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How to sustain meadow passerine populations in Europe through alternative mowing management

Joël Broyer[a,*], Olga Sukhanova[b], Alexander Mischenko[b]

[a] Office National de la Chasse et de la Faune Sauvage (ONCFS), Direction de la Recherche et de l'Expertise, Station de la Dombes, Montfort, 01330 Birieux, France

[b] Russian Society for Bird Conservation and Study (BirdsRussia), 70 Nigegorodskaja str., building 1, Moscow, Russia

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ABSTRACT

Two decades of agri-environmental policy did not prevent a long term decline of grassland birds in Europe. Additional measures are therefore needed to sustain the populations. This study explored alternative mowing management regimes likely to secure demographic sources in the early mown grassland systems of western Europe, and to limit habitat loss after farming abandonment in countries of the former Eastern Bloc. Postponing grass cutting until after mid-July from 2009 to 2014 in half of the area of 4 study sites (29–55 ha each) in the Saône Valley (France), led to increased territory density and improved hatching success. Bird response however was species-specific: Corn Bunting *Emberiza calandra* territory density benefited the most from the alternative management, Yellow Wagtail *Motacilla flava* territory distribution tended to match the late mown areas, whereas the Whinchat *Saxicola rubetra* did not change its initial distribution. Temporary interruption of mowing in 8 meadow units (11.7–15.1 ha) of the Moskva Valley (Central Russia) was similarly correlated with higher territory density. Whinchat territory density decreased after one single year of mowing. After two consecutive years of mowing, Whinchat hatching success was lower and the Lesser Citrine Wagtail *Motacilla citreola werae* virtually disappeared. The tested alternative mowing regimes may therefore locally increase population density without negative density dependent effects on hatching rates. Implementing rotational mowing could reduce habitat loss caused by farming abandonment in Russia. Postponing mowing until after mid-July in patches of hay fields may sustain meadow bird demography in the remaining strongholds of western Europe.

1. Introduction

Growing evidence suggests that we may be witnessing an unprecedented decline in farmland birds in Europe (Voříšek et al., 2010). To date, agri-environment schemes (AES), which are the main available mechanism likely to mitigate the negative effects of farming practices over large areas (Vickery et al., 2004), have not succeeded in halting the on-going, large-scale negative trends in farmland bird populations (Breeuwer et al., 2009; Davey et al., 2010; Princé et al., 2012). AES principles could be improved to better offset the detrimental consequences of modern agriculture on biodiversity. It can be predicted however that some practices such as early mowing will be extremely difficult to reverse for achieving conservation objectives in intensively managed grassland systems. This major condition for the successful reproduction of meadow birds is most often hampered by farmers' reluctance to adopt a mowing chronology in accordance with breeding cycles, even with economic compensation (Horch and Spaar, 2007). Obviously, the problem already existed before agriculture intensification. Brehm (1868) reported that the number of Corncrakes *Crex crex* killed by mowers was higher than the number of those killed by hunters. In France in 1789, royal edicts forbade mowing before a certain period to preserve game birds (Young, 1792). Nowadays, reproductive outputs of meadow birds in Europe seem to be usually too low to compensate for adult mortality (Green, 1996; Roodbergen et al., 2012). The challenge therefore is to preserve demographic sources. Grassland management subsidies should focus on areas with less intensive management that aim at attracting high densities of grassland birds with a high reproductive success. The hatching success of meadow passerines is however likely to be density dependent (Broyer, 2009, 2011) and therefore investigations of reproductive success are needed in areas with increased bird density due to management changes.

* Corresponding author.
E-mail address: joel.broyer@oncfs.gouv.fr (J. Broyer).

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Such “ecological intensification” may be sought through late enough mowing or through intermittent (not every year) hay harvesting, likely not only to prevent the risk of bird mortality by mowers, but also to boost arthropod-prey abundance (Erhardt, 1985; Cattin et al., 2003; Baur et al., 2006; Marini et al., 2009; Buri et al., 2013), thereby enhancing carrying capacity for birds in grassland habitats.

Throughout Europe, a sharp contrast exists between western countries and the members of the former Eastern Bloc (Orlowski 2005; Wretenberg et al., 2007). In Russia, where a considerable proportion of European populations of certain meadow bird species breed, key-sites may be threatened by farming abandonment as a result of a long-lasting agricultural crisis (Mischenko and Sukhanova, 2006). Rotational mowing (i.e. mowing every second-fourth year) could be a possible adaptation to prevent forest encroachment in large, otherwise unmanaged, grassland places. Intermittent mowing then could help reduce habitat loss caused by farm abandonment. In Western Europe, the prevailing issue is early hay harvesting and nest or juvenile destruction by mowers. Usually, mowing postponement through AES programmes shortly after fledging time only aims at decreasing mortality during the harvesting period. But the obtained increase in population density may theoretically lead to higher competition between neighboring pairs, with negative consequences on nesting success (Broyer, 2011). However, in a previous work in late mown French grasslands, we observed high hatching success, similar to that recorded in extensively managed grasslands in Russia, whereas passerine territory density was high (Broyer et al., 2014). This study describes the variation in meadow passerine density and hatching rate after implementation of alternative mowing management in controlled experiments: either grass cutting postponement until after 15 July in the Saône Valley (eastern France), or temporary interruption of mowing in the Moskva Valley (Central Russia). So far, efforts to counteract the negative effects of agriculture intensification (including earlier mowing of meadows) have mainly been restricted to Western Europe, while the large grassland areas in Eastern Europe (Russia in particular) have largely been neglected. The high rate of natal dispersal in some meadow birds in Russia (Shitikov et al., 2011, 2013) suggests that long distance dispersal between countries might be important for maintaining European populations of meadow birds. The scale of this natal dispersal is however largely unknown.

The hypotheses tested here were that late enough mowing (in Western Europe) and a temporary interruption of hay harvesting (in Russia) may enable to increase passerine territory density without hampering hatching success. We focused here on hatching success for investigating the existence of possible density dependent effects because: 1) food shortage in the pre-breeding or laying period can result in a lower proportion of pairs attempting to breed (Enoksson and Nilsson, 1983; Rodenhouse and Holmes, 1992; Murphy et al., 1991; Tobias, 1997; Elmegaard et al., 1999), 2) food shortage may also cause low hatching success (Martin, 1987; Hatch and Hatch, 1990; Hamer et al., 1993; Schreiber and Kissling, 2005), 3) we observed in the Saône Valley a trade-off between territory density and hatching success after AES implementation (Broyer, 2011). We expected in this experiment that hatching success will not be negatively influenced by higher territory density.

2. Method

2.1. Study areas

The study was carried out in two flood plains, the Saône Valley in eastern France (46°18′ N 04°49′ E) and the Vinogradovo plain near the Moskva river in Central Russia (55°08′ N 38°45′E).

The consequences of late mowing on meadow passerine breeding were observed in 4 study sites (29, 40, 49 and 55 ha) of the Saône Valley, in which hay harvesting was experimentally postponed to the end of July (after 15 July) in half of their total surface area (50% delayed and 50% normal in each study site), and in 2 control sites (116 and 76 ha) without mowing delay (mowing period: 20 May–20 June and 10 June–5 July, respectively). The spatial patterning of delayed and normal mowing (i.e. in June) was in single blocks, not in interspersed patches. The effects of a temporary interruption of grass cutting were studied in 8 replicates (between 11.7 and 15.1 ha each) in the Vinogradovo flood plain. The size of these experimental units was defined after the results of a preliminary survey in 2006 in different flooded plains of the Vladimir and the Ryazan regions, indicating that passerine density was >11 territories per 10 hectares on average. We therefore considered that surface areas >10 ha for each replicate was sufficient in such habitat conditions. Each study site in both countries was made up of hay meadows only. At the level of each valley, similar conditions in all replicates, experimental and control grasslands: dominant flora, management prior to the experiments, surrounding landscape with open hay-meadows (for details, see Broyer et al., 2014), enabled us to avoid confounding effects.

In the Saône Valley, the study was carried out from 2009 to 2014. Mowing was postponed each year from July 2009. Bird breeding in 2009 was considered as the reference before the experiment. We accepted the risk of relying on a single survey in 2009 to derive baseline data as the reference point before the start of the experiment as the weather conditions were normal (neither drought nor spring flood). After mowing manipulation however, the breeding conditions of meadow birds were affected by a severe drought during the spring 2011, and by heavy rainfall and late flooding in 2013. The control areas however can determine the impacts of weather vs. management. In 2013 however, we decided to discard from the analysis two manipulated study sites which have been exceptionally flooded until the end of May.

In the Moskva Valley, the objective was to compare meadow bird breeding in the year following a presence or an absence of grass harvesting. Due to the travel distance to the study sites and the difficulty to negotiate alternative management in Russia, we could not apply identical sample sizes and survey methods in both experiments. The studied meadows were left unmown for several successive years until 2009. Each one was harvested in July 2010 and submitted to various management regimes thereafter:

Table 1
Comparison using AICc of GLMs explaining the variation in passerine territory density in 4 study sites with mowing postponement and in 2 control sites, with YEAR (2009 vs. 2010 + 2011 + 2012 + 2013 + 2014, i.e. before vs. after mowing delay), MANAG (presence vs. absence of alternative mowing management), PERCB, PERYW and PERWH (proportions of Corn Bunting *Emberiza calandra*, Yellow Wagtail *Motacilla flava* and Whinchat *Saxicola rubetra* territories) (Saône Valley, France, 2009–2014).

Models	*n*	*k*	AICc	ΔAICc	*w*
YEAR + MANAG + YEAR*MANAG + PERCB	36	5	183.15	0	0.76
YEAR + MANAG + YEAR*MANAG	36	4	187.06	3.91	0.11
YEAR + MANAG + YEAR*MANAG + PERYW	36	5	188.56	5.41	0.05
YEAR + MANAG	36	3	188.92	5.77	0.04
YEAR + MANAG + YEAR*MANAG + PERWH	36	5	189.63	6.48	0.03
MANAG	36	2	191.27	8.12	0.01
YEAR	36	2	210.23	27.08	0.00
(*)	36	1	210.47	27.32	0.00

	Estimate	St. Err.	*z*	*p*
Intercept	6.241	8.509	0.733	0.47
MANAG	4.138	5.607	0.738	0.47
YEAR	12.383	4.255	2.910	0.0069
YEAR*MANAG	−6.474	3.000	−2.158	0.039
PERCB	−19.552	7.829	−2.497	0.018

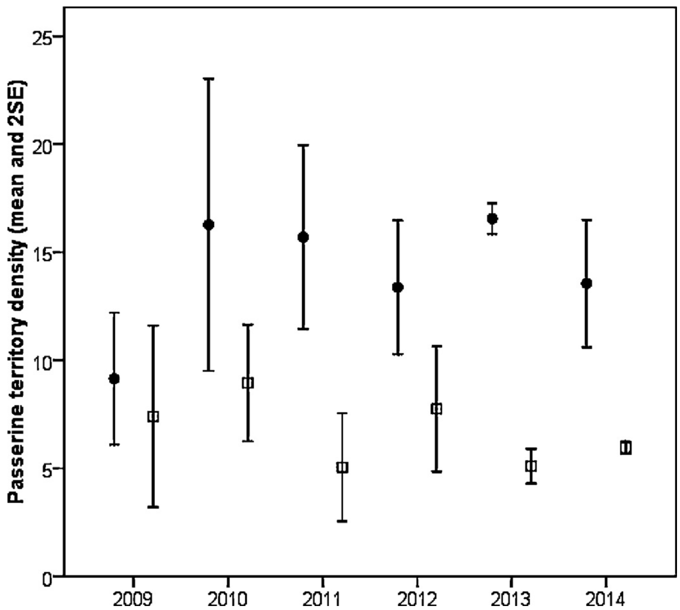

Fig. 1. Annual variation in passerine territory density after mowing manipulation (postponement to the second half of July) from 2009 onwards in 4 study sites (black circles) and in 2 control sites without mowing delay (white squares). (Saône Valley, eastern France). NB—For 2013, two manipulated study sites completely flooded until the end of May were discarded.

5 meadows were mown in July 2011 and 3 were left unmown, 2 meadows harvested in 2011 were mown again in July 2012, whereas the 6 other ones were left unmown. In Russia also, the spring 2013 was characterized by unusually late flooding in May.

2.2. Passerine territory density and hatching rate

Passerine territory density (TD) in each study site was defined by the Territory Mapping method (Pough, 1950; Enemar, 1959). A circuit was established that allowed an easy and exhaustive survey of the area with binoculars to detect ground nesting species: Whinchat *Saxicola rubetra*, Yellow Wagtail *Motacilla flava*, Lesser Citrine Wagtail *Motacilla citreola werae*, Skylark *Alauda arvensis*, Corn Bunting *Emberiza calandra*, Reed Bunting *Emberiza schoeniclus*, Tree Pipit *Anthus trivialis*, Sedge Warbler *Acrocephalus schoenobaenus*, Marsh Warbler *Acrocephalus palustris*, Grasshopper Warbler *Locustella naevia*, Common Whitethroat *Sylvia communis* (in Russia, this species may be a ground nesting meadow bird).

In the French study sites from 2009 to 2014, meadow passerines were surveyed twice every week by a walking observer, from mid-April to the end of the haymaking. During each visit, individual birds, song displays and agonistic behaviors were plotted on a 1:8 000 map. When the hatching period started, every individual Whinchat, Corn Bunting and Yellow Wagtail (the most common passerine species) was systematically checked with binoculars to verify whether it carried prey to feed its chicks. Successive visits were made every 2–3 days, but each survey was intensive (>4 h), ensuring a reliable detection rate. Passerines carrying prey were usually observed within known territories. Otherwise, prey carrying was assigned to the nearest territory after checking that corresponding adults were absent in this territory. The hatching rate was defined as the proportion of territories in which at least one prey carrying episode was observed, indicating that at least one egg hatched per territory. In the Russian study sites from 2010 to 2013, meadow birds and prey carrying by passerines were mapped only once a week between May 1 and July 30 but each survey was more intensive (notably with 2 observers instead of 1). The observation of prey carrying in such conditions cannot strictly reflect hatching success since nests may hatch and fail between visits. This indicator (that we will refer to as “hatching rate” or “hatching success”) may nevertheless enable us to describe the influence of increasing TD and possible density dependent effects on nesting success shortly after hatch.

2.3. Data analysis

In both experiments we studied to what extent the spatio-temporal variations of passerine TD in the replicates tended to reflect the expected influence of each tested alternative management. In the Saône Valley, we hypothesized that TD in manipulated study sites across the period 2010–2014 was higher than in 2009 and than in the unmanipulated control sites over the same period. We used GLMs with TD as response variable (Gaussian distribution) and YEAR (2009 vs. 2010–2014, i.e. before and after the start of management), MANAG (presence or absence of mowing postponement in half the surface area), and the proportion of Whinchat territories (PERWH), or Corn Bunting territories (PERCB), or Yellow Wagtail territories (PERYW), as explanatory variables. The main variable of interest here was the interaction between YEAR and MANAG. In the most abundant species, possible changes over time in the proportion of territories situated within the late mown parts of the manipulated sites were also studied using binomial GLMs with YEAR as explanatory variable.

In the Moskva Valley, passerine TD variation across replicates was compared according to the presence or absence of hay cutting the preceding year. The explanatory variables in the GLMs were MPY01 (presence or absence of mowing the preceding year), MPY012 (absence of mowing the preceding year, or mowing for one single year, or mowing for 2 or 3 consecutive years), the proportion of Whinchat territories (PERWH), or Yellow Wagtail territories (PERYW), or Lesser Citrine Wagtail territories (PERLCW), or Sedge Warbler territories (PERSED), or Reed Bunting territories (PERREED). A species-specific analysis in the 5 most abundant species enabled to compare, by ANOVAs with Bonferroni correction, TD after absence of mowing the preceding year to TD after one year of mowing and TD after 2 or 3 consecutive years.

We also hypothesized that the improvement of habitat quality by the alternative practices was likely to outweigh potentially negative density dependent effects on hatching success. The presence or absence of prey carrying in each individual territory was studied in the most abundant species using Generalized Linear Mixed Models (GLMMs) with binomial error distribution. In the Saône Valley, the fixed factors were meadow passerine territory density in study sites and the situation of each territory either inside (at least partly) or outside the areas devoted to mowing postponement; study sites and years were used as random effects. In the Moskva Valley, the fixed factors were mowing management the preceding year (no mowing, mowing for only one year, for several consecutive years) and passerine territory density in corresponding replicates; study sites were used as a random effect.

The different possible models, including the null model (with only the intercept as a fixed factor), were compared using their AIC scores. We only considered the models within ΔAIC < 2 (Burnham and Anderson 1998). R version 3.0.3 was used for all statistical analyses.

3. Results

3.1. Mowing postponement in the Saône Valley

3.1.1. Territory density

The top-ranked model to explain the variation in passerine TD included the interaction of YEAR (2009 vs. 2010–2014) and MANAG (presence/absence of mowing postponement in half the surface area) + PERCB (proportion of Corn Bunting territories) (Table 1). After mowing postponement in 4 study sites since July 2009, a general increase of territory density was observed in each of the 5 following years. This increase was not recorded in the 2 unmanipulated controls during the same period (Fig. 1). The Corn Bunting seems to have benefited the most from mowing postponement (Fig. 2).

The proportion of territories within the late mown parts of the 4 manipulated sites obviously did not change in the Whinchat across the experiment (Table 2). This proportion tended to increase after 2009 in the Yellow Wagtail (binomial GLM with YEAR as explanatory variable: $z = 1.889$, $P = 0.059$). In fact, the distribution of Yellow Wagtail territories differed from 2009 in 2010 ($\chi 2 = 5.23$, $P = 0.02$), in 2013 ($\chi 2 = 5.36$, $P = 0.02$) and marginally in 2014 ($\chi 2 = 3.39$, $P = 0.065$). A slight but stable increase in the percentage of Corn Bunting territories within late mown areas (Table 2) was not significant (binomial GLM with YEAR as explanatory variable: $z = 0.982$, $P = 0.33$).

3.1.2. Hatching success

In all studied species (Whinchat, Yellow Wagtail, Corn Bunting), the hatching success was significantly higher in the areas where mowing was postponed. Adding passerine territory density to the models did not improve the AIC scores (Table 3), suggesting that higher TD did not influence hatching rates. Annual hatching success in the Whinchat, the Corn Bunting and the Yellow Wagtail within late mown subunits were 72.7% ± 11.9SD, 66.8% ± 13.1SD and 68.2% ± 23.6SD respectively, against 47.5% ± 20.1SD, 34.9% ± 16.4SD and 57.6% ± 16.8SD outside, very close to the hatching rates recorded in the control sites over the same period: 50.4% ± 26.2SD, 39.6% ± 24.4SD and 53.6% ± 31.5SD, respectively.

3.2. Intermittent mowing in the Moskva Valley

3.2.1. Territory density

For explaining TD variation, three models had ΔAICc < 2. MPY01 (mown vs. not mown the preceding year) was included in each one. Adding PERLCW (proportion of Lesser Citrine Wagtail territories) or PERWH (proportion of Whinchat territories) in the models did not improve the AICc score significantly (Table 4). The specific influence of MPY01 was significant in all three models ($P < 0.02$), but P was >0.05 for PERLCW and PERWH. We found no extra explanatory power in making a difference between mowing for one single year and for 2 or 3 consecutive years (MPY012). Passerine TD in meadow areas not mown the preceding year was higher than in those mown for one or several successive years (Figs. 3 and 4). Analyzing with ANOVAs species-specific responses to mowing indicated that Whinchat TD decreased from 7.0 ± 2.7SD to 4.0 ± 2.5SD after one single year of mowing ($F = 7.313$, Bonferroni $P = 0.028$) and to 3.2 ± 1.6SD after 2 or 3 consecutive years of mowing ($F = 7.313$, Bonferroni $P = 0.007$). Lesser Citrine Wagtail TD only decreased from 3.9 ± 3.0SD to 2.7 ± 1.8SD after the first year of mowing ($F = 5.713$, Bonferroni $P = 0.718$) but the species virtually disappeared (0.3 ± 0.4SD) after at least two consecutive years ($F = 5.713$, Bonferroni $P = 0.006$).

3.2.2. Hatching success

The best model explaining Whinchat hatching success included meadow passerine TD and mowing management, both displaying negative effects (Table 5A). In fact, the hatching rates were similar in case of absence of mowing the preceding year (70.0%, $n = 166$ Whinchat territories) and in case of mowing for only one year (70.2%, $n = 47$), but decreased to 44.1% ($n = 34$) after mowing for 2 or 3 consecutive years. In the Yellow Wagtail, no model was more plausible than the null model (Table 5B). Hatching success increased from 61.2% after an absence of mowing the year before

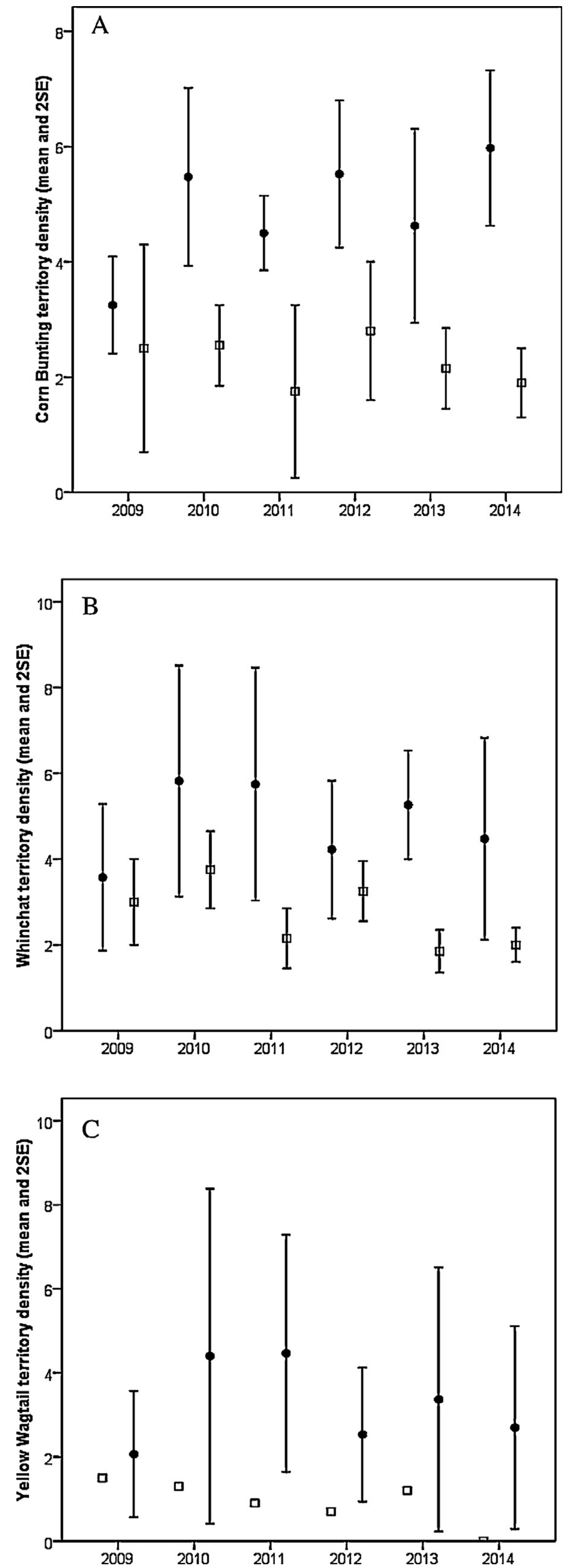

Fig. 2. Annual variation in the territory density of the Corn Bunting *Emberiza calandra* (A), the Whinchat *Saxicola rubetra* (B) and the Yellow Wagtail *Motacilla flava* (C) after mowing manipulation (postponement to the second half of July) from 2009 onwards in 4 study sites (black circles) and in 2 control sites without mowing delay (white squares). (Saône Valley, eastern France). NB—Yellow Wagtail was absent from the second control site.

Table 2
Annual variation in the proportion of territories situated inside (at least partly) the late mown areas, in study sites where mowing was postponed each year in half of their total surface area (Saône Valley, France).

	Whinchat		Corn Bunting		Yellow Wagtail	
2009	24/50	0.48	14/40	0.30	6/17	0.35
2010	34/75	0.45	29/63	0.46	19/27	0.70
2011	37/74	0.50	25/58	0.43	17/35	0.49
2012	31/56	0.42	30/72	0.42	8/17	0.47
2013	20/41	0.49	19/46	0.41	14/19	0.74
2014	25/53	0.47	30/69	0.43	9/13	0.69

Table 3
Comparison using AIC of GLMMs explaining the hatching success of Whinchat *Saxicola rubetra* (A), Corn Bunting *Emberiza calandra* (B), Yellow Wagtail *Motacilla flava* (C), with the proportion of territories in or outside areas where mowing was postponed (in-out), and with meadow passerine territory density (TD). The null model (*) includes only the intercept. (Saône Valley, 2010–2014).

A

Models	*n*	*k*	AIC	ΔAIC	*w*
in-out	418	2	537.1	0	0.73
in-out + TD	418	3	539.1	2.0	0.27
(*)	418	1	548.7	11.6	0
TD	418	2	550.5	13.4	0

	Estimate	St. Err.	*z*	*p*
Intercept	1.6799	0.4080	4.117	3.8e-5
in-out	-0.7987	0.2155	−3.706	0.000

B

Models	*n*	*k*	AIC	ΔAIC	*w*
in-out	434	2	552.2	0	0.71
in-out + TD	434	3	554.0	1.8	0.29
(*)	434	1	585.0	32.8	0
TD	434	2	586.6	34.4	0

	Estimate	St. Err.	*z*	*p*
Intercept	2.1164	0.3869	5.470	4.5e-8
in-out	−1.2371	0.2169	−5.705	1.2e-8

C

Models	*n*	*k*	AIC	ΔAIC	*w*
in-out	195	2	258.5	0	0.59
in-out + TD	195	3	260.4	1.9	0.23
(*)	195	1	261.7	3.2	0.12
TD	195	2	262.9	4.4	0.07

	Estimate	St. Err.	*z*	*p*
Intercept	1.5295	0.4540	3.369	0.0008
in-out	−0.7186	0.3127	−2.298	0.022

(n = 98 Yellow Wagtail territories), to 81.8% after one first year of mowing (n = 33), but dropped back to 65.4% after the second consecutive year of mowing (n = 26). Lesser Citrine Wagtail hatching success was not significantly affected by the first year of mowing: 60.0% (n = 30) against 64.3% when grass was not cut the preceding year (n = 98).

4. Discussion

In this study, we examined two methods likely to improve meadow passerine territory density by alternative mowing management. We expected that after mowing postponement until after 15 July or after temporary interruption of grass cutting: 1) higher breeding success would enhance the potential recruitment the next breeding season in case of natal philopatry (Shields, 1984; Gavin and Bollinger, 1988; Haas, 1998; Gauthier, 1990; Vergara et al., 2006), 2) grassland habitat would become more attractive for breeding pairs, with increased invertebrate abundance (Wettstein and Schmid, 1999; Morris, 2000; Knop et al., 2006) or with altered grass structure to the benefit of tall plant species likely to provide more efficient nest concealment against predation. Passerine territory density substantially increased in the study sites of the Saône Valley after mowing postponement in half of their surface areas, but the alternative management seemed to benefit the most to the Corn Bunting. In this species however, we observed only a marginal shift to the late mown parts of the study sites. Increased Corn Bunting territory density could then be explained by higher breeding output in late mown areas and strong natal philopatry at the scale of the whole study site. By contrast, Yellow Wagtail pairs tended to concentrate within the late mown areas, but territory density did not clearly increase in study sites. This suggests that late mown areas were more attractive for this species but that Yellow Wagtail juveniles were not site-faithful. In the Whinchat, territory density did not increase significantly in study sites and

Table 4
Comparison using AICc of GLMs explaining the variation in passerine territory density in 8 study sites, with MPY01 (presence vs. absence of mowing the preceding year), MPY012 (absence of mowing the preceding year, mowing for one single year, mowing for 2 or 3 successive years), PERLCW, PERYW, PERWH PERREE, PERSED (proportions of Lesser Citrine Wagtail *Motacilla citreola werae*, Yellow Wagtail *Motacilla flava*, Whinchat *Saxicola rubetra*, Reed Bunting *Emberiza schoeniclus* and Sedge Warbler *Acrocephalus schoenobaenus* territories) (Moskva Valley, Russia, 2010–2013).

Models	*n*	*k*	AICc	ΔAICc	*w*
MPY01 + PERLCW	32	3	205.92	0	0.32
MPY01	32	2	206.67	0.75	0.22
MPY01 + PERWH	32	3	207.84	1.92	0.12
MPY01 + PERREE	32	3	208.01	2.09	0.11
MPY01 + PERYW	32	3	208.03	2.11	0.11
MPY01 + PERSED	32	3	208.41	2.49	0.09
MPY012	32	4	211.76	5.84	0.02
(*)	32	1	215.31	9.39	0.00

	Estimate	St. Err.	*z*	*p*
Intercept	34.624	3.138	11.032	4.4 e-12
MPY01	−7.065	2.023	−3.492	0.0015

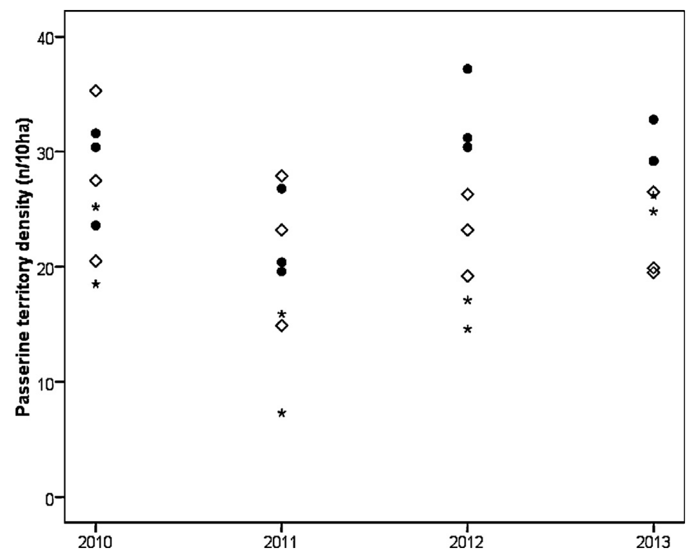

Fig. 3. Annual variation between 2010 and 2013 of passerine territory density in 8 meadow units, unmown for several years up to 2009 (n = 8) and mown in July 2010 (n = 8). In 2011 and 2012, 3 units were left unmown (black circles), 2 were mown (asterisks), whereas 3 were mown in 2011 but not in 2012 (white rhombs). (Moskva Valley, Central Russia). NB—In 2013, two black circles overlapped.

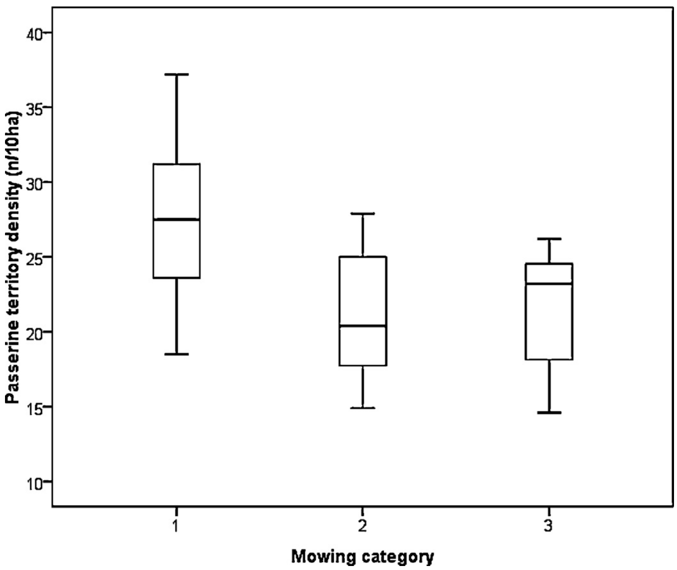

Fig. 4. Boxplot showing the variation of passerine territory density in 8 study sites between 2010 and 2013, according to mowing management in the preceding year: 1 = not mown (n = 17), 2 = mown for one year (n = 8), 3 = mown for 2 or 3 consecutive years (n = 7). (Moskva Valley, Central Russia).

Table 5
Comparison using AIC of GLMMs explaining Whinchat *Saxicola rubetra* (A) and Yellow Wagtail *Motacilla flava* (B) hatching success, with mowing management (M1 = unmown vs. mown the preceding year; M2 = unmown the preceding year vs. mown for one or more years), and with meadow passerine territory density (TD). The null model (*) includes only the intercept. (Moskva Valley, Russia, 2010–2013)

A

Models	*n*	*k*	AIC	ΔAIC	*w*
M2 + TD	248	4	308.1	0	0.60
M2	248	3	310.1	2.0	0.22
M1 + TD	248	3	312.3	4.2	0.07
M1	248	2	313.5	5.4	0.04
(*)	248	1	313.9	5.8	0.03
TD	248	2	315.2	7.1	0.03

	Estimate	St.Err.	*z*	*p*
Intercept	3.4928	1.1898	2.936	0.003
TD	−0.0708	0.0379	−1.868	0.062
M2	−0.6508	0.2211	−2.943	0.003

B

Models	*n*	*k*	AIC	ΔAIC	*w*
M1	157	2	203.7	0	0.35
(*)	157	1	204.8	1.0	0.20
M1 + TD	157	3	204.9	1.2	0.19
M2	157	3	205.7	2.0	0.13
TD	157	2	206.7	3.0	0.08
M2 + TD	157	4	207.6	3.9	0.05

the use of late mown areas remained stable throughout the experiment, as if this species was not attracted by late mown grassland areas and was characterized by a weak natal philopatry at the level of study sites (Shitikov et al., 2011; Broyer et al., 2012). However, increasing Whinchat population in the Saône Valley after AES implementation in the 1990s seems to indicate the existence of natal philopatry at the regional scale (Broyer, 2011). Higher territory density in the Corn Bunting, increased use of late mown areas by the Yellow Wagtail, are therefore robust evidences that the tested alternative management may locally improve meadow passerine abundance. In this experiment, hatching success was similar in the early mown parts of manipulated study sites and in the control sites, but was higher in late mown areas for the three most abundant species. It is not possible here to disentangle the effects of improved habitat conditions through higher invertebrate abundance (Wettstein and Schmid, 1999; Morris, 2000; Knop et al., 2006; Britschgi et al., 2006) from those of lower mortality or nest destruction by mowers. We may nevertheless conclude that increased passerine territory density did not lead to negative density dependent effects on hatching rates.

In the Vinogradovo flood plain, passerine TD was higher after an absence of mowing the preceding year. Negative effects were recorded in the Whinchat after only one year of mowing, in the Lesser Citrine Wagtail in the second year, from which this species almost disappeared in study plots. The development of tall weeds (*Rumex confertus*,*Veratrum lobelianum*, *Filipendula ulmaria*, *Thalictrum lucidum*) in meadows not regularly mown may provide preferred habitats to some species, with convenient display perches, more efficient plant cover for nests concealment, or improved conditions for invertebrate populations (Erhardt, 1985; Baur et al., 2006; Marini et al., 2009). Higher territory density after temporary mowing interruption could be the consequence of a better attractiveness of grasslands since we did not noticed important decreases in hatching rates after one year of mowing. The probability is therefore weak that reproductive outputs were strongly enhanced by intermittent mowing. Moreover, natal philopatry in meadow passerines seems to be usually low in Russia (Shitikov et al., 2011) and grass structure is a prevailing condition in habitat selection by nesting Whinchats (Broyer et al., 2012). In the Whinchat only, hatching success seemed to be negatively influenced by passerine territory density. Density dependence in Whinchat hatching success was indeed reported in France (Broyer, 2009). But the best model explaining Whinchat hatching success also contained mowing management, and the explanatory power of the model with only TD was lower than with the null model. Our results suggest that Whinchat hatching success may be density dependent in regularly mown meadows, as a possible consequence of depressed invertebrate populations or altered grass structure. We may then conclude that a temporary absence of mowing led to increased passerine density without negative consequences on hatching rates.

5. Conclusion

Despite the considerable amount of money spent annually to counteract the negative effects of modern practices in agriculture, common farmland bird numbers have on average fallen nearly by half in Europe since 1980 (Voříšek et al., 2010). This study confirms the short-term response of grassland bird density after late haying or absence of haying already described in North America (Luscier and Thompson, 2009). A further lesson is that high territory density and high nesting success are not irreducibly exclusive. We suggest to focus on a restricted network of key sites in which either late enough mowing schedules or intermittent mowing may enable to secure demographic sources for vulnerable meadow bird species. Hardly acceptable in most farming systems of Western Europe, intermittent mowing may be nowadays spontaneously implemented by farmers in Russia. Incentive to promote such a management could be a first step for this country to enter in an agri-environmental project.

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References

Baur, B., Cremene, C., Groza, L., Rakosy, Gh., Schileyko, A.A., Baur, A., Stoll, P., Erhardt, A., 2006. Effects of abandonment of subalpine hay meadows on plant and invertebrate diversity in Transylvania. Biol. Conserv. 132, 261–273.

Breeuwer, A., Berendse, F., Willems, F., Foppen, R., Teunissen, W., Schekkerman, H., Goedhart, P.W., 2009. Do meadow birds profit from agri-environment schemes in Dutch agricultural landscapes? Biol. Conserv. 142, 2949–2953.

Brehm, A.E., 1868. La vie des animaux—les oiseaux. Baillière, Paris, pp. 905.

Britschgi, A., Spaar, R., Arlettaz, R., 2006. Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the whinchat *Saxicola rubetra*: lessons for overall Alpine meadowland management. Biol. Cons. 130, 193–205.

Broyer, J., 2009. Whinchat *Saxicola rubetra* reproductive success according to hay cutting schedule and meadow passerine density in alluvial and upland meadows in France. J. Nat. Cons. 17, 160–167.

Broyer, J., 2011. Long-term effects of agri-environnent schemes on breeding passerine populations in a lowland hay-meadow system. Bird Study 58, 141–150.

Broyer, J., Curtet, L., Boissenin, M., 2012. Does breeding success lead meadow passerines to select late mown fields? J. Ornith. 153, 817–823.

Broyer, J., Sukhanova, O., Mischenko, A., 2014. Mowing management and density dependence in meadow passerine hatching success. Bird Study 61, 394–403.

Buri, P., Arlettaz, R., Humbert, J.Y., 2013. Delaying mowing and leaving uncut refuges boosts orthopterans in extensively managed meadows: evidence drawn from field-scale experimentation. Agr. Ecosyst. Environ. 181, 22–30.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Inference. Springer, Berlin.

Cattin, M.-F., Blandenier, G., Banašek-Richter, C., Bersier, L.-F., 2003. AT The impact of mowing as a management strategy for wet meadows on spider (*Araneae*) communities. Biol. Conserv. 113, 179–188.

Davey, C.M., Vickery, J.A., Boatman, N.D., Chamberlain, D.E., Parry, H.R., Siriwardena, G.M., 2010. Assessing the impact of entry level stewardship on lowland farmland birds in England. Ibis 152, 459–474.

Elmegaard, N., Andersen, P.N., Odderskaer, P., Prang, A., 1999. Food supply and breeding activity of skylarks in fields with different pesticide treatment. In: Adams, N.J., Slokow, R.H. (Eds.), Proc. 22 Int. Ornithol. Congr.. BirdLife, Durban, Johannesburg, South Africa, pp. 1058–1069.

Enemar, A., 1959. On the determination of the size and composition of a passerine bird population during the breeding season. Var Fagelvärld 2, 1–114.

Enoksson, B., Nilsson, S.G., 1983. Territory size and population density in relation to food supply in the nuthhatch *Sitta europaea*. J. Anim. Ecol. 52, 927–935.

Erhardt, A., 1985. Diurnal Lepidoptera: sensitive indicators of cultivated and abandoned grassland. J. Appl. Ecol. 22, 849–861.

Gauthier, G., 1990. Philopatry, nest-site fidelity and reproductive performance in Buffleheads. Auk 107, 126–132.

Gavin, T.A., Bollinger, E.K., 1988. Reproductive correlates of breeding site fidelity in Bobolinks (*Dolichonyx oryzirorus*). Ecology 69, 96–103.

Green, R.E., 1996. Factors affecting the population density of the corncrake *Crex crex* in Britain and Ireland. J. Appl. Ecol. 33, 237–248.

Haas, C.A., 1998. Effects of prior nesting success on site fidelity and breeding dispersal: approach. Auk 115, 926–936.

Hamer, K.C., Monaghan, P., Uttley, J.D., Walton, P., Burns, M.D., 1993. The influence of food supply on the breeding ecology of Kittiwakes *Rissa tridactyla* in Shetland. Ibis 135, 255–263.

Hatch, S.A., Hatch, M.A., 1990. Components of breeding productivity in a marine bird community: key factors and concordance. Can. J. Zool. 68, 1680–1690.

Horch, P., Spaar, R., 2007. Conservation measures for the Whinchat Saxicola rubetra in Switzerland: Struggle between effect and politic. Proceed. 6th Conference of European Ornithologists' Union, Vienna, August.

Knop, E., Kleijn, D., Herzog, F., Bernhard, S., 2006. Effectiveness of the Swiss agri-environment scheme in promoting biodiversity. J. Appl. Ecol. 43, 120–127.

Luscier, J.D., Thompson, W.L., 2009. Short-term responses of breeding birds of grassland and early successional habitat to the timing of haying in northwestern Arkansas. Condor 111, 538–544.

Marini, L., Fontana, P., Battisti, A., Gaston, K.J., 2009. Response of orthopteran diversity to abandonment of semi-natural meadows. Agr. Ecosyst. Environ. 132, 578–583.

Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. Ann. Rev. Ecol. Syst. 18, 453–487.

Mischenko, A., Sukhanova, O., 2006. Changes in agricultural land-use in Russia and their impact on wildfowl: an overview. OMPO Newsl. 26, 33–39.

Morris, M.G., 2000. The effects of structure and its dynamics on the ecology and conservation of arthropods in British grasslands. Biol. Cons. 95, 129–142.

Murphy, E.C., Springer, A.M., Roseneau, D.G., 1991. High annual variability in reproductive success of kittiwakes (*Rissa tridactyla*) at a colony in western Alaska. J. Anim. Ecol. 60, 515–534.

Orlowski, G., 2005. Endangered and declining bird species on abandoned farms in southwestern Poland. Agric. Ecosyst. Environ. 111, 231–236.

Pough, R.H., 1950. Comment faire un recensement d'oiseau nicheurs? Terre Vie 97, 203–217.

Princé, K., Moussus, J.P., Jiguet, F., 2012. Mixed effectiveness of French agri-environment schemes for nationwide farmland bird conservation. Agric. Ecosyst. Environ. 149, 74–79.

Rodenhouse, N.L., Holmes, R.T., 1992. Results of experimental and natural food reductions for black-throated warblers. Ecology 73, 357–372.

Roodbergen, M., van der Werf, B., Hötker, H., 2012. Revealing the contributions of reproduction and survival to the Europe-wide decline in meadow birds: review and meta-analysis. J. Ornith. 153, 53–74.

Schreiber, J., Kissling, W.D., 2005. Factors affecting the breeding success of arctic tern *Sterna paradisaea* in a colony at Kaldbaksbotnur, Faroe Islands. Atlantic Seabirds 7, 97–105.

Shields, W.M., 1984. Factors affecting nest and site fidelity in Adirondack born swallows (*Hirundo rustica*). Auk 101, 781–789.

Shitikov, D., Fedotova, S., Gagieva, V., Fedchuk, D., Dubkova, E., Vaytina, T., 2011. Breeding-site fidelity and dispersal in isolated populations of three migratory passerines. Orn. Fennica 88, 1–10.

Shitikov, D.A., Dubkova, E.V., Makarova, T.V., 2013. The demography of Yellow Wagtails *Motacilla flava* on abandoned fields in northern European Russia. Bird Study 60, 518–526.

Tobias, J., 1997. Food availability as a determinant of pairing behaviour in the European robin. J. Anim. Ecol. 66, 629–639.

Vergara, P., Aguirre, J.I., Fargallo, J.A., Davila, J.A., 2006. Nest-site fidelity and breeding success in White Stork *Ciconia ciconia*. Ibis 148, 672–677.

Vickery, J.A., Bradbury, R.B., Henderson, I.G., Eaton, M.A., Grice, P.V., 2004. The role of agri-environment schemes and farm management practices in reversing the decline of farmland birds in England. Biol. Conserv. 119, 19–39.

Voříšek, P., Jiguet, F., van Strien, A., Škorpilová, J., Klvaňová, A., Gregory, R.D., 2010. Trends in abundance and biomass of widespread European farmland birds: how much have we lost? B.O.U. Proceedings—Lowland Farmland Birds III . http://www.bou.org.uk/bouproc-net/lfb3/vorisek-etal.pdf.

Wettstein, W., Schmid, B., 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. J. Appl. Ecol. 36, 363–373.

Wretenberg, J., Lindström, Å., Svensson, S., Pärt, T., 2007. Linking agricultural policies to population trends of Swedish farmland birds in different agricultural regions. J. Appl. Ecol. 44, 933–9414.

Young, A., 1792. Travels During the Years 1787, 1788, & 1789: Undertaken More Particularly with a View of Ascertaining the Cultivation, Wealth Resources and National Prosperity of the Kingdom of France. W. Richardson, London.