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Survival and development of predator avoidance in the post-fledging period of the Whinchat (*Saxicola rubetra*): consequences for conservation measures

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Abstract Farmland bird populations in Europe are shrinking, largely due to modern agriculture practices. In grasslands, the shift to early mowing is believed to be particularly responsible for this decline because it is interwoven with breeding time—a change that birds in general have not adapted to. We studied the post-fledging survival of the Whinchat, an altricial grassland passerine. Based on a sample of 74 radiotagged young Whinchats, we confirmed that they fledge at 13–15 days. Twenty-four fledged birds died, while 18 of them were depredated. The survival probability of young Whinchats, calculated using Kaplan–Meier estimates, was lowest during the first day after fledging, and slowly leveled off later. In total, the probability that a juvenile survived the first month after fledging was 0.52. During the first days after fledging, all chicks were found hiding on the ground among the grass stubble. The generalized linear mixed model predicts that half of the fledglings at 20 days old and 20% at 22 days old (8–10 days after fledging) will not escape but will instead remain still when approached by a threat. Sixteen depredations occurred during this period, all by mammal predators. Afterwards, the fledglings changed their strategy, escaping through flight. After 12 days, more and more of the chicks were found exposed on top of the grass or on the bush instead of hiding on the ground. The transition from sit and hide to escape behavior reduced the predation rate considerably. Only two chicks were depredated later, both by an avian predator. Due to the initial predator avoidance strategy, the current conservation measure (to postpone mowing until the chicks in 80% of all nests have fledged) is not sufficient to halt population decline on improved meadows. We suggest that at least 10 days more, and possibly even 14 days more, are necessary to maintain viable Whinchat populations.

Keywords Whinchat · *Saxicola rubetra* · Post-fledging survival · Mortality causes · Conservation measures · Mowing regime

Zusammenfassung Die Praktiken in der modernen Landwirtschaft führen in Europa zu einer Abnahme der Vogelpopulationen auf Ackerland. Vor allem der Wechsel hin zu früher Gras-Mahd wird dafür verantwortlich gemacht, weil diese immer häufiger in die Brutzeit fällt—eine Veränderung, an die sich die Vögel nicht anpassen konnten. Wir untersuchten das Überleben in der Zeit direkt nach dem Flüggewerden bei Braunkehlchen, einem Nesthocker unter den auf Wiesen lebenden Singvögeln. Anhand von 74 mit Sendern versehenen, jungen Braunkehlchen konnten wir bestätigen, dass sie im Alter von 13 bis 15 Tagen flügge werden. 24 der markierten Vögel fielen aus, weil sie starben; 18 von ihnen wurden erbeutet. Die Überlebenswahrscheinlichkeit der jungen Braunkehlchen wurde mit der Kaplan-Meier-Methode eingeschätzt; sie war in den ersten fünf Tagen nach dem Flüggewerden am niedrigsten und pendelte sich danach langsam ein. Insgesamt lag die Überlebenswahrscheinlichkeit für den ersten Monat nach Flüggewerden bei 0,52. In den ersten Tagen versteckten sich alle Küken zwischen den Grasstoppeln am Boden. Das generalisierte lineare gemischte Modell (GLMM) sagt voraus, dass 50% der Küken am 20. Tag nach Schlüpfen, 20% im Alter von 22 Tagen (8–10 Tage nach Flüggewerden), bei einer Bedrohung nicht fliehen,

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sondern sich ganz ruhig verhalten. Sechzehn der Tiere wurden in dieser Zeit aufgestört, allesamt von Säugetieren, und änderten daraufhin ihre Strategie, indem sie aufflogen und flohen. Nach 12 Tagen gab es immer mehr Küken, die auf den Grasbüscheln zu sehen waren, anstatt sich am Boden zu verstecken. Dieser Wechsel vom sich Hinhocken und Verstecken zu einem Fluchtverhalten senkte die Rate der erbeuteten Küken beträchtlich. Nur zwei Küken wurden anschließend noch erbeutet, beide von Raubvögeln. Wegen dieser frühen Räubervermeidungs-Strategie reicht die derzeitige Schutzmaßnahme, das Mähen der Wiesen aufzuschieben, bis die Küken von 80% aller Nester flügge sind, nicht aus, um den Rückgang der Populationen auf den genutzten Wiesen aufzuhalten. Wir schlagen vor, dass mindestens 10, besser aber noch 14, zusätzliche Tage gewartet werden sollte, um lebensfähige Braunkehlchen-Populationen zu erhalten.

Introduction

When hatchlings of altricial birds hatch they are so poorly developed that they spend their first week in the nest totally dependent on parents for food and protection. After fledging, they still need parental assistance for quite some time, and the mortality rate due to predation is high. The only predator avoidance strategy they have initially is to hide or stay still when they hear a warning call from their parents (Gill 1995). However, this strategy is clearly very ineffective if you are a grassland bird living in the twenty-first century and the anti-predator warning call is issued in response to an incoming agricultural machine. Hence, being killed due to agriculture activity is an important threat to today's grassland birds. This threat became significant following changes in mowing techniques about 30 or 40 years ago (Newton 2004). This resulted in a large-scale decline in farmland bird populations all across Europe (Tucker and Heath 1994; Donald et al. 2001; Vickery et al. 2001; Henderson et al. 2004). In particular, one of the most relevant changes was the move from hay to silage, which led to earlier mowing dates (Shrubb 2003), turning meadows into ecological traps (Green et al. 1997; Wakeham-Dawson and Smith 2000; Kokko and Sutherland 2001; Schlaepfer et al. 2002).

The Whinchat (*S. rubetra*) is an altricial, insectivorous passerine and a long-distance migrant. In Europe, it is confined to grasslands, where it forages and nests (Urquhart 2002). It is considered an indicator species of traditionally managed meadows (Flade 1994; Müller et al. 2005; Britschgi et al. 2006). Large declines in Whinchat populations have been reported in recent decades in 19 western and central European countries (Bastian and

Bastian 1994; BirdLife International 2004): the species is extinct in lowland meadows of Western Europe, with the exception of some alluvial flooded plains (Maumary et al. 2007; Horch et al. 2008; Broyer 2009). In the stronghold of the Slovenian Whinchat population, Ljubljansko barje (central Europe), the population has decreased by 50% in the last 10 years (Denac 2007). Besides habitat changes and the consequent lack of invertebrate food (Britschgi et al. 2006), mortality caused by earlier mowing of grasslands is held to be the factor most responsible for this decline (Müller et al. 2005; Grüebler et al. 2008; Broyer 2009). The suggested conservation measure to tackle the problem is to postpone mowing until 80% of the population have fledged (Broyer 2009). However, it remains unclear whether this measure is appropriate, and what would constitute a successful conservation measure (Aebischer et al. 2000; Chamberlain et al. 2000; Swash et al. 2000; Kleijn and van Zuijlen 2004).

Until now, data on the mortality of young Whinchats have only been collected from nests in meadows that are heavily affected by human management, where mowing during pre-fledging time is the prime cause of the mortality (Müller et al. 2005; Britschgi et al. 2006; Grüebler et al. 2008). The other published information concerning mortality relates to their return rate in the following years and apparent annual mortality (Schmidt and Hantge 1954; Bezzel and Stiel 1975; Parker 1990; Müller et al. 2005). There is a complete lack of survival and behavioral data on juvenile Whinchats after fledging and before their first migration. Therefore, the main aim of this study was (i) to present the causes of mortality and the survival rate of fledged Whinchats in situations free of mowing interference, and (ii) to describe predator-avoidance behavior in the first week out of the nest, since juvenile escape behavior may be a key factor in the sensitivity of this species to predation and the threat from mowing. We also estimate the proportion of the population of young birds which fail to return to the natal ground in the following year that can be explained by mortality in their first year before migration.

Methods

Study species

Whinchat is a typical ground-nesting grassland bird species which usually has one brood/year (Glutz von Blotzheim and Bauer 1988). It selects a wide variety of grasslands from late mown, unimproved grasslands to intensive early mown ones for breeding (Bezzel and Stiel 1975; Opperman 1992; Britschgi et al. 2006). Relatively late (in May), adult birds build well-hidden nests on the ground between the

grass stubbles (Bastian and Bastian 1996). Eggs hatch after incubation for 12–13 days, young birds leave the nest at an age of 13–15 days, and 2 days later they are able to fly (Schmidt and Hantge 1954). Mowing while eggs or young are in the nest is fatal (Bastian and Bastian 1996).

Study area

The fieldwork was carried out on 100 ha of unimproved grasslands on Ljubljansko barje, near Ljubljana, the Slovenian capital (45°40′N, 14°30′E). Extensive grasslands mown once per year predominate (about 80%) within the area, with the rest being heavily cattle-loaded pastures. Mowing on the grasslands occurs late, starting at the end of May, with half of the area mown by the end of June (Denac 2007). Since Whinchats in the study area start to breed well beforehand (the earliest date that breeding commenced in the period 2002–2006 was 30th April; the latest was 6th June; Denac 2007), very few nests are destroyed by mowing.

Data collection

Fifty to eighty Whinchat nests were found each year from 2007 to 2009. Three in 2007, 7 in 2008 and 4 in 2009 were selected for the study. All young birds in the selected nests were fitted with radio transmitters (Biotrack PIP3 model, backpack type, weight = 0.6 g, estimated tag life = 20 - days) and rings, and their survival was monitored. All nests used for the study were visited once only prior to bird tagging, when the age of each bird was determined using wing length measurement (Tome 2007).

When selecting nests for the study, the earliest in the season and replacement nests were not considered to be very representative. In addition, the replacement broods were already at risk of being mown, which would interfere with our aims. Among the other available nests, factors such as the right age of the nestlings, weather conditions on the tagging day, available time for searching, etc., were involved in the selection process. All in all, nests were not selected strictly at random, but they were not selected with any particular pattern that would be expected to bias the results.

Young birds were tagged when 7–11 days old. Younger birds were too small to be fitted with tags, while older ones were likely to leave the nest prematurely if disturbed. Tagged birds were located every other day (in exceptional cases 1 or 3 days after they had been located previously) until the battery drained out, the tag failed, or the bird emigrated or was found dead (whichever happened first). All birds from one nest were located on the same day and the following data were recorded. (1) The *escape distance*, which was the distance from the bird to the person with receiver and antenna (telemetrist) at the moment the bird flew away. The telemetrist always approached the bird very slowly (about 5 m/min), but directly. If the bird did not move, or if the bird was engaged in a last-moment attempt to run away, the distance recorded was 0 m. (2) The *distance to the nest and position of the bird* (hiding on the ground or exposed on the vegetation) *before it moved*. If the birds were still in the nest, the distance was 0 m. All distances up to 1 m were rounded to the nearest 0.1 m, from 1 to 10 m to the nearest 0.5 m, and larger distances to 10 m. (3) The *status of the bird* (alive or dead).

Data analysis

We used the Kaplan–Meier (KM) method of analyzing failures to estimate a survival curve for young Whinchats in their last days in the nest and their first week out of the nest (Conroy et al. 1989; Pollock et al. 1989). KM analysis allows observations of animals whose fates are unknown (censored data), which is often the case in radiotagged animals (e.g., due to tag failure, battery drain, emigration from the study area). A KM estimate was calculated for the entire sample (consisting of birds with at least two successful locations). Tagged birds were not usually located every day. If more than 1 day elapsed between the last time that the bird was located and the day on which we failed to locate it or we found it dead, the middle date was taken as the last date of live observation. If the bird was successfully located and found alive, it was also considered to be alive during the days when we did not search for the birds.

To analyze the effect of age on the escape distance of young Whinchats, the dependent variable—distance—was transformed into a binary scale in two ways: (1) all of the birds that escaped irrespective of the distance from the approaching person were classified as 1 and the birds that did not escape we classified as 0, and (2) all of the birds that escaped at a distance of 5 m or more from the approaching person were classified as 1 and all of the rest were classified as 0. While an escape distance of 0 m was considered fatal to fledglings regardless of the speed of the approaching threat, we arbitrarily considered an escape distance of up to 5 m to be potentially fatal in the case of fast-moving threats such as avian predators or mowing machines. In the following, we use the following notations for these two sets of variables: 0–1 and 0–5, respectively. The same modeling procedure was applied to both binary variables. An information-theoretic model selection approach was carried out (Burnham and Anderson 2002) with generalized linear mixed modeling (GLMM) to analyze the age dependence of the escape behavior (Zuur et al. 2009). The age of the juveniles was modeled in days, where day 1 was the hatching day. Escape distances were considered for juveniles aged 13 days and more, as no juveniles left the nest before that age.

We controlled for the effects of both shared nests and repeated measures of the same individual by including a hierarchical random effect (individuals nested in the nest) in the models. We created three models for each response variable (0–1 and 0–5): a squared age term (nonlinear relationship: $age^2 + age$), a linear age effect, and a null model (only the intercept). Using AIC values of these generalized linear mixed models, we selected the best model. Predicted escape probabilities were calculated from the best models. The 95% confidence interval of the prediction was drawn. GLM modeling was carried out using the *glmer* function from the package *lme4* in R.

Results

In 3 years, 74 young birds were tagged. All juveniles survived the remaining nestling period and were located at least twice after tagging. The data were censored for 24 birds (32%) due to tag failure or loss. The signal was lost for 26 birds (35%), but only after 18 days of operation or more. Battery drainage was assumed, so they were all considered to have survived the study period. Twenty-four birds (32%) failed due to mortality.

At an age of 12 days, all of the birds were still in the nest; the first chicks left the nest on the 13th day. At day 14 almost half and at day 15 about 80% of the birds had left the nest by inspection time (around noon). By day 16, all birds has left their nests. In the first 3 days after fledging, most of the birds were found in a 20 m perimeter around the nest. Until the age of 29 days, the median distance from the nest to the bird was <100 m. From the next day on, the median distance increased to over 200 m (Fig. 1). Eighty percent of the located birds that were younger than 25 days could not be spotted from the distance. They were hiding among the grass, probably sitting on the ground or on the grass stubbles close to the ground. From 30 days onwards, all juveniles were found sitting on a bush, on a tree branch or on top of the grass, clearly visible from the distance.

The largest drop in cumulative survival was recorded on the day immediately following fledging. It decreased from 1.0 at age 12 days to 0.7 at age 16 days. By the end of the study period, when the chicks were 1 month old, cumulative survival was 0.52 (±0.27, 95% confidence interval; Fig. 2). The survival probability pattern from the day the first birds fledged (day 13) to the end of our study period (day 32) was fitted extremely well by a power regression line ($y = 0.963\ x^{-0.206}$; $R^2 = 0.983$).

Out of the fledglings found dead ($n = 24$), 3 were killed by a mower and the rest by natural causes. There were no external signs of the cause of death on 3 of them, while 18 were depredated. On 2 occasions (11% of all depredations) the predator was a bird (1 tag was found in the active nest
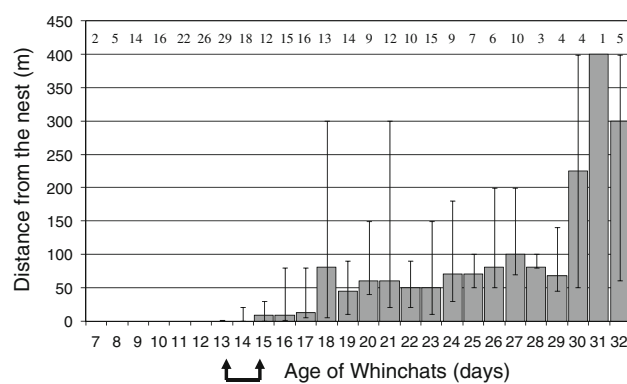

Fig. 1 Median distances of young Whinchats from the nest (*bars*), with *minimum and maximum lines* also shown. *Arrows* indicate the period when the birds were leaving the nest; *numbers at the top* are sample sizes
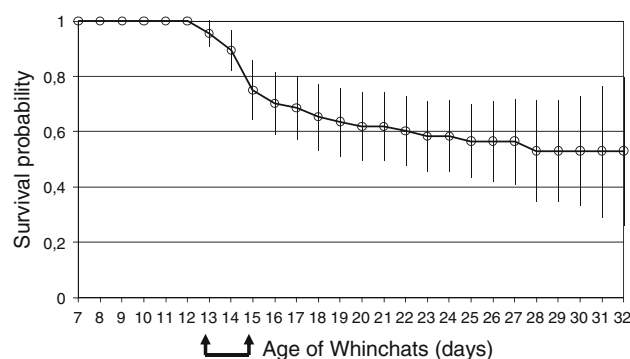

Fig. 2 Cumulative survival probability of young Whinchats versus age, calculated using Kaplan–Meier estimates ($N = 74$). *Vertical lines* are 95% confidence intervals, *arrows* indicate the period when birds were leaving the nests

of a Common Buzzard, *Buteo buteo*), in 14 cases (78% of all depredations) the predator was an unknown mammal, and for 2 depredations (11% of all of them) the predator could not be determined, even roughly. Mammals depredated 2 complete nests (6 birds in each nest). Since the birds were already fledged at the time of predation, not all were depredated on the same day. All mammal depredations occurred before the birds reached the age of 22 days. Avian predation occurred only after day 22 (days 26 and 29).

Two fledglings escaped upon the approach of the telemetrist on the third day after they left the nest, and continued to do so at all later visits. They were about 17 days old at that time, and the lengths of their escape flights were <5 m.

For both binary-dependent variable sets (0–1 and 0–5), the model selection revealed that the model with age used as the explanatory variable was the most well supported one (Tables 1, 2). Predicted probabilities calculated from the best models indicate that there is a 50% probability that

Table 1 Models used to investigate the age-dependent escape probabilities of Whinchat (*S. rubetra*) juveniles

Set	Fixed eff.	Rand. eff.	K	AIC	Δi	Model lik.	wi
0–1	**Age**	**Nest/ind**	**4**	**122.30**	**0.00**	**1.00**	**0.69**
0–1	Age^2 + age	Nest/ind	5	123.90	1.60	0.45	0.31
0–1	Null	Nest/ind	3	277.60	155.30	0.00	0.00
0–5	**Age**	**Nest/ind**	**4**	**61.90**	**0.00**	**1.00**	**0.69**
0–5	Age^2 + age	Nest/ind	5	63.48	1.58	0.45	0.31
0–5	Null	Nest/ind	3	193.40	131.50	0.00	0.00

GLMMs with hierarchical random effect were used

Models are ranked by ascending AIC within the model set

The model with best support from the data is shown in bold

Set set of dependent binary variables used in the modeling (see "Data analysis"), *K* number of parameters in the model, *AIC* Akaike's information criterion, *Δi* AIC differences, relative to the smallest AIC value in the set of models, *Model lik.* model likelihood, *wi* Akaike weights

Fig. 3 Predicted escape probabilities of Whinchat fledglings in relation to their age. *Left solid line* (*a*) represents the probability that fledglings will escape from the approaching threat irrespective of the distance; *right solid line* (*b*) represents the probability that they will escape when the threat is at a distance of 5 m or more. *Dashed lines* show the 95% confidence intervals of the predicted values

a 20 day old Whinchat juvenile will stay hidden and will not escape when approached by a threat. The probability reduces to 20% by the age of 22 days. There is a 50% probability that fledglings will escape from a fast-moving threat at the age of 25 days, which increases to 80% at 26 days (Fig. 3).

Discussion

Post-fledging survival, causes of mortality, and predator avoidance

It is well known that in the post-fledging period the mortality rates of birds are very high (Gill 1995). The Whinchat is no exception in this respect. We noted a steep mortality rate for the very first day after fledging, which leveled off with age (Fig. 2). Similar results have been found for other altricial birds that were also investigated using radio telemetry, which leaves little doubt about the accuracy of the pattern (e.g., Adams et al. 2006; King et al. 2006; Berkeley et al. 2007; Rush and Stutchbury 2008; Wightman 2009; Grüebler and Naef-Daenzer 2010).

The marginal importance of mowing as a cause of mortality indicates that the selected study site was good for investigating mortality under natural conditions. Out of 21 retrieved dead bodies (not including the three killed by a mower), we found predation to be the most important cause of mortality in 18 cases. Since the majority of the depredations occurred before the age of 25 days, when fledged birds were found hidden in the grass close to the ground, the high ratio of mammal to bird predators is understandable.

In our study, we assumed that a telemetrist slowly and directly walking towards a young Whinchat is a good approximation of an approaching threat of any type, even a slow ground predator. If the bird did not escape before we reached it, there is probably little chance that it would survive such an attack. So, during the first 10 days after fledging, when alarm calls of parents prompted the birds to hide close to the ground and stay still, the birds are as vulnerable to predators as they were in the nest. Since siblings of this age are not far from each other, they can all

Table 2 Coefficients for models with the best support from the data

Set	Best model	Model parameters					
		a	SE	b	SE	SD ind:nest	SD nest
0–1	logit(p) = a × age + b	0.644	0.090	−12.554	1.743	0.303	2.363×10^{-8}
0–5	logit(p) = a × age + b	0.992	0.200	−24.620	4.895	1.108×10^{-7}	1.043

Set set of dependent binary variables used in the modeling (see "Data analysis"), *SE* standard error of the model coefficient, *SD ind:nest, SD nest* standard deviation of the hierarchical random intercept in GLMM
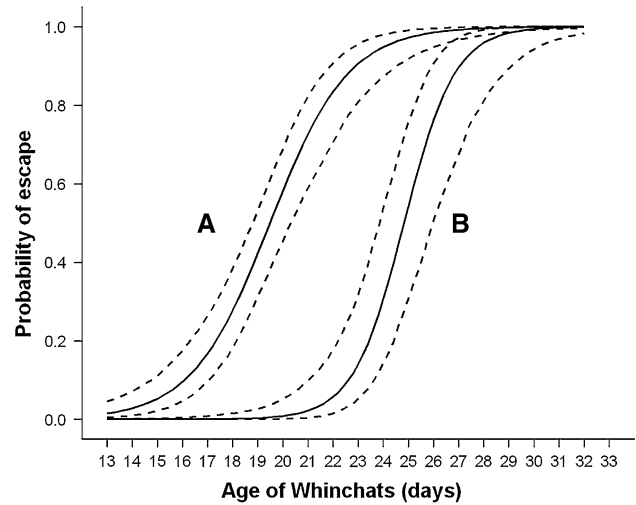
quickly fall victim to the same predator. This is supported by two observations of already fledged siblings that were all depredated in the course of 2 or 3 days. After 10–15 days out of the nest, the young birds developed the habit of waiting for parents with food at more exposed positions, and in the case of alarm calls, their avoidance strategy was to fly away rather than hiding on the ground. This behavioral change was likely to reduce predation rate and led to a change in predator type, too. In our case, heavy predation by mammals stopped completely and was replaced with much less pronounced avian predation.

Conservation measures

Various agri-environmental schemes aimed at conserving farmland biodiversity have been proposed in the EU (European Union) since 1992 in order to stop severe environmental degradation. They came into force with the Agri-Environment Regulation 2078/92 (Wilson et al. 1999). During the following year, these measures showed different levels of success (Kleijn et al. 2001, 2004; Bradbury and Allen 2003; Kleijn and van Zuijlen 2004; Breeuwer et al. 2009). What became clear was that reliable and detailed insights into the behavior and the ecological processes of the target species are essential if the design and implementation of a conservation scheme is to be successful (Aebischer et al. 2000; Chamberlain et al. 2000; Swash et al. 2000; Kleijn and van Zuijlen 2004). For example, if postponing mowing is to give any positive results in terms of the survival of fledged birds, we must know exactly when they are old enough to evade the oncoming machine. Here, we demonstrate that the age at which juvenile Whinchats show the behavior required to avoid an approaching mowing threat is far past fledging.

The 5-year average data for Ljubljansko barje show that practically the entire population starts nesting within a month (Denac 2007). Findings elsewhere in Europe are similar (Bezzel and Stiel 1975; Parker 1990; Müller et al. 2005). If mowing is postponed until 80% of the nests in a population are fledged—the suggested conservation measure (Broyer 2009)—many young Whinchats are still at risk of being killed by mowing, despite the fact that they are already away from the nest and capable of flying (Fig. 4). This is due to their initial predator-avoidance strategy, which, in the case of mowing, makes them "sitting ducks." The postponement period should therefore be longer if it is to be effective.

Our results show that half of the fledglings develop a strategy of escaping from the threat by the time they are 20 days old, and this increases to 80% by the age of 22 days, which is approximately 8–10 days after fledging. For this reason, mowing must be postponed 10 days more than suggested in order to conserve Whinchat populations
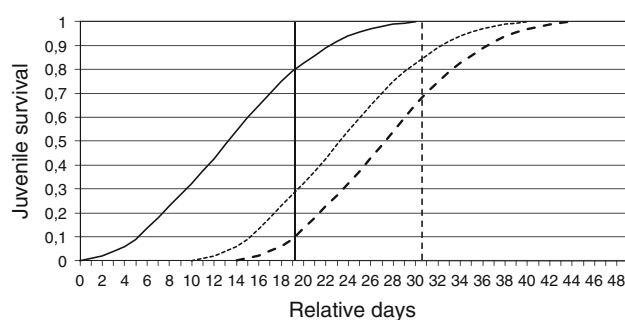

Fig. 4 Influence of date of mowing on the survival of Whinchat chicks; the figure shows a schematic presentation of meadows mown completely in 1 day. The *solid curve* shows fledgling survival assuming that the juveniles are safe after fledging; i.e., the proportion of fledged nests over time in Ljubljansko barje according to Denac (2007). A logistic curve is assumed. The *dotted curve* shows fledgling survival assuming that the surviving juveniles have to escape before they are reached by a threat; i.e., that they are not safe before 10 days from fledging. The *dashed curve* shows fledgling survival assuming that the surviving juveniles have to escape before the threat is within 5 m; i.e., assuming that they are not safe before 14 days from fledging. The *full vertical line* shows the effect of postponing mowing to the time when 80% of the chicks are fledged (the current conservation measure). Less than 30% of all young are old enough at that time to avoid an oncoming mower, and only about 10% if an escape distance of 5 m is required. On the day when all of the nests are fledged (*dashed vertical line*), 70–80% of the young can avoid the mower

in early-mown meadows. However, we believe that even this might not be enough. Modern mowing machines move much faster than a man on foot. They can easily cover 5 m/s. When a mower is heading directly at the bird, even if the bird tries to escape, it could be too late to do so if the distance to the machine is too small. This is true of adult birds (Grüebler et al. 2008), and is probably even more so for young, inexperienced birds during the first 15 days after fledging, when they are hiding close to the ground and their escape route is hindered by the grass above them. Thus, if a minimum escape distance of 5 m is necessary, the mowing date with a minimal probability of killing juveniles is 14 days later than previously suggested. This is also our recommendation for a conservation measure on grasslands, at least until more is known about the reaction of fledglings to fast-incoming mowing machines.

Mortality or emigration?

After the first week of the fledging period, Whinchats face about 3 months of learning tough survival skills, for which the mortality rate is unknown. However, if the survival trend calculated for birds aged between 13 and 32 days is extrapolated to the entire juvenile period, the survival probability of juveniles by the time they start to migrate (mid-September, personal observation) decreases to about 0.35. Thus, roughly two-thirds of fledged Whinchats from

Ljubljansko barje are estimated to die on their natal grounds before the first migration. Given that roughly 10% return in the following spring (Denac 2007), this means that for about 20% of the population of the first-year birds, we still do not know how many die during migration and how many emigrate to new locations.

Censored data

In our study, we experienced a rather high percentage of censored data. Eleven out of 24 tag losses occurred on the first day after activation. All young birds were tagged while still in the nest. Flight feathers are not fully developed at that time, and we suspect that the presence of several birds side by side in a small nest increased the possibility of accidental or deliberate dismantling of the harnesses. After tagging, we avoided approaching the nest too closely in order to reduce the possibility of premature chick departure. For this reason, we usually confirmed tag loss only after the chicks were already out of the nest, and were difficult to find and retag. We lost track of the other tags after 9–17 days, for unknown reasons.

References

Adams AAY, Skagen SK, Savidge JA (2006) Modeling post-fledging survival of lark buntings in response to ecological and biological factors. Ecology 87:178–188

Aebischer NJ, Green RE, Evans AD (2000) From science to recovery: four case studies of how research has been translated into conservation action in the UK. In: Aebischer NJ, Evans AD, Grice PV, Vickery JA (eds) Ecology and conservation of lowland farmland birds. Proc 1999 British Ornithologists' Union Spring Conf, Southampton, UK, 27–28 March 1999, pp 43–54

Bastian A, Bastian HV (1994) Bestände und Bestandstrends des Braunkehlchens S. rubetra. Limicola 8:242–270

Bastian A, Bastian HV (1996) Das Braunkehlchen. Opfer der ausgeräumten Kulturlandschaft. AULA-Verlag, Wiesbaden

Berkeley LI, McCarty JO, Wolfenbarger LL (2007) Postfledging survival and movement in dickcissels (S. americana): implications for habitat management and conservation. Auk 124:396–409

Bezzel E, Stiel K (1975) Zur verbreitung und ökologie des braunkehlchens (S. rubetra) am Deutschen nordalpenrand. Ardeola 21:841–859

BirdLife International (2004) Birds in Europe (BirdLife Conservation series no. 12). BirdLife International, Cambridge

Bradbury RB, Allen DS (2003) Evaluation of the impact of the pilot UK arable stewardship scheme on breeding and wintering birds. Bird Study 50:131–141

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

Britschgi A, Spaar R, Arlettaz R (2006) Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat S. rubetra: lessons for overall alpine meadowland management. Biol Conserv 130:193–205

Broyer J (2009) Whinchat S. rubetra reproductive success according to hay cutting schedule and meadow passerine density in alluvial and upland meadows in France. J Nat Conserv 17:160–167

Burnham KP, Anderson DR (2002) Model selection and multimodel inference. Springer, New York

Chamberlain DE, Fuller RJ, Shrubb M, Bunce RGH, Duckworth JC, Shrubb M (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J Appl Ecol 37:771–788

Conroy MJ, Costanzo GR, Stotts DB (1989) Winter survival of female American black ducks on the Atlantic coast. J Wildl Manag 53:99–109

Denac D (2007) Populacijska dinamika repaljščice (S. rubetra) v mozaiku nižinskih habitatnih tipov. Population dynamics of Whinchat (S. rubetra) in the mosaic of lowland habitat types (dissertation). University of Maribor, Maribor

Donald PF, Green RE, Heath MF (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. Proc R Soc Lond B 268:25–29

Flade M (1994) Die Brutvogelgemeinschaften Mittel- und Norddeutschlands. IHW-Verlag, Eching

Gill FB (1995) Ornithology. WH Freeman and Co., New York

Von Glutz Blotzheim UN, Bauer KM (1988) Handbuch der Vögel Mitteleuropas, Band 11/I Passeriformes (2. Teil). AULA-Verlag, Wiesbaden

Green RE, Tyler GA, Stowe TJ, Newton AV (1997) A simulation model of the effect of mowing of agricultural grassland on the breeding success of the corncrake (C. crex). J Zool Lond 243:81–115

Grüebler MU, Naef-Daenzer B (2010) Survival benefits of post-fledging care: experimental approach to a critical part of avian reproductive strategies. J Anim Ecol 79:334–341

Grüebler MU, 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 Conserv 141:3040–3049

Henderson IG, Fuller RJ, Conway GJ, Gough SJ (2004) Evidence for declines in populations of grassland-associated birds in marginal upland areas of Britain. Bird Study 51:12–19

Horch P, Rehsteiner U, Berger-Flückiger A, Müller M, Schuler H, Spaar R (2008) Bestandsrückgang des Braunkehlchens S. rubetra in der Schweiz, mögliche Ursachen und Evaluation von Fördermassnahmen. Der Ornithologische Beobachter 103:267–298

King DI, Degraaf RM, Smith ML, Buonaccorsi JP (2006) Habitat selection and habitat-specific survival of fledgling ovenbirds (S. aurocapilla). J Zool Lond 269:414–421

Kleijn D, van Zuijlen GKC (2004) The conservation effects of meadow bird agreements on farmland in Zeeland, The Netherlands, in period 1989–1995. Biol Conserv 117:443–451

Kleijn D, Berendse F, Smit R, Gillisen N (2001) Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. Nature 413:723–725

Kleijn D, Berendse F, Smit R, Gilissen N, Smit J, Brak B, Groeneveld R (2004) Ecological effectiveness of agri-environment schemes in different agricultural landscapes in the Netherlands. Conserv Biol 18:775–786

Kokko H, Sutherland WJ (2001) Ecological traps in changing environments: ecological and evolutionary consequences of a behaviourally mediated allee effect. Evol Ecol Res 3:537–551

Maumary L, Vallotton L, Knaus P (2007) Die Vögel der Schweiz. Schwaizerische Vogelwarte Sempach und Nos Oiseaux, Montmollin

Müller M, Spaar R, Schifferli L, Jenni L (2005) Effects of changes in farming of subalpine meadows on a grassland bird, the Whinchat (*S. rubetra*). J Ornithol 146:14–23

Newton I (2004) The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. Ibis 146:579–600

Opperman R (1992) Das resourcenangebot verschiedener Grünland-Gesellschaften und dessen Nutzug durch Brutvögel. Phytocoenologia 21:15–89

Parker JE (1990) Zur Biologie und Ökologie einer Btraunkehlchen-Population (*S. rubetra*) im Slazburger Voralpengebiet (Österreich). Egretta 33:63–76

Pollock KH, Winterstein SR, Conroy MJ (1989) Estimation and analysis of survival distributions for radio-tagged animals. Biometrics 45:99–109

Rush SA, Stutchbury BJM (2008) Survival of fledgling hooded warblers (*W. citrina*) in small and large forest fragments. Auk 125:183–191

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. Trends Ecol Evol 17:474–480

Schmidt K, Hantge E (1954) Studien an einer farbig beringten population des Braunkehlchens (*S. rubetra*). J Ornithol 95:130–173

Shrubb M (2003) Birds, scythes and combines. Cambridge University Press, Cambridge

Swash ARH, Grice PV, Smallshire D (2000) The contribution of the UK biodiversity action plan and agri-environment schemes to the conservation of farmland birds in England. In: Aebischer NJ, Evans AD, Grice PV, Vickery JA (eds) Ecology and conservation of lowland farmland birds. Proc 1999 British Ornithologists' Union Spring Conf, Southampton, UK, 27–28 March 1999

Tome D (2007) Rast mladičev repaljščice *S. rubetra* na Ljubljanskem barju. Growth of young Whinchats *S. rubetra* on Ljubljansko barje. Acrocephalus 28:51–55

Tucker GM, Heath MF (1994) Birds in Europe: their conservation status. Birdlife International, Cambridge

Urquhart E (2002) Stonechats. Christopher Help, London

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J Appl Ecol 38:647–664

Wakeham-Dawson A, Smith K (2000) Birds and lowland grassland management practices in the UK: an overview. In: Aebischer NJ, Evans AD, Grice PV, Vickery JA (eds) Ecology and conservation of lowland farmland birds. Proc 1999 British Ornithologists' Union Spring Conf, Southampton, UK, 27–28 March 1999

Wightman CS (2009) Survival and movements of fledgling western bluebirds. Southwest Nat 54:248–251

Wilson GA, Petersen JE, Höll A (1999) EU member state responses to agri-environment regulation 2078/92/EEC: towards a conceptual framework? Geoforum 30:185–202

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York