologda region, Russia. We modelled daily survival rates (DSR) using data on 250 nests found in 2002–2011. We compared relative effects of year, nest age, date, weather conditions and nest placement characteristics. Clutch size did not vary over the study period and was on average 5.69 ± 0.04 eggs. Inter-seasonal variability was the most important component of DSR variation. The top model included a year effect, a quadratic nest age term and an interaction between year and quadratic age. Overall nest success varied greatly from 0.03 in 2008 to 0.7 in 2007. Nest height was an important nest placement covariate, nest remoteness from villages and roads were not influential. We detected the species composition of predators by watching nests of Booted Warblers and other grassland passerines as well as by observing the artificial nests. The main predators were carnivorous mammals, Common Viper *Vipera berus*, Harriers and corvids. Predator pressure was the main factor that determined nest success of Booted Warblers. Intra- and inter-annual fluctuations in the activity of predators may cause corresponding changes in nest success of Booted Warbler.

INTRODUCTION

Predation is the main cause of nesting failure in most songbirds (Ricklefs 1969, Martin 1992). Nest predation can be highly variable in space and time because of the diversity of predators, habitats and landscapes to which birds are exposed (Hartley & Shepherd 1994, Thompson 2007). It has received great attention in recent years due to concern about the effects of high levels of predation on the demography (e.g. Rogers et al. 1997, Thompson 2007) and in relation to habitat fragmentation (e.g. Howard et al. 2001, Mazgajski & Rejt 2005, Svobodová et al. 2012). Despite the general conviction that nesting losses in birds are caused primarily by predators, there is little definitive evidence of the nest predator identity in different geographical areas, habitats and prey species (Weidinger 2009). Yet, nest success may be affected by area-dependent changes in predator assemblages (Zanette & Jenkins 2000). Anti-predator strategies evolved by birds include direct effects of parental behaviour (nest defence) as well as indirect ones, such as decision where (nest site selection) and when (timing) to breed (Weidinger 2002). Weather conditions can have significant impact on breeding success of birds besides predation (Dinsmore et al. 2002, Collister & Wilson 2007). Weather might directly affect nest survival if extreme conditions decrease hatchability of eggs and/or increase nestling mortality, whereas indirect impacts might arise through effects on food abundance and the behavior of predators (Morrison & Bolger 2002, Collister & Wilson 2007).

In this study, we examined the nest survival of a Booted Warbler *Iduna caligata* (formerly *Hippolais caligata*) population in Vologda region, north of European Russia at the northern edge of the species range. Booted Warbler is a common widespread passerine species of steppe and forest-steppe regions of European Russia East, West Siberia and Kazakhstan (Ptushenko 1954, Korovin

2004). By the end of 20th century the species has settled practically in all areas of north-west regions of Russia; random cases of nesting were registered in Estonia and Finland (Lilleleht & Leibak 1992, Iovchenko 2004, Butyev et al. 2007, Lindblom 2008). Booted Warbler inhabits different open habitats preferring wet meadows with shrubs in abandoned farmlands. Nests are arranged on the ground or suspended on vertical shoots of plants (Mugwort *Artemisia vulgaris*, Meadowsweet *Filipendula ulmaria*).

Most of agricultural areas were abandoned in European part of Russia at the end of 20th and the beginning of 21st century and that led to significant changes in farmland bird populations, including significant increase in Booted Warbler density (Galushin et al. 2001, Vengerov 2005, Melnikov & Khruleva 2006). Booted Warbler was registered in Vologda region for the first time at the beginning of 1970th (Butyev 1978), and by the end of 20th century its breeding has been demonstrated in the whole region (Butyev et al. 1997, 2007). Booted Warbler arrives to the breeding location at the end of May and begins to breed several days after arrival. Booted Warbler is a single-brooded species (Butyev et al. 2007).

We modelled the impact of weather, nest age, and nest placement on daily nest survival rates of Booted Warbler on abandoned fields. We then described the predator fauna that can be responsible for the observed patterns and we reported breeding performance.

METHODS

Study site
The study was conducted in 2002–2011 in the southern part of National Park "Russky Sever" near Topornya village (59°76´N, 38°22´E), Vologda region, north of European Russia. Sowing of spring crops (wheat, oat) and perennial grasses (Cock's-foot *Dactylis glomerata*, Meadow Fescue *Festuca pratensis*) were dominant on our study site of 400 ha in the beginning of our research. Abandoned fields and wet meadows with shrubs were not more that 15% of the area. After 2005 abandoned fields occupied more than 90% of the study site. Colony of Rooks *Corvus frugilegus* of about 30 nests was situated in Topornya village at a distance of 2 km from the study site. Maximum size of feeding Rook flock on fields varied from 50 birds (2010) to 150 (2008) and in other years it was about 60–70 birds.

Field methods
Annually the fieldwork started on 15–25th of May and lasted till 20–21st of July. Nests were located every day by observing the behavior of adult birds and systematically searching all suitable nesting habitats throughout the season. In total, 308 nests of Booted Warbler were found. Every nest location was determined using a Geographic Positioning System (GPS). All positions were transferred to digital maps using Mapinfo 10.5 (Pitney Bowes MapInfo Corporate 2010) software. After the onset of incubation, nests were visited every 2–3 days except near the expected hatching and fledging date, when they were checked on alternate days. During each nest check, we recorded the presence or absence of adults, the number of eggs or chicks, and, if appropriate, the developmental stage of the chicks. At the age of approximately 7–9 day, nestlings were banded with an aluminium band on one tarsus and a color plastic band on the other. Adults were captured with mist nets set near nests that had clutches and were banded with aluminium bands and individual combinations of color plastic bands. Monitoring individually marked young and adult birds was used to detect the fates of nests. If a nest was found empty around the expected time of fledging, we confirmed a successful nesting by locating the fledglings and observing parents carrying food and engaged in defensive behavior. The nest was considered unsuccessful if its content disappeared or adult birds did not appear near the nest for two or more control visits in a row. For unsuccessful nests we visually detected a probable cause of destruction based on characteristic signs (abandoned nest, unsuccessful because of the weather causes, destroyed by predators etc.). We measured height of the nests above ground (in centimetres). The distance to the roads and villages was measured in meters on digital maps that had all coordinates of found nests.

Data analysis
For the nests found after clutch completion, first egg dates (FED) were calculated from hatching date or nestling age, using the formula: FED = hatch date – 13 – clutch size + 2 (Butyev et al. 2007). Then we calculated the mean onset of initiation for each year. This estimate may be biased if not adjusted for nests that failed before they were found. Therefore, we used the Horvitz-Thompson estimator described by Dinsmore et al. (2002). This method uses the top nest survival model (see below) to calculate the probability that each found

nest survived until it was found. By dividing the observed frequency of each nest by this probability, we can estimate how many other nests might have been initiated on the same day but failed before they were found. We applied this approach to each nest in the sample and used the expected number of nest initiations as our corrected estimate of mean initiation date for each year.

We used average temperature values and total precipitation for 10 days after first egg date for each year (this was the period when most of the Booted Warbler nests were built) to detect the impact of weather on nests height. We received the weather data from Belozersk weather station situated 40 km north-west from the study site.

To calculate daily survival rates (DSR) we used data on 250 nests that were found in 2002–2011 (12 nests in 2002, 8 in 2003, 7 in 2004, 17 in 2005, 43 in 2006, 39 in 2007, 32 in 2008, 34 in 2009, 23 in 2010, 35 in 2011). Nests were monitored over 3369 exposure days.

We examined potential causes of variation in nest survival by fitting logistic regression models using program MARK 6.0 (White & Burnham 1999, Dinsmore et al. 2002). This approach requires the following assumptions: 1) nest ages are correctly determined, 2) nest fates are known with certainty, 3) investigator disturbance does not influence nest survival, and 4) nest fates are independent. We determined fate of a nest with the additional visiting after fledglings had left it according to individually marked parents' behavior and by observing the juveniles. For successful nests we considered the last day the nest was active to be the date of last observation (Weidinger 2007). For nests with uncertain fates we only used nest information up to the last date the nest was confirmed active and then denoted the nest as successful over that period. If there was uncertainty in nest age (7 nests) or if survival was clearly influenced by observer disturbance (3 nests), then such nests were not used in the analysis.

We constructed a set of 26 candidate models to examine how nest survival might be affected by year, nest age, weather conditions and nest placement. We began with a constant survival model and then added year as a categorical factor because annual variation in weather, predator abundance, and food availability might lead to yearly differences in nest survival. Nest survival might vary with nest age because of the susceptibility of eggs or nestlings to weather or predators, or changes in parental behavior through the nest cycle (Martin et al. 2000, Grant et al. 2005, Grant &

Shaffer 2012). We considered models that included linear, quadratic, and cubic effects of age, linear and quadratic effects of date. We included cubic effect of age in the models because previous studies of passerines have demonstrated a nonlinear decrease in daily survival rate as the breeding season progresses (Grant et al. 2005, Grant & Shaffer 2012). As the next step we added interaction terms with year to the models obtained from previous step to determine whether age and date patterns were consistent among years. Then we added weather and nest placement covariates to the model with the most support to examine how nest survival might be affected by mean daily temperature, daily precipitation, nest height and distance from nests to roads and villages.

We used a logit link function for all models. There is currently no suitable goodness of fit test for nest survival models in MARK (Dinsmore & Dinsmore 2007), and therefore, we have not used one here. We used Akaike's information criterion for small samples (AICc) to rank candidate models. We constructed a confidence set on the models and considered models with ΔAICc ≤ 2 to be well supported by the data (Burnham & Anderson 2002).

As a best estimate of year–specific nest survival, we used the adjusted mean initiation date for each year and the logistic regression equation from the best model without nest placement covariates. To compute nest survival we produced 29 consecutive daily nest survival estimates from the best fitting model without nest placement covariates, beginning with the adjusted mean nest initiation date (Dinsmore et al. 2002, Shaffer & Thomson 2007).

Predator assemblage composition
Systematic affiliation of predators was determined in several ways: 1) direct observation of the predators destroying Booted Warbler nests, 2) camera shooting of the nest destruction process, 3) direct observations of the artificial nests or destruction of nests of other ground-nesting passerines, 4) analysis of the eggshell remains in/near artificial nests. Under the direct observations we considered the visual detection of a predator near the nest or registration of its movement to the nest area (for example, a bird of prey landing in the nest clump area) with the following confirmation of the nest predation case by examining of the nest content. As an additional method of predator detection, we used installed video cameras near the nests at the distance of 1 m.

Cameras were set to 5 active Booted Warbler nests in 2009 only. In the same area in 2005–2011 we controlled 171 Whinchat *Saxicola rubetra* nests (49 of them were predated) and 62 Yellow Wagtail *Motacilla flava* nests (26 of them were predated). We also managed to detect several cases of predation for these species. Thereby we suggested these predator species could also destroy Booted Warbler nests in the area.

The artificial ground nests were established in 2007–2011. There were 245 of them in total. Artificial nests were put in those parts of study site where we did not have Booted Warbler and other grassland passerines real nests under control. The location of the artificial nests imitated nests of ground-nesting passerines: nests were located at the base of the grass clumps (wormwood, meadowsweet, cornflower, cock's-foot). Two quail *Coturnix japonica* eggs were put into each artificial nest. The use of quail eggs in nest predation studies allows us to detect the most of nest predators (corvids, predatory mammals and snakes) except small mammals (Buler & Hamilton 2000, Pärt & Wretenberg 2002). Artificial nests were checked daily. We considered the nest destroyed if eggs disappeared (one or both), if they were damaged or placed outside the nesting hollow. We did not estimate daily survival rates of artificial nests. In this study we use data on artificial nests only to identify the species composition of potential predators. Predator taxonomic groups were identified by the eggshell remains of the quail eggs that could be found near the artificial nests. Using this method we distinguished artificial nests destroyed by birds (triangle mark on the eggshell left by a bird's beak) from the nests destroyed by large mammals (round-shaped marks on the eggshell left by canine teeth). Also, direct observations were conducted from the shelter established at the distance of 30–50 m from the artificial nests. In total we did 24 hours of observation.

RESULTS

Timing of breeding and clutch size
The earliest first egg date (FED) was 31st of May (2010), the latest FED was 8th of June (2008). FED correlated with mean diurnal temperature of the last decade of May (r = -0.79, p < 0.01). First eggs appeared during 10 days after the beginning of egg-laying in earliest nest. There was between 4 and 7 eggs in a complete clutch, on average (± SE) 5.69 ± 0.04 eggs (n = 225, without renesting attempts). Clutch size did not vary systematically over the study period (Kruskal-Wallis ANOVA, H = 9.55, p = 0.15).

Repeat and second clutches
We found repeat clutches for 10 pairs out of 33 pairs that had unsuccessful first breeding attempt and where at least one adult was ringed. We also found 2 likely cases of repeat breeding (new nests were found after previous nests death on the same territories; adult individuals were not ringed). The only documented case of second brood attempt after first successful attempt was registered in 2006, when after fledglings successfully left the nest and stayed with the male, female formed a pair with another male in two days and proceeded to the second clutch.

The height of nests
Among 308 found nests 189 were on the ground, 119 were suspended on height from 1 to 40 cm (on average 8.99 ± 0.58 cm). Mean nest heights differed significantly over the years (Kruskal-Wallis ANOVA: H = 20.97, p = 0.01). More suspended nests were found in years with more rain in the period of active nest building process (r = 0.72, p = 0.02). Nest height poorly correlated with nest initiation date (r = 0.4, p < 0.01). Pairs that lost their nests built repeated nests higher (7.8 ± 2.1 cm), than previous nests (3.3 ± 1.9 cm) but differences were slightly non-significant (Wilcoxon pairs test: z = 1.75, p = 0.08, n = 10).

Partial brood losses and predation on adult individuals
One to three nestlings died in 9 nests out of 126 nests that were successful during nestling period (at least one fledgling left the nest). In 2 cases there was 1 dead nestling left in nest after other fledglings left; in the remaining 7 cases nestlings vanished from nests during the nestling period and reasons were unknown. In 2008 incubating females were predated from 3 nests by unknown predator. And in 2 out of 3 nests eggs were not touched. Survived males did not attempt to continue incubation.

Daily survival rate
An estimate of daily nest survival from the constant model without year or covariates was 0.978 (95% CI: 0.973, 0.982). Inter-seasonal variability was the most important component of DSR variation; total AICc weight of the models with year effect was 0.99 (Table 1). The top model with time

Table 1. Summary of model selection results for nest survival of Booted Warbler in 2002–2011. † — the AICc of the best model was 552.34.

Model	ΔAICc†	AICc Weights	K	Deviance
Year + age^2 + year*age^2 + year*height	0	0.24	40	479.56
Year + age^2 + year*age^2	0.50	0.19	30	494.33
Year + age^2 + year*age^2 + precipitation	0.90	0.15	31	490.66
Year + age^2 + year*age^2 + height	2.11	0.08	31	493.91
Year + age^2 + year*age^2 + temperature	2.34	0.07	31	494.13
Year + age^2 + year*age^2 + road	2.46	0.07	31	494.25
Year + date^2 + year*date^2	2.48	0.07	30	496.31
Year + age^3 + year*age^3	3.01	0.05	40	490.73
Year + age^2 + date + year*age^2 + year*date	3.92	0.03	40	481.43
Year + date^2 + age + year*date^2 + year*age	4.95	0.02	40	482.46
Year + date + year*date	8.23	0.00	20	520.33
Year + age + year*age	8.66	0.00	20	520.76
Year + age^3 + date + year*age^3 + year*date	8.96	0.00	50	478.28
Year + age	11.06	0.00	11	541.32
Year + date	11.27	0.00	11	541.54
Year	11.75	0.00	10	544.02
Year + age^2 + year*age^2 + year*road	12.55	0.00	40	483.92
Year + age^2	12.99	0.00	12	541.24
Year + date^2	13.23	0.00	12	541.48
Year + age3	14.99	0.00	13	541.23
Age	45.97	0.00	2	594.31
Date	46.40	0.00	2	594.73
Constant survival	46.61	0.00	1	596.95
Age^2	47.96	0.00	3	594.29
Date^2	48.32	0.00	3	594.65
Age^3	49.88	0.00	4	594.20

specific covariates only included a year effect, a quadratic nest age term and an interaction between year and quadratic age. The models with the interaction between year and quadratic age had a combined AICc weight of 0.8. The second most supported model with time specific covariates only contained a year effect, quadratic date effect and interaction between year and quadratic date effect. Using the top nest survival model without nest placement covariates, we estimated the nest survival probability for each year. This probability varied from 0.03 ± 0.01 in 2008 to 0.70 ± 0.02 in 2007 (Table 2).

To study the influence of the weather conditions and nest placement we added covariates which took into account the effect of the precipitation, temperature, nest height and distance from the nearest road to the best model obtained at the previous stage of analysis. The best model additionally contained the effect of nest height (Table 1). Survival was higher when nests were higher in 2003–2005 and 2010–2011 (Table 3). Models that took into account the influence of temperature

and precipitation were less important than the top model with time specific covariates only. Distance from roads and villages did not show any effect on DSR.

Nest predation

We managed to trace the fate of 234 nests of which 87 nests were unsuccessful. Among them 74 were

Table 2. Nest survival calculated from Year+age^2+year*age^2 model.

Year	Nest survival (± SE)
2002	0.43 ± 0.04
2003	0.45 ± 0.04
2004	0.28 ± 0.05
2005	0.69 ± 0.03
2006	0.43 ± 0.02
2007	0.70 ± 0.02
2008	0.03 ± 0.01
2009	0.50 ± 0.02
2010	0.31 ± 0.03
2011	0.64 ± 0.02

Table 3. β-estimates for nest height effect on daily survival rate obtained from model (Year+age^2+year*age^2+year*height).

Year	Estimate (β ± SE)	95% CI (LCI, UCI)
2002	-0.03 ± 0.12	-0.27, 0.20
2003	9.48 ± 0.00	9.48, 9.48
2004	17.56 ± 0.00	17.56, 17.56
2005	0.11 ± 0.12	-0.13, 0.35
2006	-0.09 ± 0.05	-0.19, 0.00
2007	0.09 ± 0.14	-0.20, 0.37
2008	-0.01 ± 0.04	-0.09, 0.07
2009	-0.06 ± 0.08	-0.22, 0.11
2010	3.49 ± 0.00	3.49, 3.49
2011	0.25 ± 0.16	-0.07, 0.57

destroyed by predators, 11 were left by adults without obvious reasons, 1 was dropped by strong wind, 1 nest had 3 infertile eggs and the female left it after 19 days of incubation. With direct observations of Booted Warbler nests we proved involvement of 4 species of predators. Three species were identified by direct observations from predating on other grassland passerine nests (Table 4). Among 245 artificial nests 120 (49%) were depredated (Table 5). All cases of predation by large mammals were registered only in 2008, while birds predated artificial nests annually. Main predators of artificial nests identified by direct observations were corvids (Table 6).

DISCUSSION

Nest survival in relation to year
Year effect had the greatest impact on Booted Warbler nest survival. Nest survival (Dinsmore et al. 2002) varied greatly from year to year with some years of almost total failure (estimated 0.03 in 2008) and other years with high nest survival (estimated 0.7 in 2007). This is the distinctive feature that distinguishes Booted Warbler from other grassland passerines for which year effect does not have an impact on nest survival (Grant et al. 2005, Collister & Wilson 2007) or is less important predictor than nest age effect (Davis et al. 2006, Grant & Shaffer 2012). High inter-annual variations in DSR can be most likely explained by between-year differences in the species composition of nest predators (Schmidt & Ostfeld 2003, Brzezinski et al. 2010, Svobodová et al. 2012). Similar results were obtained in 12-year study of variation in predation on artificial ground nests in northeastern Poland (Brzezinski et al. 2010) where high year-to-year variation in the predation pressure was recorded.

Nest survival in relation to age of a nest
Our data show a strong impact of nest age on DSR of Booted Warbler nests. The quadratic age effect on daily survival rate of passerine nests was reported by some researches (Collister & Wilson 2007, Post van der Burg et al. 2010). In our case such effect means that DSR is at its maximum during laying and nestling periods (i.e. in the very beginning and end of breeding cycle) and is at its minimum in the middle of nestling period (Fig. 1A). Similar dependence of DSR on nest age was found for ground nesting passerines in mixed-grass prairies in North Dakota (Grant et al. 2005, Davis et al. 2006, Grant & Shaffer 2012). The only difference of North American passerines was DSR increase during the period of egg laying, i.e. cubic age effect on DSR.

Table 4. Observed and likely nest predators of Booted Warbler.

Predator	Identification method
Reptiles	
Common Viper *Vipera berus*	direct observation, other passerines (Yellow Wagtail), videotaping
Birds	
Marsh Harrier *Circus aeruginosus*	other passerines (Whinchat)
Hen Harrier *Circus cyaneus*	other passerines (Yellow Wagtail)
Short-eared Owl *Asio flammeus*	direct observation, other passerines (Yellow Wagtail)
Gulls (*Larus canus*, *Chroicocephalus ridibundus*)	artificial nests (direct observation)
Magpie *Pica pica*	artificial nests (direct observation)
Hooded Crow *Corvus cornix*	artificial nests (direct observation)
Rook *Corvus frugilegus*	other passerines (Whinchat); artificial nests (direct observation)
Mammals	
Weasel *Mustela nivalis*	videotaping
Fox *Vulpes vulpes*, Domestic Dog *Canis familiaris*	artificial nests (marks on the eggshell)
Feral Cat *Felis catus*	direct observation

Table 5. Predators of artificial nests due to the analysis of eggshell marks.

Nests fate	Number of nests
predated by large mammals (foxes or domestic dogs)	30
predated by birds	10
eggs disappeared completely	80
Total	120

The relationship of DSR with nest age changed through the years. Increase of DSR in the end of breeding cycle was registered in 2009–2010 only. In 2002 and 2006 daily survival rate declined during the nesting period reaching its minimum by the end of nestling period (Fig. 1B), while in 2007 and 2008 nests with eggs were most exposed to predation (Fig. 1C). We suggest that observed differences are associated with the preferred activity of different predator groups in different years.

Nest survival in relation to nest height and nest concealment

We tested influence of two components of the nest placement on DSR of Booted Warbler: nest height and distance from roads and villages. Some studies have associated higher nests with greater nest survival (Wilson & Cooper 1998, Burhans et al. 2002, Peluc et al. 2008), and there is experimental evidence that adult birds can actively assess the risk of predation, recognize specific predators, and adjust the height at which they build nests accordingly (Peluc et al. 2008). Proportion of Booted Warbler suspended nests can vary on different territories and in different years (Butyev et al. 2007, our data). Booted Warblers build higher nests later in the breeding season and build higher nests following nest failure. Our data suggest that the height of nests affects the DSR strongly but only during some years. Most strongly its influence was obvious in 2003–2004 and 2010–2011 while in 2005 and 2007 it was rather weak. In 2006 and 2009 suspended nests were predated slightly more often than ground nests. It is important to point out that all nests were predated

Table 6. Predators of artificial nests due to observations from shelter.

Predator	Number of predation cases
Magpie	17
Hooded Crow	6
Rook	5
Black-headed Gull	1
Total	29
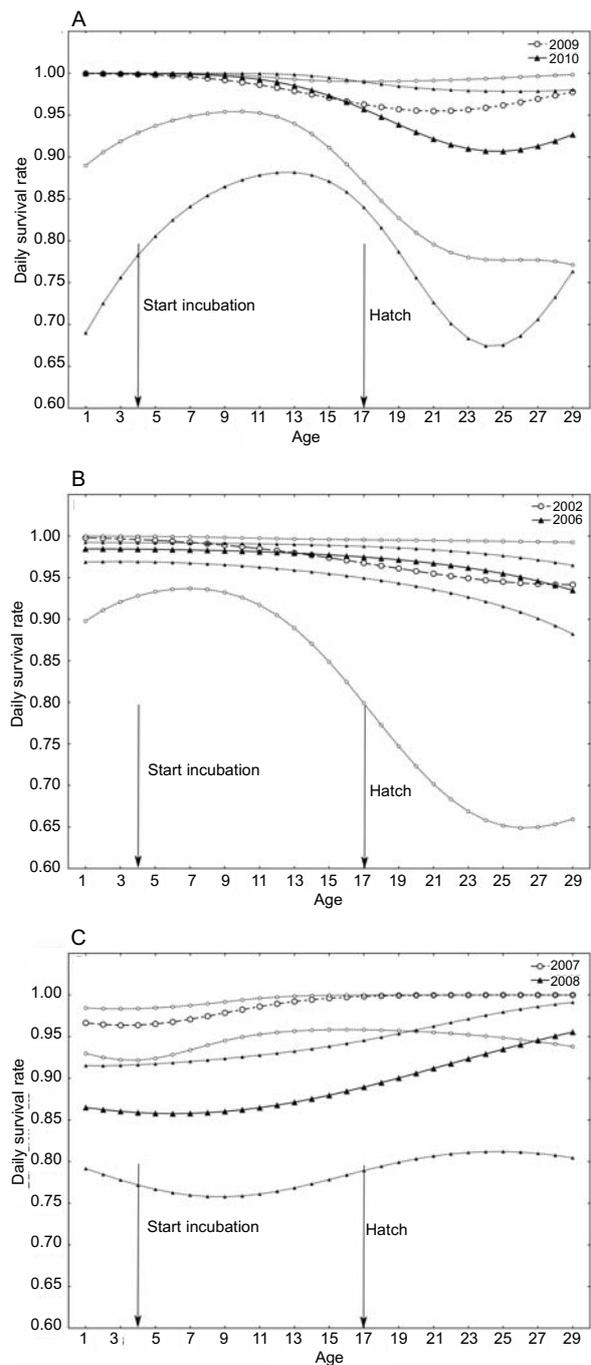
Fig. 1. Changes in daily nest survival across 29-days nest cycle for Booted Warbler in 2009–2010 (A), 2002 and 2006 (B) and 2007-2008 (C). Dashed lines represent 95% confidence intervals for the daily survival rate.

equally in catastrophic 2008 regardless of their location. This year predators destroyed 7 nests located at the height of 10 cm, and such high located nests were never predated during previous years (n = 37). Thereby nest location above the

ground does not guarantee more successful nesting; successful nesting depends on what group of predators destroys nests more actively during current year.

Butyev et al. (2007) showed that proportion of suspended nests in a local population depends on amount of precipitations: during wet years Booted Warblers build suspended nests more often than ground nests. The proportion of suspended nests in our study depended on amount of precipitation in the period of mass nest building. It has been suggested (Butyev et al. 2007) that ground nests are more frequently subject to soaking than suspended nests. We did not observe cases of ground nests destruction after heavy rains. Thus quantity of precipitation can only indirectly influence the height of the nests, perhaps this is related to different level of activity of predators in wet and dry seasons.

Predator composition and predation impact on nest survival

Our data show that predator pressure is the main factor that determines nest success of Booted Warbler on our study site. The most of identified predators are typical destroyers of open-nesting passerine birds in farmland areas across Europe (Söderström et al. 1998, Evans 2004). Direct observations confirmed the participation of Common Viper, harriers and small carnivores (Weasel) in Booted Warbler nest predation. Predation by Common Viper can be one of the reasons for DSR decrease during the nestling period in some years. Passerine nestlings are from 6% to 100% of Vipers' diet in various regions of European Russia (Belova 1978, Korosov 2010), but there are no cases of predating on eggs detected. All observations of Common Viper predation on Booted Warbler and other passerines nests that we had were also made during nestling period. Relation between DSR and nest age can reflect changes in predator activity during breeding season (Hartley & Shepherd 1994, Thompson 2007). Possible decrease of DSR during the nestling period may be related to enhancing the role of birds of prey in nest destroying, above all Marsh Harrier and Hen Harrier. At our study site all cases of harriers predating nests of Booted Warbler were registered during nestling period, particularly in the second half of June.

Corvids, especially Hooded Crow, Jackdaw and Magpie may be one of the most important predator groups of ground-nesting farmland birds across Europe (Angelstam 1986, Andren 1992, Söderström et al. 1998, Suvorov et al. 2012).

In our study site, corvid flocks consisted of mostly Rooks (70–80%), Jackdaws, Hooded Crows and Magpies. Mixed flocks of up to several tens of individuals regularly fed on the abandoned fields. Though we never witnessed direct predation by corvids, numerous cases of destruction of artificial nests by them and total disappearance of quail eggs confirm corvids to be important predators (Mazgajski & Rejt 2005, Suvorov et al. 2012).

It is generally accepted that nest height lowers the risk of predation by ground predators (snakes and mammals), while birds can equally successful predate nests located at any height (Schmidt 1999, Kleindorfer et al. 2005). At the same time it is known that Common Viper in the north of Russia predates passerine nests that are located at the height of up to a few tens of centimeters (Korosov 2010), small predatory mammals are also capable of ruining suspended Booted Warbler nests (our data obtained with videotaping). We assume that suspended nests were rarely depredated by corvids. Feeding flocks of corvids successively inspect fields and peck surface-active invertebrates from the ground that are the main food type in the first half of summer (Korovin 2004). Using this way of feeding birds can destroy nests that they find on the way, and ground nests are more likely to be predated.

We assume that the coincidence of the annual peaks of activity of different groups of predators caused a catastrophic decrease in nest success of Booted Warbler in 2008. For example, in 2008 there was abnormally high level of predation pressure on the territory of our study. Predators destroyed more than 80% of 49 found nests and most part was destroyed during first 1–3 days of finding. 2008 was an abnormal year not only for Booted Warbler but also for most ground-nesting passerines at our study site. Nest success of Whinchat estimated using Mayfield method (Mayfield 1975) in 2008 was as low as nest success of Booted Warbler and made 0.03 ± 0.02 (our unpublished data). In addition in 2008 three cases of incubating females death were registered, which clearly points to predatory mammals, for example mustelids (Björklund 1990); also in 2008 all cases when canines predated artificial nests were registered.

Thus, our data suggest that the expanded population of Booted Warbler on abandoned fields in north-east of European Russia is under the influence of different predators who can limit the nest success of the species significantly. Intra- and

inter-annual fluctuations in the activity of predators may cause corresponding changes in nest success of Booted Warbler.

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STRESZCZENIE

[Biologia lęgowa, przeżywalność lęgów oraz zagrożenie drapieżnictwem gniazdowym lęgów zaganiacza małego na opuszczonych terenach uprawnych w Rosji]

Celem pracy było zbadanie biologii lęgowej, przeżywalności lęgów oraz zagrożenia drapieżnictwem gniazdowym i składu zespołu drapieżników lęgów zaganiacza małego gniazdującego na opuszczonych terenach uprawnych na północy europejskiej części Rosji. Badania prowadzono w latach 2002–2011. Zebrano dane o 250 lęgach, dla których przeanalizowano wpływ sezonu (rok), stopnia zaawansowania lęgu (określanego jako „wiek gniazda"), daty, warunków pogodowych (średnia dzienna temperatura, dzienne opady) oraz położenia gniazda (wysokość nad powierzchnią ziemi, odległość od dróg i wiosek) na dzienne prawdopodobieństwo przeżycia lęgu (DSR daily survival rate).

Wielkość zniesienia była podobna w całym badanym okresie i wynosiła 5.96 ± 0.04 jaj. Najlepszy model wyjaśniający dzienne prawdopodobieństwo przeżycia lęgu zawierał sezon, wiek gniazda oraz wysokość gniazda and powierzchnią ziemi (Tab. 1). Sukces lęgowy były bardzo zmienny pomiędzy sezonami (Tab. 2) i wahał się od 0.03 w 2008 r. do 0.7 w 2007 r. Wysokość gniazda nad powierzchnią ziemi była ważną, szczególnie w niektórych sezonach (Tab. 3), zmienną towarzyszącą natomiast odległość gniazda od dróg, czy zabudowań nie wpływała na prawdopodobieństwo przeżycia lęgu. Stopień zaawansowania lęgu także wpływał na dzienne prawdopodobieństwo przeżycia lęgu, jednak wzorzec strat w zależności od wieku gniazda różnił się pomiędzy sezonami (Fig. 1). Główną przyczyną strat lęgowych było drapieżnictwo. Na podstawie obserwacji autorów, nagrań z kamer oraz obserwacji gniazd innych ptaków wróblowych na badanym terenie, a także losów sztucznych gniazd z jajami przepiórczymi, określono skład zespołu drapieżników odpowiedzialnych za straty lęgowe zaganiacza małego. Były to głównie drapieżne ssaki, żmija zygzakowata, błotniaki oraz krukowate (Tab. 5, 6). Autorzy sugerują, że zmiany w zespole drapieżników pomiędzy latami powodują obserwowane duże różnice w sukcesie lęgowym zaganiacza pomiędzy sezonami.