



Effects of grassland intensification on Whinchats *Saxicola rubetra* and implications for conservation in upland habitats

GAVINO STREBEL,^{1,2} ALAIN JACOT,^{3,4*} PETRA HORCH¹ & RETO SPAAR¹

¹Swiss Ornithological Institute, Sempach CH-6204, Switzerland

²Department of Geography, University College London, Gower Street, London WC1E 6BT, UK

³Valais Field Station, Swiss Ornithological Institute, Sion CH-1950, Switzerland

⁴Institute of Ecology and Evolution - Conservation Biology, University of Bern, Erlachstrasse 9a, Bern CH-3012, Switzerland

Modern, intensive grassland management has led to strong declines in ground-nesting grassland birds, and is now increasingly threatening the last remaining strongholds of the Whinchat *Saxicola rubetra* in the Central European uplands. In this study, we assess key threats to Whinchat populations in these uplands in order to suggest appropriate conservation measures. We compared the direct threat of early mowing as well as the indirect threat resulting from a deteriorating arthropod food source in an inner-alpine valley. Five of our seven study sites were mown too early with respect to the chicks' fledging date. Such early mowing was particularly evident on the more intensively farmed, earlier mown valley bottoms than on the valley slopes. Arthropod abundance and biomass did not differ between valley bottoms and slopes. However, valley bottoms had a greater amount of unprofitable prey items such as flies. Breeding bird density was mainly determined by the degree of overlap between the mowing schedule and breeding phenology. These findings suggest that in upland grasslands at an early stage of intensification, early mowing is of greater importance for populations than possible negative effects of a reduced food source. We suggest that mowing is delayed until a sufficient proportion of nestlings are safely fledged.

Keywords: agricultural intensification, Alps, breeding phenology, grassland birds, mowing regime.

During the second half of the last century, agricultural intensification severely degraded the quality of many farmland habitats for plant and animal species (Benton *et al.* 2003, Geiger *et al.* 2010). Mechanization, use of fertilizers and pesticides, destruction of natural grassland and hedgerows, and increasing field sizes following land consolidation have greatly impoverished the structure of agricultural landscapes and have been accompanied by a widespread decline in biodiversity (Donald *et al.* 2001, Boatman *et al.* 2004, Flohre *et al.* 2011, Storkey *et al.* 2011).

Ground-nesting grassland birds in particular have shown strong declines in both Europe and

North America (Vickery *et al.* 2001, Perlut *et al.* 2008a,b) as a result of intensified meadowland management. The increased application of fertilizers, often in combination with irrigation, leads to a faster growth of grass and allows for earlier and more frequent harvests (Shrubb 2003). Such advanced mowing causes an overlap of the mowing cycle with the vulnerable nestling period, which directly threatens ground-nesting grassland birds through high nest destruction rates (Newton 2004, Perlut *et al.* 2006) and an increased mortality of incubating females (Grüebler *et al.* 2008). Strong population declines of formerly widespread European grassland breeding birds such as the Corn-crake *Crex crex* (Green & Stowe 1993) and Skylark *Alauda arvensis* (Donald *et al.* 2002) have been attributed to the direct threat of early mowing.

*Corresponding author.

Email: alain.jacot@vogelwarte.ch

Modern intensive grassland management also affects grassland birds by changing the diversity, abundance and availability of arthropod prey (Di Giulio *et al.* 2001, Marini *et al.* 2008). Fertilization and frequent mowing changes grassland structure towards a dense and tall sward with reduced plant diversity (Bastian *et al.* 1994, Fenner & Palmer 1998) and a reduced availability of invertebrate prey (Vickery *et al.* 2001, Schaub *et al.* 2010). Prey availability may further be hampered by early and frequent mowing, which increases the mortality of arthropods (Humbert *et al.* 2010), thereby reducing the number of larger insects, which are a preferred component in the nestling diet of grassland birds (Beintema *et al.* 1991, Britschgi *et al.* 2006).

Both the direct effects resulting from grassland intensification on nests and incubating females together with the indirect effects on the invertebrate food source may impact on the population persistence of grassland birds (Brickle *et al.* 2000, Schekkerman & Beintema 2007). Evidence from species such as the Whinchat *Saxicola rubetra*, a typical example of a declining, ground-breeding grassland bird, suggests that both processes can be important (Müller *et al.* 2005, Britschgi *et al.* 2006). For example, Müller *et al.* (2005) showed that the percentage of successful Whinchat broods strongly depended on mowing date, whereas Britschgi *et al.* (2006) found that nestlings were fed lower biomass in intensively managed areas and had lower fledging rates. Gruebler *et al.* (2008) showed that population decline can be further accelerated by losing incubating females due to mowing. As a result of these processes, Whinchat populations have virtually disappeared in the lowlands of Western Europe in the last 60 years and their main distribution is now confined to upland areas (Hagemeyer & Blair 1997, Schmid *et al.* 1998, Horch *et al.* 2008, Broyer 2009). According to Hulme and Cresswell (2012), recent population declines in Europe are unlikely to be explained by conditions in the wintering grounds. In their breeding grounds, grassland farming intensification is increasingly advancing towards higher altitudes (Müller *et al.* 2005, Graf & Korner 2011) and threatening the last remaining Central European strongholds of Whinchats and other grassland breeding birds. Typically, at an early stage of intensification, mowing starts to be incompatible with the Whinchat's nestling phase, whereas at an advanced stage mowing can also lead to the loss of

incubating females (Gruebler *et al.* 2008). With initial intensification processes having started in the uplands, there is now an urgent need to re-assess the effects of grassland farming intensification on Whinchats. With the aim to identify possible conservation measures, this study therefore addresses the important question of whether recent declines of Whinchats in uplands are mainly caused by immediate destructive effects of mowing on nests, or by indirect effects resulting from a deteriorated food source. We therefore investigate exposure of nests to early mowing by establishing the relationship between breeding and mowing, defined as the overlap between the period of mowing activity and the period when Whinchat young are most vulnerable to mortality caused by mowing. In addition, we estimate the arthropod abundance on hay meadows managed at different intensities.

METHODS

Study area and territory mapping

The study was conducted during the summers of 2011 and 2012 in the Upper Goms Valley (46°49'N, 8°27'E), an inner Alpine valley in the southern canton of Valais, Switzerland. Alongside the Engadine Valley, the Goms Valley now hosts one of the largest remaining Whinchat populations in Switzerland (Müller *et al.* 2005, Horch *et al.* 2008). The study area has a mean annual temperature of 3.7 °C and an annual precipitation of 1200 mm, which is distributed regularly throughout the year. Hay meadows farmed for dairy cattle are the main land cover type in the study area. The degree of grassland intensification varies over the study area. Meadows in the easily accessible valley bottoms (1350 m asl) are farmed intensively and mowing starts from mid-June, with the aim to harvest a second time at the end of August. Furthermore, liquid manure fertilizer is commonly used after harvest. Meadows on the valley slopes (1350–1550 m asl) are farmed less intensively, with later mowing and a lower fertilizer input. Seven study sites known to host breeding Whinchats were selected that differed in terms of location (valley bottom (V), valley slope (S)), field size and management intensity. The selected seven sites were in the municipalities of Geschinen (GeV, 67.67 ha), Obergesteln (OgV, 40.11 ha), Ulrichen (UIV, 19.81 ha), Oberwald (OwV, 66.21 ha), Ritzingen (RiS, 78.45 ha), Reckingen (ReS, 52.02 ha) and Geschinen (GeS,

92.55 ha). Covering a total area of 417 ha, the study sites were mostly open grassland areas with a few hedges, pastures and small fields.

In 2011, we mapped Whinchat territories in the seven selected sites, before mowing had started, along predefined routes according to standard mapping techniques (Bibby *et al.* 2000). Over six visits per site, carried out in the mornings from end May until mid-July, we mapped all Whinchats and recorded their behaviour (e.g. singing, territorial disputes, feeding behaviour). We then segregated territories based on these behavioural variables according to Schmid and Spiess (2008).

Breeding phenology

In 2011, we collected data on breeding phenology and daily extent of mowing in order to estimate the conflict between breeding and mowing schedule. A total of 27 nests (three to six per site) were surveyed at 3-day intervals to determine key data on breeding phenology of Whinchats. Hatching and fledging dates were calculated by comparing photographs of nestlings with reference images from Castell and Castell (2009), and the laying date of the first egg was estimated using data from Glutz von Blotzheim and Bauer (1988). We calculated the date by which fledglings are safe from mowing according to Tome and Denac (2011), who found that during the first days after leaving the nest, all chicks hid on the ground as a strategy to avoid predators, and did not escape if a mowing machine approached. On day 22 after hatching, 80% of the fledglings were safely fledged and would fly away from an approaching mowing machine. Our study assumes that 22 days can be considered a threshold at which the majority of nestlings avoid mortality due to mowing. We protected the 27 nests in our study from mowing by leaving an area of 100 m² around the nest unmown if the corresponding field was mown before young fledged. This nest protection method had already been successfully applied in the Engadine Valley as a conservation tool (Horch *et al.* 2008, Gruebler *et al.* 2012) and allowed us to collect data on nestling development from hatching until fledging.

Mowing schedule and conflict between breeding and mowing schedule

We surveyed the daily extent of mowing on all seven study sites in 2011. GPS-based

measurements of individual cuts were recorded from the first mowing event until 15 July, the mowing deadline for set-aside meadows at this altitude in Switzerland, using the GIS software QGIS 1.8 (Sherman 2011). We then used records in Julian date format to quantify the magnitude of overlap between breeding phenology and mowing regime per site. For each nest, we first calculated a conflict potential per nest (CN) as the date by which 80% of nestlings would be safely fledged (Tome & Denac 2011) minus the date on which 50% of the meadowland per site was cut. We then calculated the conflict potential per site (CS) as the mean of the CN from each nest within the site. Positive values of the CS indicate an overlap between breeding cycle and mowing and, thus, indicate the number of days mowing should be postponed. Negative values show that there is no acute conflict between mowing and the average breeding cycle of Whinchats.

Arthropod sampling

Arthropod sampling was performed to get an estimate of the availability and abundance of potential Whinchat prey per site. Sampling was performed in 2012, a year after the collection of Whinchat data. We performed sweep-net sampling according to Standen (2000) to collect arthropods, a method that has previously been shown to be a good indicator for Whinchat diet (Bastian *et al.* 1994). On each of the seven study sites we randomly chose 10–12 transects of 20-m length on which we performed 20 strokes through the sward at equal intensity (Oppermann 1999, Di Giulio *et al.* 2001). Sweep netting was done on 20 and 21 June 2012 between 10:00 and 17:00 h and under good weather conditions (≥ 16 °C, sunshine, windspeed < 2 on the Beaufort scale). Mowing of meadows had not yet started, and therefore there were no effects of mowing on arthropod numbers (Humbert *et al.* 2010). Arthropod samples from each transect were immediately conserved in 70% ethanol. We later identified arthropod abundance to order (Aranea, Coleoptera, Orthoptera, Hymenoptera) and suborder (Brachycera, Nematocera, Auchenorrhyncha, Sternorrhyncha, Heteroptera). Due to their clumped occurrence (i.e. large numbers caught close to anthills), ants (Formicidae) were not included in the analysis, and larval stages of holometabolic insects were grouped as larvae. To estimate the arthropod biomass of each

transect, arthropods were dried in an oven for 48 h at 60 °C (Southwood 1978) and weighed with a precision balance to the nearest 0.001 g.

Statistical analyses

All statistical analyses were performed with R 3.0.2 (R Development Core Team 2013). Mowing schedule was analysed by partitioning each site into 100 units where the exact date of mowing was known for each unit. Differences in mowing dates between sites were analysed comparing the dates of the 100 units in a non-parametric approach with a Kruskal–Wallis test. Laying date, mowing date, arthropod abundance, biomass and composition (i.e. principal components, function ‘*princomp*’) in relation to study site and location (valley bottom/valley slope) were analysed with linear models (function ‘*glm*’) with site and location as fixed factors. When analysing the relationship between mowing conflict and breeding density, we used the mean CS per site.

RESULTS

Breeding phenology and mowing schedule

The breeding cycle of the observed nests ranged between 22 May (first clutches initiated) and 17 July (fledging, day 22 of latest nest). The last clutches were initiated on 8 June. The laying date of the first egg differed between sites ($F_{6,20} = 13.21$, $P < 0.01$) but there was no effect of location ($F_{1,25} = 3.38$, $P = 0.09$). Post-hoc tests revealed that the laying date at the site OwV differed from all other sites (all $P < 0.01$), showing a delay of 9 days compared with the mean laying date of other sites. Nestlings reached the fledging age of 22 days between 30 June and 17 July (Fig. 1a), and 80% of the nests were safely fledged (day 22) by 6 July.

Mowing in the Goms Valley strongly depended on weather conditions and took place only on days without precipitation. Over the whole observation period of 53 days, mowing of hay meadows occurred on 19 days. We found significant differences in the timing of mowing between sites ($\chi^2_6 = 507$, $P < 0.001$), with sites ReS and GeS being mown the latest (see Fig. 1a). Furthermore, intensively farmed valley bottoms were mown earlier than the more extensively farmed valley slopes ($\chi^2_1 = 342$, $P < 0.001$).

Conflict between breeding and mowing

CS differed between sites ($F_{5,20} = 50.31$, $P < 0.001$) and location ($F_{1,25} = 196.78$, $P < 0.001$), with an increased conflict in the valley bottom compared with the slopes. Only the latest mown sites, ReS and GeS, showed no conflict between mowing and breeding; in all other sites, half of the area was mown before 80% of the offspring were safely fledged (Fig. 1a). The variation in CS is largely due to the time of mowing ($r = -0.89$, $n = 27$; conflict vs. 50% mown date) and to a lesser degree to the onset of Whinchat breeding ($r = 0.51$, $n = 27$, conflict vs. day 22 when 80% of young safely fledged), indicating that early mowing and not differences in the breeding phenology among sites was primarily responsible for the conflict. Mowing did not coincide with the incubation period on any of the sites.

We found a total of 184 territories before mowing, with an average territory density across the whole study area of 4.4 territories per 10 ha. Territory density varied between sites (Fig. 1c), ranging from a maximum of 6.3/10 ha (ReS) to a minimum of 1.2/10 ha (OwV), and was affected by the location (mean \pm 1 se difference between bottom and slope = -0.13 ± 0.046 , $t = -2.95$, $P = 0.03$) with higher densities on the slopes. Variation in breeding density was significantly explained by the magnitude of CS (-0.015 ± 0.005 , $t_5 = -3.08$, $P = 0.03$; Fig. 2).

Site-specific arthropod abundance and composition

We collected a total of 15 101 arthropods (Table 1). They were mainly Diptera (55%) and Hemiptera (33%). Arthropods varied between sites (abundance: $F_{6,65} = 2.74$, $P = 0.02$, Fig. 1b; biomass: $F_{6,50} = 1.33$, $P = 0.26$), whereas there was no difference in relation to location (abundance: $F_{1,70} = 0.18$, $P = 0.67$; biomass: $F_{1,55} = 0.24$, $P = 0.63$). Further, there was no detectable relationship between arthropods and CS (abundance: $t_5 = -0.36$, $P = 0.73$; biomass: $t_5 = -1.15$, $P = 0.30$). Using a principal components analysis, we detected significant differences in arthropod composition among sites (PC1: $F_{6,65} = 12.86$, $P < 0.001$; PC2: $F_{6,65} = 2.22$, $P = 0.05$; PC3: $F_{6,65} = 2.70$, $P = 0.02$; see Tables 1 & 2), location (PC1: $F_{1,70} = 75.40$, $P < 0.001$; PC2: $F_{1,70} = 3.00$, $P = 0.09$; PC3: $F_{1,70} = 0.68$, $P = 0.41$;

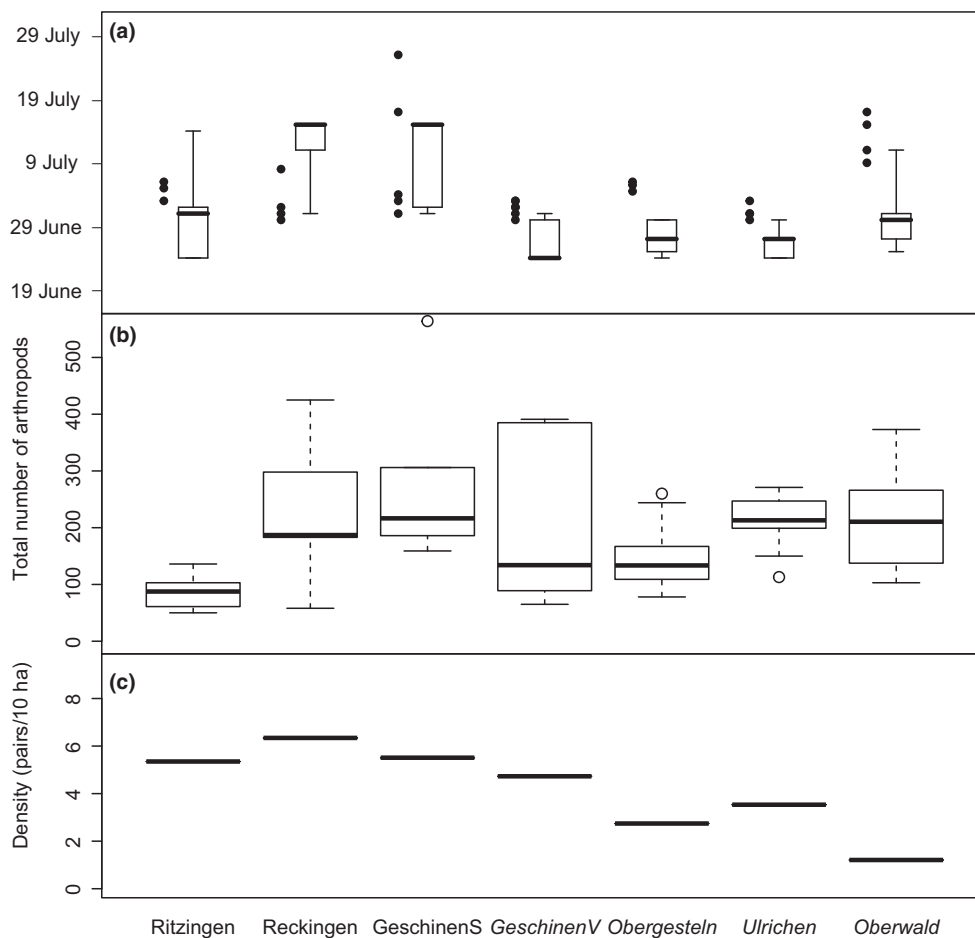


Figure 1. (a) Conflict between breeding phenology and mowing schedule per site, where sites in the valley bottom are indicated in italics (dots: day 22 when 80% of young are safe from mowing; boxplots: the 25%, 50% (bold line) and 75% limits of the grassland area mown; whiskers: 10% and 90% deciles). (b) Total number of arthropods per site. The boxplots indicate the 25%, 50% (bold line) and 75% limits of arthropod abundance, whiskers the 10% and 90% deciles. Open dots indicate outliers. (c) Territory density of Whinchats in the seven study sites.

Tables 1 & 2) and in relation to CS (PC1: $t = -3.69$, $P = 0.01$; PC2: $t = 1.03$, $P = 0.35$; PC3: $t = 0.35$, $P = 0.74$). The first principal component (PC1) was positively related to the number of orthopterans (i.e. grasshoppers) and heteropterans (i.e. bugs), and the second component (PC2) mainly represented an increased number of Brachycera (flies), Nematocera (mosquitoes) and Sternorrhyncha (mainly aphids; see Table 2 for details).

DISCUSSION

We assessed the effects of grassland intensification on the overlap between the Whinchat breeding period and timing of mowing activities, and the

abundance of arthropod food. We observed a considerable conflict for nearly all sites, indicating that early mowing is impacting on the breeding schedule of Whinchats in large parts of our study area. Similar to other inner-alpine valleys (Schifferli *et al.* 1999, Müller *et al.* 2005), we found valley bottoms to be mown earlier, indicating an advanced stage of intensification compared with areas on the slopes. Müller *et al.* (2005) estimated that at least 40% of Whinchat pairs must successfully raise young to maintain the local population. These reference values are very unlikely to be matched in valley bottoms in our study area, where we found 88% of meadows to be mown too early. Our estimates of the conflict may be slightly underestimated, as we most likely found early

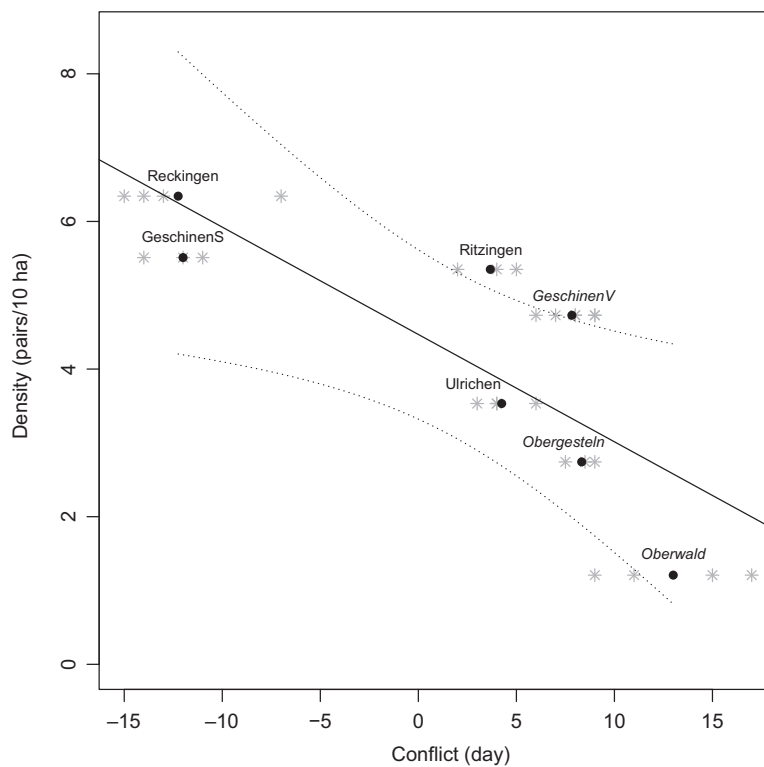


Figure 2. Relationship (\pm 95%CI) between the mowing conflict and the breeding density ($n = 27$). The grey stars show the data for each nest and the black dots show the mean value per site. Sites in the valley bottom are indicated in italics.

nests within the season and did not specifically search for late nests or replacement clutches later in the season. Despite this, our data on breeding phenology and mowing dates indicate that early mowing does not yet conflict with the incubation period of first broods and will not affect female mortality. This is in contrast to results from the Engadine Valley (Grüebler *et al.* 2008), where female mortality strongly increased during the period of mowing. In our study population, females losing a first brood may still be able to invest in a replacement clutch, thereby ensuring some current reproductive success, which may prevent or at least slow down the population decline, and may temporarily blur the negative impacts of agricultural intensification. Mowing does not yet seem to constitute a considerable threat to Whinchats on only a few sites on the valley slopes. Under these mowing regimes, Whinchat populations should still be able to persist over a long term, and could even act as source populations for marginal populations in the intensified valley bottoms that persist over the years with a few individuals (Watkinson

& Sutherland 1995, Müller *et al.* 2005). However, our results demonstrate that the mowing schedule has also started to be incompatible with populations breeding on the slopes, and we therefore expect an overall population decline over the longer term in the whole study area.

Regarding the food source of Whinchats, we found that biomass did not significantly differ between valley bottoms and slopes and was unrelated to the mowing conflict, which suggests that even on more intensively farmed meadows, there should still be enough prey available for Whinchats. Despite the arthropod data being collected a year later than the Whinchat data, we believe that a comparison is legitimate, as variation in arthropod abundance and diversity among sites in relation to an intensification process is likely to be highly repeatable among years (e.g. Potts *et al.* 2009). While there might be strong year differences in the overall abundance of arthropods, we expect similar within-year differences in abundance and diversity among sites (Potts *et al.* 2009). Although overall arthropod abundance and biomass have not yet been affected by management

Table 1. Mean (± 1 sd) number per visit ($n = 6$) of arthropod taxa collected in the seven study sites using the sweep-netting method. Sites in the valley bottom are indicated in italics.

Invertebrate group	Ritzingen	Reckingen	Geschinen Slope	Geschinen Valley	Ulrichen	Obergesteln	Oberwald
Araneae	0.1 \pm 0.32	0.4 \pm 0.70	0.9 \pm 0.99	0.2 \pm 0.42	0.6 \pm 0.70	0.3 \pm 0.67	0.33 \pm 0.65
Diptera (Brachycera)	30.5 \pm 15.45	60.2 \pm 29.26	52.2 \pm 18.30	267.1 \pm 494.95	111.8 \pm 29.87	81.8 \pm 39.85	138.58 \pm 51.23
Diptera (Nematocera)	5.7 \pm 5.46	6.1 \pm 4.91	16.8 \pm 14.57	8.8 \pm 10.03	15.7 \pm 9.87	3 \pm 4.16	8.83 \pm 11.57
Hymenoptera (other)	1.5 \pm 1.27	4.4 \pm 2.84	3.7 \pm 2.31	3.2 \pm 4.66	2.3 \pm 2.21	3 \pm 2.11	3.67 \pm 3.70
Coleoptera	10.5 \pm 4.55	5.2 \pm 3.22	12.3 \pm 9.23	3.5 \pm 4.72	5.5 \pm 4.01	3.7 \pm 2.83	2.67 \pm 3.58
Orthoptera	0.6 \pm 0.70	0.8 \pm 1.48	2.8 \pm 1.93	0.8 \pm 1.32	0.6 \pm 1.07	0.1 \pm 0.32	0.08 \pm 0.29
Hemiptera (Heteroptera)	3.3 \pm 3.40	86.8 \pm 68.68	115.7 \pm 101.01	4.4 \pm 3.2	6.6 \pm 4.81	5.9 \pm 5.80	3.42 \pm 3.84
Hemiptera (Stenomorrhyncha)	14.5 \pm 12.33	2.6 \pm 2.22	17.8 \pm 17.52	12.2 \pm 10.10	8.6 \pm 7.03	5.6 \pm 4.70	22.08 \pm 24.60
Hemiptera (Auchenorrhyncha)	13.9 \pm 9.64	45.4 \pm 52.38	27.1 \pm 16.33	20.4 \pm 32.14	30.8 \pm 12.04	15.9 \pm 10.37	6.92 \pm 8.40
Larvae	4.2 \pm 3.94	9.8 \pm 7.91	4.5 \pm 3.50	9.2 \pm 11.25	27.1 \pm 21.63	27 \pm 24.50	23.83 \pm 31.16

Table 2. The first three principal components of the sampled invertebrate taxa. Values indicate the factor loadings, i.e. the correlation coefficients between the components and the collected invertebrate abundance. Loadings below 0.1 are represented by a dash.

Variable	PC 1	PC 2	PC 3
Araneae	0.229	–	–0.176
Brachycera	–	0.465	–
Nematocera	0.234	0.631	–
Hymenoptera	0.149	0.211	0.628
Coleoptera	0.415	–	–0.460
Orthoptera	0.538	–	–0.259
Heteroptera	0.369	–0.127	0.251
Stenomorrhyncha	–	0.525	–
Auchenorrhyncha	0.376	–0.123	0.475
Larvae	–0.354	0.160	–
Eigenvalue	1.49	1.29	1.18
Cumulative %	20.09	37.33	51.02

intensity in our study area, we still found effects of intensification on arthropod composition. Particularly striking was the higher abundance of Diptera on several intensified areas (Britschgi *et al.* 2006), which is likely to be a consequence of intensive fertilization with dung or liquid manure (D'Arcy-Burt & Blackshaw 1991). Early and more frequent mowing is known to be particularly detrimental to larger and less mobile insects (Beintema *et al.* 1991, Bastian *et al.* 1994, Humbert *et al.* 2010), which may partly explain the near absence of grasshoppers in intensified areas. If the intensification process is on-going, such changes in arthropod composition may have effects on Whinchat reproduction. Zalik and Strong (2008) have shown that the destruction of arthropods through mowing may not be a serious threat to reproduction of grassland birds. In their study, Savannah Sparrows *Passerculus sandwichensis* were able to re-nest successfully shortly after mowing. Despite the reduction in invertebrate biomass by up to 82% on cut fields, there was no reduction in clutch size or average nestling mass. Although Whinchats would not show the same behaviour as Savannah Sparrows and re-nest in fully harvested fields, the study by Zalik and Strong (2008) indicates that nest destruction can be the limiting factor for population persistence of grassland birds.

Overall, our results suggest that in the Goms Valley and other upland grasslands at an initial stage of intensification, early mowing is the key threat to Whinchat nestling survival and reproduction. In comparison, the threat from a deterioration

of the arthropod food source seems to be of less concern, at least at an early stage of intensification. For the conservation of Whinchats and other ground-nesting grassland birds, it is therefore essential to avoid mowing during the critical nestling stage. Setting aside grassland areas to be harvested after nestlings are safely fledged is the most commonly used solution for several ground-nesting grassland birds (Müller *et al.* 2005, Perlut *et al.* 2006, Gruebler *et al.* 2012). Our data indicate that mowing should be postponed by an average of 8 days to ensure a survival of 80% of the nestlings. However, in hay meadows managed for dairy cattle, such as in our study site, postponing mowing is problematic from a farmer's perspective, as the nutritional value decreases if grass is cut later. Therefore, Perlut *et al.* (2011) have presented an alternative conservation model for North American grassland breeding birds in intensively managed lowland hayfields whereby mowing is advanced to the egg-laying or incubation period. This allows farmers to get in an early first harvest with sufficient protein content, but also allows birds to re-nest if their breeding cycle was interrupted by mowing activities. Farmers were then allowed to collect a late harvest of greater quantity, but decreased nutritional quality, after the nesting cycle was completed. This alternative model is interesting but is expected to be a less viable option for Whinchat populations breeding in upland meadows. First, advancing the mowing date to the incubation period is likely to increase female mortality (Gruebler *et al.* 2008). Secondly, a further advancement of on average 32 days into the pre-nesting period is not feasible given the low sward height in upland regions, but may be an interesting alternative for lowland populations of Whinchats or other ground-breeding grassland species. Consequently, precise knowledge about a species' breeding phenology at specific locations is essential for the appropriate recommendation of mowing schedules.

For the preservation of Whinchat populations and other ground-nesting grassland birds in upland regions, we therefore recommend first and foremost that grassland areas are set aside to be harvested after nestlings are safely fledged. In accordance with previous studies (Gruebler *et al.* 2008, Fischer *et al.* 2013) we recommend a delay in cutting until at least mid-July in the Goms Valley in order to reduce significantly the probability of loss of Whinchat broods and incubating females.

Ideally, such earlier dates for cutting should be implemented within agri-environmental schemes (Fischer *et al.* 2013). As Whinchats seem to favour south- over north-facing slopes for settlement decisions (Calladine & Bray 2012), the aspect of a given site should be considered within efforts to delay mowing schedules. Given that most intensification processes are on-going, we might also need conservation measures targeted at maintaining arthropod-rich grasslands. In particular, set-asides as refuges for arthropods and low input of fertilizers would be a key combination to promote both plant and arthropod diversity and hence grassland bird populations.

We would like to thank David Berthold, Daniel Muff and Stephanie Michler for assistance in the field. Furthermore, we thank all the farmers in the Goms Valley who collaborated within the framework of this study.

REFERENCES

- Bastian, A., Bastian, H.-V. & Sternberg, H.E. 1994. Ist das Nahrungsangebot für die Brutrevierwahl von Braunkehlchen *Saxicola rubetra* entscheidend? *Vogelwelt* **115**: 103–114.
- Beintema, A.J., Thissen, J.B., Tensen, D. & Visser, G.H. 1991. Feeding ecology of Charadriiform chicks in agricultural grassland. *Ardea* **79**: 31–43.
- Benton, T.G., Vickery, J.A. & Wilson, J.D. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.* **18**: 182–188.
- Bibby, C.J., Burgess, N.D., Hill, D.A. & Mustoe, S.H. 2000. *Bird Census Techniques*, 2nd edn. London: Academic Press.
- Boatman, N.D., Brickle, N.W., Hart, J.D., Milsom, T.P., Morris, A.J., Murray, A.W.A., Murray, K.A. & Robertson, P.A. 2004. Evidence for the indirect effects of pesticides on farmland birds. *Ibis* **146**: 131–143.
- Brickle, N.W., Harper, D.G.C., Aebischer, N. & Chockayne, S.H. 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. *J. Appl. Ecol.* **37**: 742–755.
- 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.
- Calladine, J. & Bray, J. 2012. The importance of altitude and aspect for breeding Whinchats *Saxicola rubetra* in the uplands: limitations of the uplands as a refuge for a declining, formerly widespread species? *Bird Study* **59**: 43–51.
- Castell, P. & Castell, R. 2009. *Breeding Birds of the Western Palearctic: Nests, Eggs, Nestlings, Fledglings and Habitats, DVD-Rom*. London: Birdguides Ltd.

- D'Arcy-Burt, S. & Blackshaw, R.P.** 1991. Bibionids (Diptera: Bibionidae) in agricultural land: a review of damage, benefits, natural enemies and control. *Ann. Appl. Biol.* **118**: 695–708.
- Di Giulio, M., Edwards, P.J. & Meister, E.** 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *J. Appl. Ecol.* **38**: 310–319.
- Donald, P.F., Green, R.E. & Heath, M.F.** 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R. Soc. Lond. B* **268**: 25–29.
- Donald, P.F., Evans, A.D., Muirhead, L.B., Buckingham, D.L., Kirby, W.B. & Schmitt, S.E.** 2002. Survival rates, causes of failure and productivity of Skylark *Alauda arvensis* nests on lowland farmland. *Ibis* **144**: 652–664.
- Fenner, M. & Palmer, L.** 1998. Grassland management to promote diversity: creation of a patchy sward by mowing and fertilizer regimes. *Field Stud.* **9**: 313–324.
- Fischer, K., Busch, R., Fahl, G., Kunz, M. & Knopf, M.** 2013. Habitat preferences and breeding success of Whinchats (*Saxicola rubetra*) in the Westerwald mountain range. *J. Ornithol.* **154**: 339–349.
- Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clemet, L.W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M.B., Oñate, J.J., Pärt, T., Weisser, W.W., Winqvist, C., Thies, C. & Tschardtke, T.** 2011. Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids, and birds. *Ecol. Appl.* **21**: 1772–1781.
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W. & Inchausti, P.** 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic Appl. Ecol.* **11**: 97–105.
- Glutz von Blotzheim, U.N. & Bauer, K.M.** 1988. *Handbuch der Vögel Mitteleuropas*, Vol. 11. Wiesbaden: Aula.
- Graf, R. & Korner, P.** 2011. *Veränderungen in der Kulturlandschaft und deren Brutvogelbestand im Engadin zwischen 1987/88 und 2009/10*. Sempach: Schweizerische Vogelwarte.
- Green, R.E. & Stowe, T.J.** 1993. The decline of the corncrake *Crex crex* in Britain and Ireland in relation to habitat change. *J. Appl. Ecol.* **30**: 689–695.
- Grübler, M.U., Schuler, H., Müller, M., Spaar, R., Horch, P. & Naef-Daenzer, B.** 2008. Female biased mortality caused by anthropogenic nest loss contributes to population decline and adult sex ratio of a meadow bird. *Biol. Cons.* **141**: 3040–3049.
- Grübler, M.U., Schuler, H., Horch, P. & Spaar, R.** 2012. The effectiveness of conservation measures to enhance nest survival in a meadow bird suffering from anthropogenic nest loss. *Biol. Cons.* **146**: 197–203.
- Hagemeijer, E.J.M. & Blair, M.J.** 1997. *The EBCC Atlas of European Breeding Birds*. London: Poyser.
- Horch, P., Rehsteiner, U., Berger-Flückiger, A., Müller, M., Schuler, H. & Spaar, R.** 2008. Bestandesrückgang des Braunkehlchens *Saxicola rubetra* in der Schweiz, mögliche Ursachen und Evaluation von Fördermassnahmen. *Ornithol. Beobacht.* **105**: 267–298.
- Hulme, M.F. & Cresswell, W.** 2012. Density and behaviour of Whinchats *Saxicola rubetra* on African farmland suggest that winter habitat conditions do not limit European breeding populations. *Ibis* **154**: 680–692.
- Humbert, J., Ghazoul, J., Sauter, G.J. & Walter, T.** 2010. Impact of different meadow mowing techniques on field invertebrates. *J. Appl. Entomol.* **134**: 592–599.
- Marini, L., Fontana, P., Scotton, M. & Klimek, S.** 2008. Vascular plant and orthoptera diversity in relation to grassland management and landscape composition in the European Alps. *J. Appl. Ecol.* **45**: 361–370.
- Müller, M., Spaar, R., Schifferli, L. & Jenni, L.** 2005. Effects of changes in farming of subalpine meadows on a migrant bird, the Whinchat (*Saxicola rubetra*). *J. Ornithol.* **145**: 14–23.
- Newton, I.** 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* **146**: 579–600.
- Oppermann, R.** 1999. Nahrungsökologische Grundlagen und Habitatansprüche des Braunkehlchens *Saxicola rubetra*. *Vogelwelt* **120**: 7–25.
- Perlut, N.G., Strong, A.M., Donovan, T.M. & Buckley, N.J.** 2006. Grassland songbirds in a dynamic management landscape: behavioral responses and management strategies. *Ecol. Appl.* **16**: 2235–2247.
- Perlut, N.G., Strong, A.M., Donovan, T.M. & Buckley, N.J.** 2008a. Grassland songbird survival and recruitment in agricultural landscapes: implications for source-sink demography. *Ecology* **89**: 1941–1952.
- Perlut, N.G., Strong, A.M., Donovan, T.M. & Bugter, R.** 2008b. Regional population viability of grassland songbirds: effects of agricultural management. *Biol. Cons.* **141**: 3139–3151.
- Perlut, N.G., Strong, A.M. & Alexander, T.J.** 2011. A model for integrating wildlife science and agri-environmental policy in the conservation of declining species. *J. Wildl. Manage.* **75**: 1657–1663.
- Potts, S.G., Woodcock, B.A., Roberts, S.P.M., Tschudin, T., Pilgrim, E.S., Brown, V.K. & Tallowin, J.R.** 2009. Enhancing pollinator biodiversity in intensive grasslands. *J. Appl. Ecol.* **46**: 369–379.
- R Development Core Team.** 2013. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. www.R-project.org/.
- Schaub, M., Martinez, N., Tagmann-Isoset, A., Weisshaupt, N., Maurer, M.L., Reichlin, T.S., Abadi, F., Zbinden, N., Jenni, L. & Arlettaz, R.** 2010. Patches of bare ground as a staple commodity for declining ground-foraging insectivorous farmland birds. *PLoS ONE* **5**: 1–5.
- Schekckerman, H. & Beintema, A.J.** 2007. Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management. *Ardea* **95**: 39–54.
- Schifferli, L., Fuller, R.J. & Müller, M.** 1999. Distribution and habitat use of bird species breeding on Swiss farmland in relation to agricultural intensification. *Vogelwelt* **120**: 151–161.
- Schmid, H. & Spiess, M.** 2008. *Brutvogelaufnahmen bei BDM-Z7 und MHB: Anleitung zur Entscheidungsfindung bei*

- Grenzfällen und zur Revierausscheidung*. Sempach: Schweizerische Vogelwarte.
- Schmid, H., Luder, R., Naef-Daenzer, B., Graf, R. & Zbinden, N.** 1998. *Schweizer Brutvogelatlas. Verbreitung der Brutvögel in der Schweiz und im Fürstentum Liechtenstein 1993–1996*. Sempach: Schweizerische Vogelwarte.
- Sherman, G.E.** 2011. Quantum GIS 1.8.0. Available at: www.qgis.org (13 December 2013).
- Shrubb, M.** 2003. *Birds, Scythes and Combines*. Cambridge: Cambridge University Press.
- Southwood, T.R.E.** 1978. *Ecological Methods*. London: Chapman and Hall.
- Standen, V.** 2000. The adequacy of collecting techniques for estimating species richness of grassland invertebrates. *J. Appl. Ecol.* **37**: 884–893.
- Storkey, J., Meyer, S., Still, K.S. & Leuschner, C.** 2011. The impact of agricultural intensification and land-use change on the European arable flora. *Proc. R. Soc. Lond. B* **279**: 1421–1429.
- Tome, D. & Denac, D.** 2011. Survival and development of predator avoidance in the post-fledging period of the Whinchat (*Saxicola rubetra*): consequences for conservation measures. *J. Ornithol.* **153**: 131–138.
- Vickery, J.A., Tallowin, J.R., Feber, R.E., Asteraki, E.J., Atkinson, P.W., Fuller, R.J. & Brown, V.K.** 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food. *J. Appl. Ecol.* **38**: 647–664.
- Watkinson, A.R. & Sutherland, W.J.** 1995. Sources, sinks and pseudo-sinks. *J. Anim. Ecol.* **64**: 126–130.
- Zalik, N.J. & Strong, A.M.** 2008. Effects of hay-cropping on invertebrate biomass and the breeding ecology of Savannah Sparrows (*Passerculus sandwichensis*). *Auk* **125**: 700–710.

Received 1 April 2014;
 revision accepted 4 February 2015.
 Associate Editor: Robert Fletcher.