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Impact of grassland farming intensification on the breeding ecology of an indicator insectivorous passerine, the Whinchat *Saxicola rubetra*: Lessons for overall Alpine meadowland management

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ARTICLE INFO

Article history:

Received 8 June 2005

Received in revised form

24 November 2005

Accepted 15 December 2005

Available online 3 February 2006

Keywords:

Agro-ecosystems

Farmland birds

Grassland management

Saxicola rubetra

Biodiversity conservation

ABSTRACT

The decline of insectivorous farmland passerines has been attributed mostly to global decrease in arthropod availability, as a result of intensification of agricultural practices. The diminution of the Alpine Whinchat, once a widespread insectivorous passerine, has been ascribed to nest losses due to earlier and more frequent mowings. However, potential conjugated effects of deteriorated arthropod food availability had yet to be investigated. We compared food supply and nestling diet in intensively vs. traditionally managed grassland. Abundance and diversity of arthropods were much lower in intensive areas, where small-sized invertebrates, which do not enter nestling diet, were also predominant. Parents breeding in intensive habitats fed less biomass to nestlings than adults from traditional habitats. Nestling diet was less diverse and dominated by less profitable prey items in intensive than in traditional habitats. Feeding rate did not differ between the two habitats, but foraging distances from nest tended to be greater in intensive farmland. There were no significant differences in clutch sizes and hatching success with respect to management intensity, but fledging success was higher in traditional habitats. The recent intensification of farming practices has led to a decrease in the availability of grassland invertebrates, and of important Whinchat nestling food in particular, affecting parents' foraging efficiency and reproductive success. Conservation actions must not only reduce nest losses by postponing mowing, but should also promote grassland farming that is less detrimental to invertebrates. Dominant at the study site, organic grassland farming does seemingly not provide sufficient conditions for Alpine Whinchats.

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1. Introduction

The populations of many farmland birds have declined severely across Western Europe over the past decades (Fuller et al., 1995; Siriwardena et al., 1998; Donald et al., 2001). This

phenomenon coincided with marked changes in the agricultural landscape, especially land use intensification (Benton et al., 2002, 2003), although the actual mechanisms involved are still widely debated (Schifferli et al., 1999; Di Giulio et al., 2001; Freemark and Kirk, 2001; Vickery et al., 2001;

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doi:10.1016/j.biocon.2005.12.013

Stephens et al., 2003; Chamberlain, 2004; Newton, 2004). In regard to insectivorous birds inhabiting cultivated grassland, modern agriculture may exert detrimental effects in different ways: (1) earlier mowings than in the past, which tend now to overlap with breeding season, destroy nests mechanically or render them more conspicuous to predators; (2) earlier and/or more radical mowing extirpates prey during critical nestling feeding stage; (3) denser grass cover and reduced plant species diversity, resulting from excessive fertilization, affect negatively arthropod community, availability and/or accessibility (Sotherton and Self, 2000; Di Giulio et al., 2001; Vickery et al., 2001). According to several studies, a conjunction of these factors decreases feeding efficiency and, ultimately survival, affecting in turn population density (Wilson et al., 1997; Peach et al., 1999; Brickle et al., 2000). Although this link has been established in the Grey Partridge (Potts and Aebischer, 1995), and is suspected in other insectivorous farmland birds, the evidence remains contradictory (Bradbury et al., 2003).

The Whinchat (*Saxicola rubetra*), a ground-breeding passerine, inhabits primarily cultivated grassland, especially agricultural landscapes managed traditionally. It used to be common and widespread throughout western and central Europe (Bastian and Bastian, 1996) but drastic population declines have been documented over the past 20 years (Callion, 1993; Rheinwald, 1993; Bastian and Bastian, 1994; Yeatman-Berthelot and Jarry, 1994). Its conservation status is of concern in many European countries today (Tucker and Heath, 1994). In Switzerland, the Whinchat is red-listed as it has disappeared almost completely from the lowlands (Keller et al., 2001); it is one of the 50 priority species for species action plans in Switzerland (Bollmann et al., 2002).

Nest losses due to a shift towards earlier mowing have been described to be one key factor harming the reproductive output of Whinchats, and may hence explain their current population dynamics (Müller et al., 2005). Yet, Whinchat food availability in intensively and traditionally managed grassland have not been investigated specifically, though they might indirectly contribute to species' decline through an alteration of the reproductive performance (Labhardt, 1988; Oppermann, 1999). We studied the foraging and breeding ecology of Whinchats in the same Alpine population investigated by Müller et al. (2005), who demonstrated the negative effect of early mowing. In that area both types of grassland management are applied. We assessed first the arthropod abundance and diversity within grassland cultivated either intensively or traditionally, in order to confirm possible patterns of invertebrate food impoverishment due to the intensification of meadow cultivation (Sotherton and Self, 2000; Benton et al., 2002). Secondly, we studied nestlings' diet and adults' hunting and provisioning behaviour at 18 breeding sites, 9 in each habitat type, looking for a possible impact of farming intensification on diet profitability and energy intake. Thirdly, we attempted to identify the fitness costs possibly imposed, both on adults and broods, by the hypothesized altered food composition in intensively managed areas (Borg and Toft, 2000; Bradbury et al., 2003; Boatman et al., 2004). Poor food supplies can provoke brood size reduction and low fledging success if some nestlings suffer from starvation; they could also induce state-dependent predation risks due to conspicuous begging (Cotton et al., 1996). Parents may com-

pensate for the negative impacts of a deteriorating environment by working harder to get the same or a reduced amount of food for their young, and so maintain a standard reproductive output (Brickle et al., 2000; Morris et al., 2001), but they would so irremediably reduce their own survival and residual reproductive value (Richner and Tripet, 1999); we accounted for these possible effects only prospectively, by analysing food provisioning frequency, prey provisioning loads and foraging distances from the nest, this in the context of optimal foraging theory (Andersson, 1981; Stephens and Krebs, 1986). Pooled together, the results of this comparative approach should lead to a more comprehensive understanding of the problems faced by Whinchats and, by extension, other insectivorous birds inhabiting cultivated farmland in a rapidly changing environment. This is an essential step to propose effective conservation measures.

2. Methods

2.1. Study area

The study was conducted from May through to July 2002 in Lower Engadin (inner Alpine valley, SE Switzerland). This area has a dry and mild summer climate (total precipitation of 271 mm in June and July 2002, for a mean ambient temperature of 15 °C). As we could not work experimentally, by applying at random a given treatment to a selected location, we had to rely on a comparative approach instead. Six sampling plots were chosen for the assessment of food abundance, three in intensively managed grassland (henceforth INT, mainly silage grass and pastures, fertilized with liquid manure) and three in traditionally managed grassland (TRAD, 70% hay meadows, 20% pastures, low input of manure if any) (Table 1). These plots were very much representative of the two management practices present. For analyses of nestlings' diet and feeding behaviour, we followed breeding pairs from four additional plots (Table 1). The discrimination of the study plots in two grassland management regimes was based upon three variables (Di Giulio et al., 2001), which enabled a clear plot separation (Table 1): (I) number of cuts per year averaged over the last 5 years (information was provided by the corresponding farmers); (II) date when 50% of the area was mown; (III) average flower diversity at the end of May, estimated from three randomly selected 1-acre large plots at each sampling site in which the diversity of flowering species was assessed. Thereby, the number of flower colours present in the plots was counted by the same observer within a 15 m radius, and was used as an estimate for the actual flower diversity (Arlettaz, unpublished data). Though this method seems to be quite imprecise compared to the identification of single plant species, it yielded robust results and led to a reasonable separation of the study plot groups. The two groups also differed in other management variables (e.g., fertilizer input, see above), but since the latter were more difficult to collect and correlated with the variables measured, they were not taken into account. The TRAD-plots were located at higher altitudes than the INT-plots (1597 ± 99 vs. 1290 ± 149 m elevation, respectively), which was due to more farming intensification close to the valley bottom. However, due to the scatter of the plots with respect to management

Table 1 – Characteristics of the study plots investigated for food abundance, nestling diet and feeding behaviour

Plot	Grassland management	Altitude (m)	Area (ha)	Coordinates	N of cuts/year	Date with 50% of area mown	Mean flower diversity
<i>Food abundance, nestling diet and feeding behaviour</i>							
Scuol	INT	1243	31	46°48'N, 10°18'E	2–3	13.6	1.3
Sent	INT	1150	35	46°48'N, 10°20'E	2–3	13.6	1.3
Ramosch	INT	1160	41	46°49'N, 10°23'E	2	14.6	1.6
Vnà	TRAD	1540	35	46°50'N, 10°21'E	1–2	7.7	2.3
Chantata	TRAD	1680	40	46°48'N, 10°18'E	1	10.7	3.3
Tschlin	TRAD	1580	38	46°51'N, 10°25'E	1–2	8.7	2.3
<i>Nestling diet and feeding behaviour only</i>							
Lavin	INT	1430	24	46°46'N, 10°06'E	2	15.6	1.6
Ardez	INT	1464	26	46°46'N, 10°11'E	2–3	16.6	1.6
Zernez	TRAD	1473	18	46°42'N, 10°05'E	1–2	3.7	2.3
Griosch	TRAD	1711	19	46°52'N, 10°19'E	1–2	12.7	2.3

INT, intensively managed; TRAD, traditionally managed. Flower diversity classes: 1 for 0–2 flowering colour classes, 2 for 3–5, 3 for 5–8, 4 for more than 8 colour classes (see Section 2 for more details).

type along the altitudinal gradient (Table 1), phenological differences were assumed to be negligible. Moreover, since the arthropod biomass is commonly expected to decrease with increasing altitudes (Wettstein and Schmid, 1999), we are conservative concerning the hypothesis tested. The density of breeding pairs at the beginning of the season on TRAD-plots ranged from 3.3 to 8.1 pairs per 10 ha within the last 13 years, whereas density on INT-plots laid between 4.1 and 6.8 pairs per 10 ha in the same time range. Figures from the year 2002 were 3.6 pairs per 10 ha for TRAD-plots and 2.3 pairs per 10 ha for INT-plots (Müller et al., 2005).

2.2. Arthropod abundance

To estimate accurately arthropod abundance and species diversity in the six grassland study plots, we used a combination of pitfall traps (epigeal fauna) and sweep-net sampling (epiphytic fauna) (Standen, 2000). On each study plot, we chose three collecting points (pitfalls) and three transects (sweep-netting) randomly, but ensuring they would properly reflect the composition of the different agricultural parcels present. Since grassland management is very homogeneous within cultivation practice we considered the number of collecting points being sufficient. At collecting points, we burrowed 4 plastic cups, with a diameter of 7 cm, 3 m apart in a row. Ethylene glycol was used as a preservative. We set the traps every ten days, between 23 May and 24 July (i.e., 7 sampling periods), for a period of 72 h. We took sweep-net samples in the vicinity of the collecting points mentioned above also every ten days, between 10 and 17 h, under good weather conditions (≥ 16 °C, sunshine, < 2 Beaufort). One sweep-net subsample was defined as 20 strokes performed at equal intensity along a ca. 20 m long transect through the sward, or, in case of mown meadows, straight over the ground, respectively (standardized sweep-net method according to Oppermann (1999), Di Giulio et al. (2001)). We varied the sampling order of the plots randomly among the periods. This design hence produced two samples (one pitfall trap sample, one sweep-net sample) per collecting point and sampling transect, i.e., six samples per study plot and period. In addition,

sweep-netting was also performed on the home ranges of the breeding pairs followed, as we needed information about instantaneous food abundance (comparison of nestlings' diet with food supply). We collected samples on the same day as for nestlings' diet assessment at four different places corresponding to the locations where adults preferentially foraged. This data was used for a compositional analysis of prey selection in provisioning parents.

We conserved all the arthropods collected in 70% ethanol in small vacuum plastic bags. In the laboratory, we identified the food items down to suborder or family level using reference guides (Chinery, 1993; Zettel, 1999) and a binocular microscope (Leica MZ95), if necessary. Then, the arthropods were dried in an oven for 72 h at 60 °C according to Southwood (1978) and biomasses were determined to the nearest 0.001 g with a Mettler precision balance. According to their body lengths, we also assigned the arthropods to three size-classes (< 6 , 6–14, > 14 mm). A total of 126 taxa- and size-classes resulted. For the calculations of the Shannon indices of diversity (Shannon and Weaver, 1949) and index of richness (Krebs, 1989), these 126 size and taxa classes were regrouped in a logical taxonomic way into 53 major prey categories so as to avoid data over-dispersion. Since both indices of diversity gave very similar results and the sampling effort was even between the study plots and throughout the season, we used the Shannon index only (Krebs, 1989).

2.3. Nestling diet

We determined nestling diet at 18 breeding sites (9 TRAD-plots, 9 INT-plots), by video filming prey items delivered by parents (camera: Videotronic, CCD-7012P, Neumünster, Germany; time-lapse video recorder: Sanyo, SRT 7168P, Osaka, Japan). Video sessions took place on two successive mornings, when nestlings were 8–11 days old, from 6 to 12 h am, under optimal weather conditions (i.e., sunshine $\geq 75\%$ of recording time). We protected the appliances by specially designed cases that were hidden with camouflage nets and placed them the evening before a given recording session at 3–5 m distance from the nest. Power supply came from a generator

(Honda EU 10l, Tokyo), which was set 40–50 m farther away. The use of two video sets permitted to monitor two nests simultaneously. For 8 out of the 9 pairs breeding on INT-plots, we had to convince the farmers not to mow nest surroundings within a circular patch of ca. 3 m radius around nests. Without that measure, the nests would have been destroyed by mowing. We marked all nest locations with a 1.20 m high vertical wooden stick, which was readily adopted and served as an almost exclusive perch (in 94% of feeding events) by provisioning adults (Labhardt, 1988); this enabled focusing the video camera.

We analysed the video tapes using the frame-by-frame and freeze facilities of the same video cassette recorder. The two mornings of filming were pooled resulting in a period of 12 h of uninterrupted feeding per brood. We identified arthropods down to order or family level (26 taxonomical categories were recognized), and estimated prey body sizes by comparing them to bird beak length. Referring to the size and weight of the various arthropods collected from the home ranges of the videotaped pairs, we estimated biomass delivered to the nest. About 15% of prey items could not be identified; this was due exclusively to blurred video pictures. This, however, did not hamper biomass attribution. Body size composition of these unidentifiable items turned out to be a representative subsample of the overall body size composition, hence smaller invertebrate groups were not under-recorded.

2.4. Feeding behaviour

We calculated the feeding rate (number of feedings per nestling and hour) and number of prey items delivered to the nest per feeding event (load size) from the 11 h of video sequences available for each pair. We excluded the first 30 min following the start of videotaping in the mornings from the analysis to make sure birds' feeding behaviour was not influenced by the presence of the observer switching on the video system. Data on parents' foraging distances from the nest were collected during two hours per pair, between 8 and 11 h am; we used a laser rangefinder (LEICA Geovid Binocular 7 × 42) and a dictaphone. Distances to the nest and the locations of foraging were measured (accuracy ±1 m) and the angles between the two ranges were taken (at an accuracy of ±1°) to calculate foraging distances. If an adult visited several foraging locations prior to returning to the nest, we calculated the total distances flown between capture sites and the nest, for any provisioning event. Position of the observer was always outside home ranges, at a minimum distance of 130 m from the nest. Foraging adults were always in sight of the observer.

2.5. Breeding success

The reproductive variables we collected were clutch size, hatching rate and number of nestlings reaching 12 days of age. Variables were calculated with the brood being the statistical unit to avoid pseudo-replication. Fledging takes place between 12 and 14 days in the Whinchat (Bastian and Bastian, 1996), but then young are very difficult to spot when hidden in the swards; we thus used the latter variable as a proxy for the number of fledglings. We visited broods only 3–4 times

to avoid excessive disturbance. One predated brood had to be excluded from the analysis as we wanted to get rid, as far as possible, of destruction by mowing and predation in our comparison. Since this brood was located on an INT-plot where smaller breeding success compared to TRAD-plots was hypothesized, its exclusion was considered conservative.

2.6. Timing of mowing

To assess dates and extent of mowing in the six study plots, scenery pictures were taken every ten days throughout the season and every five days during the mowing peak (1st June – 15th June for INT-plots, 25th June – 15th July for TRAD-plots). From these pictures, percentages of mown area were estimated and for each of the 13 sampling dates averaged within the two groups. Logistic regression was used to fit a line through the data points.

2.7. Weather data

Data on mean daily ambient temperature and precipitation came from the weather station Scuol (Federal Office of Meteorology and Climatology, MeteoSwiss 2002). Additionally, we measured temperatures at 6 and 12 h am at every video recording site; on that basis, an average ambient temperature for the two days of videotaping per nest was calculated.

2.8. Statistical analysis

All variables were tested for homoscedasticity and normality prior to running analysis of variance (ANOVAs). To test for differences in food abundance and diversity between INT and TRAD, the biomass variables, the proportions of arthropods <6 mm and the Shannon indices of diversity had to be square root transformed (Zar, 1999). For the analysis of the Shannon indices, data from both trap types were averaged for each sampling point and period, respectively, since their separate consideration did not change the outcome of the analysis and it was the overall grassland diversity that was of interest (Arlettaz and Perrin, 1995). Factors included in the nested ANOVA analyses were: grassland management (INT vs. TRAD), study plot nested within grassland management, season, mean temperature, mean rainfall, as well as related interaction terms. Non-significant factors and interactions were dropped during a backward elimination procedure. Tukey post hoc tests were applied on the biomass dataset to perform pairwise multiple comparisons (Tukey, 1953).

Regarding nestling diet, Shannon indices of diversity were calculated using the 26 prey groups mentioned above. Tests consisted of Mann–Whitney *U*-tests when variables were not normally distributed (feeding rate per nestling * h, beak loads, clutch size, hatching success, number of fledglings). Otherwise, we applied multiway nested ANOVAs, with backward elimination procedures (biomass delivered per nestling * h and mean foraging distances from nests), including the following factors: grassland management (INT vs. TRAD), study plot nested within grassland management, age of nestlings, number of nestlings, time period, mean temperature, mean rainfall and resulting interactions. Since backward elimination procedures applied on models with small number of

replicates in relation to the number of independent variables are subjected to “over-fitting” (Harrell, 2001; Burnham and Anderson, 2002), we set two-tailed P-values for variable elimination at 0.01.

Prey selection analysis, i.e., availability and use of different invertebrate groups, was analyzed with a compositional analysis (Aebischer et al., 1993). Due to limitations on the number of groups that can be statistically compared with this method, the analysis was carried out on eight numerically dominant invertebrate groups using a Microsoft Excel Macro (Compositional analysis software V4.1 © Peter Smith, Smith Ecology Ltd.). Zeros in the available matrices were replaced with percentage values an order of magnitude smaller than the smallest non-zero value. If applied to the used matrix, this procedure is recognized to increase the type I error (Bingham and Brennan, 2004), but since there were no invertebrate groups in the available matrix that were never used by the birds, the analysis is considered both robust and appropriate. For all other data analyses performed, the program JMP4 (SAS Institute 2001, Cary, NC, USA) was used. Values reported are means ± SD or SE, or medians with box plots (quartiles). For analysis other than ANOVAS (see above), P-values are two-tailed, with rejection levels set at 5%.

3. Results

3.1. Arthropod abundance

During the seven sampling periods (May–July), a total number of 25,670 arthropods (304 g dry biomass) were collected with pitfall traps and sweep-net sampling. Out of these, 10,100 arthropods (39% of total number, 33% of total dry biomass), mainly Diptera, were smaller than 6 mm, thus not considered as being part of the Whinchat’s nestling diet (Labhardt, 1988). The composition of the remaining 15,570 arthropods was dominated by Coleoptera (39% of number, 47% of dry biomass), Arachnida (36% and 21%, respectively) and Diptera (10% and 2%, respectively).

The total biomass of arthropods collected with both sampling techniques was significantly lower, almost throughout the season, on the three intensively managed plots (INT) compared with the three traditionally managed plots (TRAD) (Fig. 1(a) and (b)). In the model, the factors “grassland management”, “study plot [grassland management]”, “season” and the interaction term “grassland management × season” explained a significant part of the overall variance (Table 2). Concerning the pitfall traps, TRAD-plots yielded significantly more biomass on the 13th June and 23rd June, but not on the other sampling dates. In contrast, the arthropod biomass caught with sweep-net was significantly higher in TRAD-plots during five out of seven sampling periods (3rd June, 13th June, 23rd June, 3rd July, 13th July; Fig. 1). Note that the number of arthropods smaller than 6 mm was higher on INT- than on TRAD-plots with the factor “grassland management” explaining most of the variance in the models (Table 2). The Shannon indices of diversity of arthropods collected with both trap types throughout the season were significantly higher on TRAD-plots than on INT-plots (Fig. 1(c)); here, “grassland management” and “season” were the most significant factors in the model (Table 2).

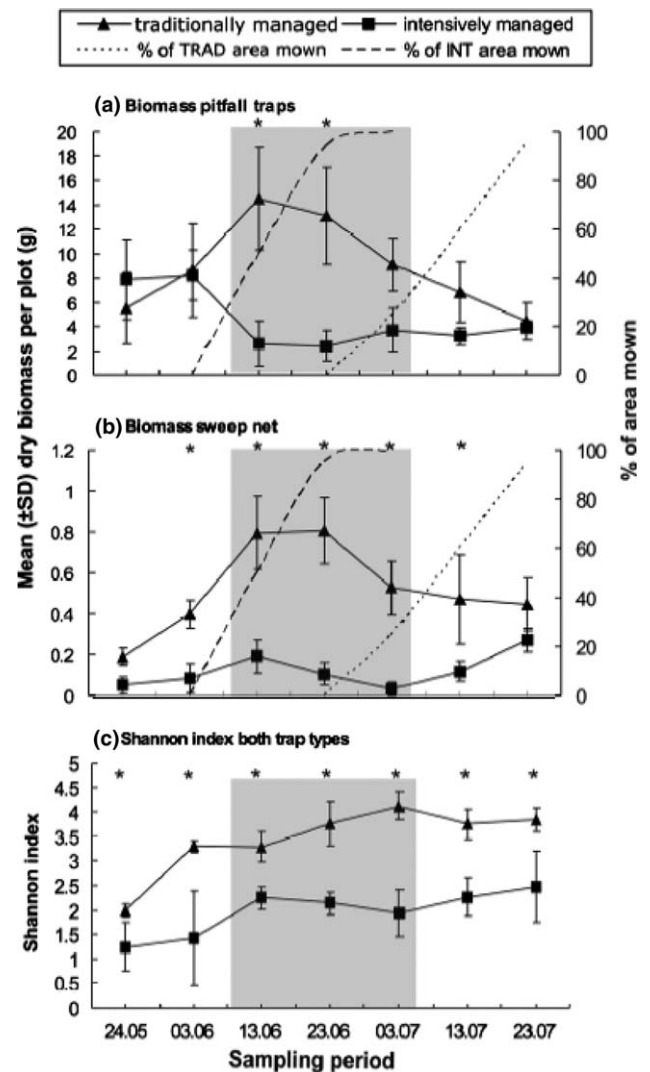


Fig. 1 – Seasonal trends in the overall dry arthropod biomass obtained from pitfall trapping (a) and sweep-netting (b) in INT-plots vs. TRAD-plots, and seasonal trends in the Shannon index of diversity of arthropods collected with both trapping techniques (c); the overlay block indicates the nesting period in the 18 Whinchat pairs followed. Significant differences between INT- and TRAD-plots are depicted by a star (Tukey post hoc test from ANOVA, $P < 0.05$).

3.2. Nestling diet

An overview of the proportions of the various invertebrate groups fed to Whinchat nestlings is given in Table 3. TRAD-nestlings were fed, on average, a significantly higher arthropod biomass (mean: 129.8 mg/nestling × h) than INT-young (mean: 101.7 mg/nestling × h), i.e., about 30% more biomass. The factor “grassland management” significantly accounted for the difference ($P = 0.0021$; Fig. 2(a)). Also, the diet of TRAD-young was significantly more diverse than the diet of INT-young (Median of Shannon index: 2.85 vs. 2.06, respectively; $P < 0.001$; Fig. 2(b)). Over 85% by number of the arthropods fed ranged in size from 9 to 16 mm, thus reflecting the main prey spectrum. The smallest prey items occasionally

Table 2 – Effects of the factors “grassland management” (INT vs. TRAD), “study plot nested within grassland management” and “season” on the total biomass, on the biomass percentages of arthropods smaller than 6 mm, and on the Shannon index of diversity of arthropods caught with pitfall-trapping and by sweep-netting (multiway nested ANOVA)

Source of variation	Sum of squares	df	Variance	F ratio	P
<i>Total biomass</i>					
Pitfall trapping					
Grassland management	7208.7	1	7208.7	58.2	<0.0001
Study plot [Grassland management]	3146.4	4	786.6	6.3	<0.01
Season	2824.1	6	470.7	3.8	<0.01
Grassland management × Season	9407.3	6	1567.9	12.7	<0.0001
Error	2973.3	24	123.9		
Sweep-netting					
Grassland management	1486.9	1	1486.9	219.7	<0.0001
Season	517.2	6	86.2	12.7	<0.0001
Grassland management × Season	227.3	6	37.9	5.6	<0.001
Error	162.4	24	6.8		
<i>Percent biomass of arthropods <6 mm</i>					
Pitfall trapping					
Grassland management	1660.7	1	1660.7	22.8	<0.0001
Season	2102.9	6	350.5	4.8	<0.01
Error	2477.2	34	47.4		
Sweep-netting					
Grassland management	6960.2	1	6960.2	118.4	<0.0001
Error	2115.9	36	58.8		
<i>Shannon index of diversity</i>					
Grassland management	2.19	1	2.19	334.7	<0.0001
Study plot [Grassland management]	0.18	4	0.05	7.0	<0.001
Season	1.15	6	0.19	29.1	<0.0001
Grassland management × Season	0.17	6	0.03	4.4	<0.01
Error	0.16	24	0.01		

Only the final models are shown, after removal of the non-significant factors and interactions dropped in the backward elimination procedure (“Study plot [Grassland management]”, “mean temperature”, “mean rainfall”). df, degrees of freedom; F, F statistic; P, probability.

brought to the nest were Formicidae with a body length of 7 mm. Overall, the proportions of fed arthropods smaller than 9 mm were significantly higher in INT-broods (median: 8.7%) than in TRAD-broods (median: 3.6%; $P < 0.001$; Fig. 2(c)). Muscidae and Calliphoridae were the most numerous insects in INT-nestlings’ diet, accounting for almost a fifth of the prey (Table 3). In TRAD-broods, they were fed less often making up around 7.5% in number. Regarding Coleoptera, dung beetles (Scarabaeidae) were most abundant with a number of nearly 15% in INT-broods, while in TRAD-broods they were fed less than half as often (6%). Hymenoptera larvae, mainly sawflies, were a favoured prey in all 18 broods. They accounted for more than 16.5% in number in TRAD-broods, thus being the main prey type, and for about 11% in INT-broods. The numerical abundance and use of eight major invertebrate categories were compared through compositional analysis; the adult Whinchats showed a significant departure from random choice in both farmland regimes (Wilk’s lambda, $n = 18$, weighted mean = 0.035, $P < 0.001$ by randomization). Hymenoptera larvae turned out to be the significantly most preferred taxa in terms of frequency. In TRAD-broods, Saltatoria and the Diptera group Muscidae/Calliphoridae were significantly less preferred than all other taxa (Table 4).

3.3. Feeding behaviour

Among the variables reflecting adults’ foraging behaviour, the feeding rate did not differ significantly between INT- and TRAD-adults (median of INT = 7.2 feedings events per nestling * h; median of TRAD = 7.9, $P = 0.251$; Fig. 2(d)). In TRAD-broods, the median number of prey items brought to the nest per feeding event was 1.7, i.e., significantly higher than in INT-broods (median: 1.2, $P < 0.001$; Fig. 2(e)). Adults on INT-plots had a tendency to longer foraging distances (mean: 54.7 m) than breeding adults hunting on TRAD-plots (42.2 m), with “grassland management” being the factor explaining almost significantly most of the observed variation ($P = 0.016$, remember that P -rejection value was here set at 0.01; Fig. 2(f)).

3.4. Breeding success

Clutch size did not differ significantly between INT- and TRAD-broods (mean: 5.6 vs. 5.3 eggs, respectively; Mann-Whitney U -test, $Z_{9,9} = -1.01$, $P = 0.315$). The differences in hatching rate were also negligible (mean for INT: 0.98, mean for TRAD: 0.92, Mann-Whitney U -test, $Z_{9,9} = -1.57$, $P = 0.12$). The only parameter to show a significant difference between

Table 3 – Mean percentage by number (\pm SD expressing inter-brood variation) of the main invertebrate groups provisioned to nestlings according to grassland management (INT, intensively managed; TRAD, extensively managed)

Invertebrate group	INT (n = 9)		TRAD (n = 9)		Mean biomass per item (mg) (sample size n)
	Mean	sd	Mean	Sd	
Aranaeidae ^a	1.8	1.5	2.1	0.5	10.6 (98)
Thomisidae ^a	–	–	1.3	0.8	9.8 (45)
Coleoptera (Cantharidae)	1.0	1.1	3.9	3.3	13.3 (36)
Coleoptera (Elateridae)	2.0	2.4	4.4	1.8	16.4 (31)
Coleoptera (Scarabaeidae) ^a	14.9	11.0	6.1	3.3	13.4 (109)
Coleoptera larvae	0.8	1.6	–	–	14.1 (22)
Coleoptera (other)	1.3	1.9	3.2	1.5	14.6 (39)
Diptera (Muscidae, Calliphoridae) ^a	18.5	8.2	7.3	1.2	13.2 (337)
Diptera (Rhagionidae, Empididae) ^a	9.2	4.6	4.8	1.5	11.4 (35)
Diptera (Syrphidae)	0.9	0.9	3.9	1.0	9.7 (27)
Diptera (Syrphidae larvae)	–	–	1.5	0.8	21.1 (11)
Diptera (Tipulidae) ^a	5.7	5.2	4.7	2.2	9.1 (36)
Diptera (other)	–	–	2.3	1.1	9.9 (103)
Gastropoda (shell)	0.9	0.8	0.8	0.7	19.3 (24)
Gastropoda	–	–	0.5	0.5	12.4 (18)
Hymenoptera-Larvae (Symphyta) ^a	10.9	5.7	16.6	3.8	25.3 (22)
Hymenoptera (Formicidae)	–	–	1.7	1.2	4.7 (113)
Hymenoptera (Ichneumonidae)	–	–	0.9	0.6	6.9 (62)
Hymenoptera (Apoidea)	–	–	–	–	20.1 (34)
Hymenoptera (Vespidae)	–	–	–	–	18.2 (21)
Lepidoptera ^a	0.6	0.3	5.5	2.3	17.5 (52)
Lepidoptera larvae ^a	1.9	0.6	5.2	1.5	32.3 (27)
Saltatoria ^a	10.8	13.0	7.5	4.7	26.7 (69)
Lumbricidae, Diplopoda	0.7	0.6	0.6	0.4	27.3 (98)
Others	–	–	–	–	17.1 (108)
Undefined	15.3	5.8	15.1	4.6	

–, values smaller than 0.5%.

a, categories used for prey selection analysis (compositional analysis).

INT- and TRAD-plots was fledging rate (mean for INT: 0.87, mean for TRAD: 0.98, Mann–Whitney *U*-test, $Z_{8,9} = -2.14$, $P = 0.028$). Significantly more nests on INT-plots suffered from partial brood losses (five out of eight) compared to broods on TRAD-plots (one out of nine) ($\chi^2 = 4.898$, $P = 0.027$).

4. Discussion

4.1. Arthropod abundance and diversity with respect to grassland management

This study establishes that arthropod abundance and diversity was higher in traditionally managed than in intensively managed areas, this almost throughout the season. Numbers were 2.5 and 6.5 times higher, as regards pitfall trapping and sweep-netting, respectively, and biomasses 7–8 times larger (both sampling techniques) in traditionally managed grassland than in the intensively managed one. Compared to previous studies (Oppermann, 1999; Brickle et al., 2000), the order of magnitude of the observed difference is striking for a region in the Swiss Alps. As grassland intensification started in the 1980s in our study area (Schifferli et al., 1999), this indicates that arthropod communities inhabiting Alpine grassland are very susceptible to changes in management practices.

In traditionally managed areas, biomasses sampled with pitfall traps and sweep-netting showed a clear peak from

mid until late June (Fig. 1). This pattern did not emerge in the intensively farmed grassland, where arthropod biomasses at the very beginning of the season were not significantly different from the ones collected on traditionally managed areas, but then dropped to a very low level. This decline in abundance coincided with the onset of mowing, especially regarding biomasses collected with pitfall traps. Either arthropods were killed when cutting the grass, removed with the cuttings, or they moved to adjacent habitats (Curry, 1994). In both cases Whinchats breeding in intensively managed habitats must have suffered from this sudden and drastic reduction of prey biomass. As evidenced by Oppermann (1999), Whinchats adjust their breeding cycle on the phenology of their main prey so that invertebrate prey availability peaks during nestling rearing. These conditions were met in traditionally managed areas, but not in intensively managed ones.

Diversity indices increased slightly over time, in both intensively and traditionally managed habitats, reaching a plateau in early and mid July, but they were at least twice as high in traditionally managed areas than in intensively managed ones throughout the season. In addition, intensively farmed habitats were also characterized by higher proportions of tiny insects (<6 mm body size), which were particularly unattractive for Whinchats (see diet composition). That management intensity influences fauna diversity and even average invertebrate body size was already demonstrated by Bastian et al. (1994) who collected more smaller arthropod

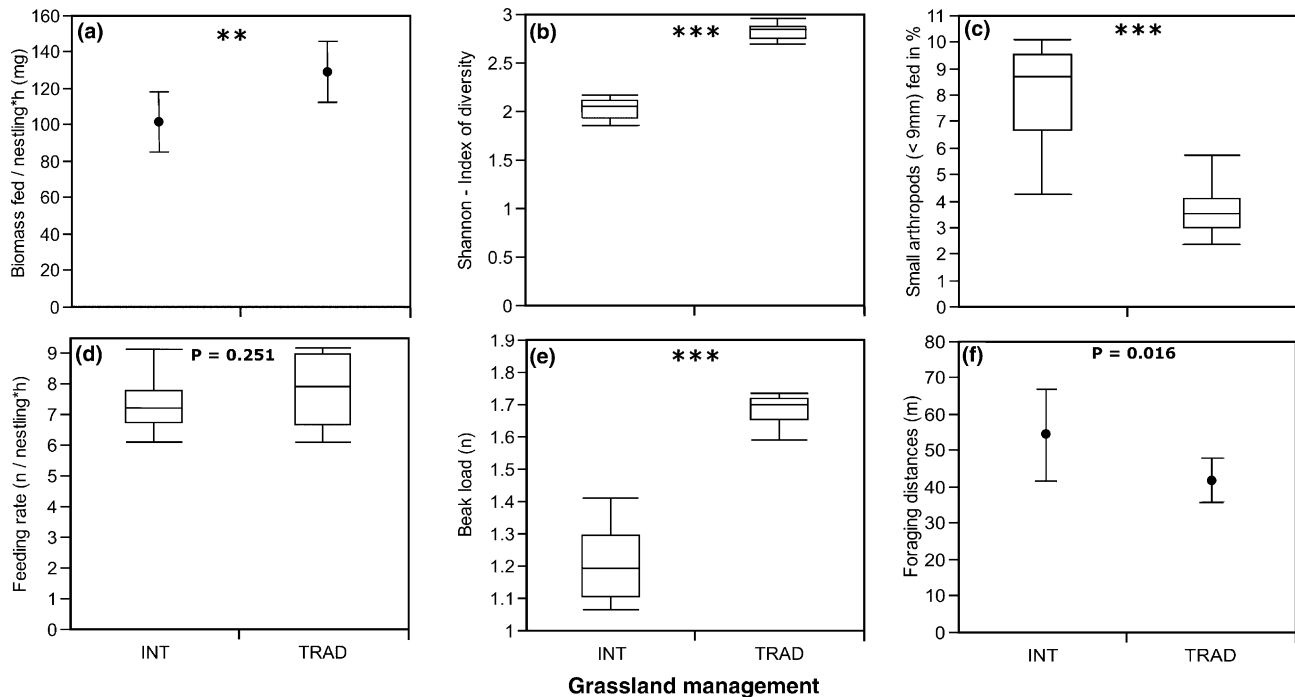


Fig. 2 – Food of nestlings (a–c) and parents’ foraging characteristics (d–f) at 18 Whinchat broods ($n = 9$ in INT-plots, 9 in TRAD-plots). Among-brood means (\pm SD) or medians with quartiles, maxima and minima are given: (a) biomass [mg/nestling * h (multiway nested ANOVA: grassland management: $F_{1,16} = 13.46$, $P = 0.0021$)]; (b) Shannon index of prey diversity (Mann–Whitney U-test, $Z = -3.53$, $P < 0.001$); (c) relative proportion of arthropods smaller than 9 mm body size (Mann–Whitney U-test, $Z = 3.45$, $P < 0.001$); (d) feeding rate (n/nestling * h) (Mann–Whitney U test, $Z = -1.15$, $P = 0.251$); (e) beak load (number of prey items in the bill at feeding event) (Mann–Whitney U-test, $Z = -3.54$, $P < 0.001$); (f) foraging distances from the nest (m) (multiway nested ANOVA: grassland management: $F_{1,16} = 7.2$, $P = 0.016$). Other non-significant factors in the models for (a) and (f) were sampling plot nested within grassland management, age of nestlings, number of nestlings, time period, mean temperature, mean rainfall. ** = $P < 0.01$; *** = $P < 0.001$.

species on intensively managed plots, where Whinchats were absent, in comparison with extensive meadowland. Indeed, besides altering the habitat structure and the overall arthropod community (Schmidt et al., 2005), mowing is particularly detrimental to larger insects (Beintema et al., 1991).

Spiders (Arachnida) and beetles (Coleoptera) were by far the most frequent orders caught in intensively managed grassland, whereas other groups were only present in very small numbers in that habitat type. These taxa that were rare in intensively managed areas occurred more abundantly in traditionally farmed ones; although they still represented a tiny part of items frequency, they played a crucial role in nestlings’ diet (Lepidoptera, Hymenoptera, larvae).

Our results provide support to the hypothesis that intensification of grassland management has a negative impact on the grass-dwelling invertebrate fauna: in all our statistical models, grassland management (intensive vs. traditional) was the most significant factor explaining overall among-plots variation. This outcome is particularly striking as the agriculture of the Alpine valley where we worked consists predominantly of hay meadows and involves almost no inorganic fertilizers, contrary to lowland farmland across western and central Europe. We can thus easily figure out why and how Whinchats have become extinct in most agricultural lowland areas. Indeed, the major switch from hay to silage grass production which occurred over the past decades could

be the principal reason for the decline of Whinchats (Ackermann, 1999; Müller et al., 2005). As a matter of fact, only one out of nine nests investigated for food provisioning in our study would have survived mowing without specific measures agreed upon with the farmers. At present, we can thus not say what affects mostly Whinchat’s population dynamics. Yet, the present study suggests that the timing of mowing – although it remains an important issue because of direct nest destruction – is not the only problem faced by Whinchats which also have to find invertebrate-rich grassland habitats.

4.2. Nestling diet and feeding behaviour: impact of grassland intensification

The video method we used for quantifying nestling diet yielded excellent results since most prey items delivered to nestlings could be identified with sufficient taxonomical resolution. As regards prey loads, biases that are assumed to be associated with any method relying on direct observation (Moreby and Stoate, 2001) were not obvious in our study. Nestlings in traditionally managed habitats were fed, on average, about 30% more arthropod biomass than nestlings of intensively managed ones, with other factors besides grassland management such as weather (Labhardt, 1988), season or nestling age (Poulsen et al., 1998) having no significant influence.

Table 4 – Simplified ranking matrices derived from the compositional analysis of prey selection (nestlings' diet vs. prey abundance)

	Rhagionidae, Empididae	Tipulidae	Scarabaeidae	Hymenoptera larvae (Symphyta)	Araneae	Lepidoptera	Saltatoria	Muscidae, Calliphoridae	Rank
Rhagionidae, Empididae		–	–	–	+	+	+	+	4
Tipulidae	+		+	–	+	+	+++	+++	6
Scarabaeidae	+	–		–	+	+	+	+	5
Hymenoptera larvae (Symphyta)	+	+	+		+++	+	+++	+++	7
Araneae	–	–	–	----		–	–	----	0
Lepidoptera	–	–	–	–	+		+	+	3
Saltatoria	–	----	–	----	+	–		–	1
Muscidae, Calliphoridae	–	----	–	----	+++	–	+		2
Hymenoptera larvae > Tipulidae > Scarabaeidae > Rhagionidae/Empididae > Lepidoptera > Muscidae/Calliphoridae > Saltatoria > Araneae									
Rhagionidae, Empididae		–	–	–	+	–	+	+	3
Tipulidae	+		+	–	+	+	+	+	6
Scarabaeidae	+	–		----	+	–	+++	+++	4
Hymenoptera larvae (Symphyta)	+	+	+++		+++	+++	+++	+++	7
Araneae	–	–	–	----		–	+++	+++	2
Lepidoptera	+	–	+	----	+		+++	+++	5
Saltatoria	–	–	----	----	----	----		+	1
Muscidae, Calliphoridae	–	–	----	----	----	----			0
Hymenoptera larvae > Tipulidae > Lepidoptera > Scarabaeidae > Rhagionidae/Empididae > Araneae >>> Saltatoria > Muscidae/Calliphoridae									
Upper part (INT-plots), n = 9 broods, Wilk's lambda: weighted mean = 0.002, P < 0.05, through randomization. Lower part (TRAD-plots), n = 9 broods, Wilk's lambda: weighted mean = 0.004, P < 0.01, through randomization. For clarity, each standardized logratio difference has been replaced by a + or – sign, showing the direction of selection; a triple sign represents a significant deviation from random at P < 0.05. The resulting ranked variable sequences from the most (7) to the least preferred taxa (0) are given below the tables; >>> denotes a significant difference (at P < 0.05) between two consecutively ranked variables.									

The lower prey diversity found in the diet of broods in intensively managed habitats reflects poor local arthropod availability. This corroborates the results of Bastian et al. (1994) who showed that in areas occupied by breeding Whinchats species richness of arthropods was greater than in unoccupied areas; arthropod diversity was the best predictor in separating the two groups. Other studies on birds have demonstrated that nestlings benefit from eating a mixed insect diet (Krebs and Avery, 1984). The fact that Whinchat nestlings of pairs breeding in intensively managed habitats were fed significantly more small prey items, whilst provisioning adults were carrying more single-prey-loads, can be interpreted in the context of optimal foraging theory (Anderson, 1981; Stephens and Krebs, 1986). A clear preference for large-sized prey items has been evidenced in several bird species (Davies, 1977; Bastian and Bastian, 1996; Grieco, 2001); it is certainly due to reduced searching time and a higher energy gain per feeding trip (Naef-Daenzer and Keller, 1999). Whinchats' parents in intensively managed areas could have compensated for smaller prey items and reduced prey loads by increasing feeding frequency (Siikamaki et al., 1998), but there was no evidence of this in our study where feeding rates did not differ significantly between grassland management regimes. Yet, a tendency towards an increased searching effort was noticeable in parents breeding in intensively managed habitats who tended to capture prey farther away from nest; this could be due to a higher proportion of multiple location foraging trips and/or less successful hunting. Breeding habitat quality hence appears to be lower in intensively managed areas as already suggested by Morris et al. (2001) for Yellowhammers. How intensification of farming practices actually affects prey availability is debated; some authors argue that it is foraging efficiency which is affected as prey items are less accessible in tall and dense swards (Vickery et al., 2001), whereas others believe that the reduction of prey body size within invertebrate communities is the principal cause (Blake et al., 1994; Blake and Foster, 1998; this study). In an interesting study of Skylarks, Poulsen et al. (1998) found that abundance of nestling food was much greater in set-aside, whilst distances traveled by parents during feeding trips there were significantly shorter compared to silage grass plots. They did not find differences in feeding frequencies, either, and suggested, as we do, that parents may have fed their young as often and as much as possible. Such a behaviour is likely to result in extra fitness costs for parents breeding in intensively managed habitats, since they devote less time for own maintenance (Martin, 1987).

As shown for other bird species, food items may be selected not only to maximize biomass brought to nestlings but also nutrient quality (Krebs and Avery, 1985; Naef-Daenzer et al., 2000). A high proportion of soft-bodied arthropods, especially lepidopteran and sawfly larvae, is known to be present in the nestling diet of many bird species, most probably because caterpillars are both nutritionally optimal and easy to handle and swallow (Banbura et al., 1999). In our compositional analysis of prey selection, sawfly larvae (Symphyta, Hymenoptera) were over-represented in nestling diet, whereas Diptera, Saltatoria and Aranae tended to be avoided. Due to their high amount of chitin (Saltatoria), or their relatively small biomass and high mobility (Diptera), these

arthropods are considered being among the least profitable prey items for Whinchats (Bastian and Bastian, 1996). In the broods of intensively managed habitats, they apparently play the role of substitution food since optimal prey is rare or absent. Similar roles are played by flies in Great tit diet (Naef-Daenzer et al., 2000) and spiders in the nestling diet of skylarks (Poulsen et al., 1998).

4.3. Breeding success

There are several, mutually non-exclusive mechanisms through which poor feeding conditions can harm breeding success or fitness. First, exploiting a poor foraging habitat may constrain parents to increase their rearing effort, with associated reduction in survival and residual reproductive value (Richner and Tripet, 1999); in this respect, a trend for longer foraging trips in intensively managed areas in this study is a symptom of poor habitat quality (Morris et al., 2001; Poulsen et al., 1998; this study). Secondly, females can adjust clutch size (see the review by Martin, 1987); however, there was no evidence for this in our Whinchat population. Thirdly, shortage of food resources can result in nestlings suffering reduced condition or growth rates (Brickle et al., 2000), with associated state-dependent predation due to conspicuous begging (Evans et al., 1997). This aspect was not investigated specifically here. Fourth, low food supplies can increase nestling mortality through starvation (Poulsen et al., 1998), or can result in a higher post-fledging mortality (Martin, 1987). In our study, there were significantly more partial losses of nestlings at 2–5 days of age in intensively managed habitats than in traditionally managed ones (5/9 vs. 1/9, respectively), probably caused by starvation, which is the main cause of fledgling mortality at that age (O'Connor, 1984).

4.4. Implications for conservation

Current farming practices within grassland and cropland are likely to affect tremendously the arthropod fauna and nestling food resources for farmland birds (e.g., Newton, 2004; this study). Especially important nestling food items for insectivorous birds, like sawfly and lepidopteran larvae, typically occur in lower densities in intensively managed areas, and such a lack of invertebrate food during the breeding season has been suggested as contributing to the widespread declines in populations and range of insectivorous farmland passerines (e.g., Benton et al., 2002; Fuller et al., 1995; Vickery et al., 2001). Results strongly supporting this view have been obtained in several species: Grey Partridge (Potts and Aebischer, 1995), Skylark (Poulsen et al., 1998; Wilson et al., 1997), Corn bunting (Brickle et al., 2000), Yellowhammer (Hinsley, 2000). Our study of the Whinchat is consistent with the hypothesis of a link between grassland management practices, arthropod abundance, feeding behaviour, nestling diet and reduced breeding success: differences in biomass, diversity and sizes of available arthropods in intensively vs. traditionally managed areas were precisely mirrored in nestling diet. Insectivorous farmland birds facing limited food resources are obviously no longer able to compensate for the numerous, newly imposed ecological constraints of modern agriculture. In regard to our Whinchat population, the contrasted patterns

found were particularly surprising as the Lower Engadine valley was till recently considered as one of the last typical Swiss landscapes with widespread traditionally managed meadowland harbouring several declining farmland birds (Schifferli et al., 1999).

Today, 84% of farmers in Lower Engadine, our study area, produce organically, with the remaining 16% fulfilling the standard, less stringent ecological requirements of the Swiss agriculture policy (R. Pedotti & Ch. Buchli, pers. comm.). Clearly this mode of supposed environment-friendly management is not providing optimal ecological conditions for Whinchats breeding in Alpine grassland, as it may do in the lowlands for other insectivorous birds (Beecher et al., 2002). Ineffectiveness of agri-environment schemes on target meadow birds have been found in a recent study in the Netherlands (Kleijn et al., 2004). Maybe it is time to envision agricultural policies that not only diminish the impact of production on the environment *sensu lato* (quality of air, water and soil), but that also favour explicitly emblematic flora and fauna elements through carefully targeted prescription as proposed by other authors (Vickery et al., 2004; Hole et al., 2005). In the future, indicator species of “natural” farmland may be used to evaluate the benefit of nature-friendly agri-environment schemes. In the case of the Whinchat, the combination of mowing practices respecting species’ breeding phenology (Müller et al., 2005) and low input fertilization in grassland (e.g., further restriction of liquid manure, a very common practice in Switzerland which is tolerated by organic production!) would certainly be key conservation measures. These measures would benefit the whole community of wild plants and animals inhabiting Alpine grassland.

Acknowledgements

Special thanks to M. Müller for information about the Whinchat and for support and encouragement during the field season. H. Schuler also provided support during field work. We are indebted to W. Nentwig and S. Bacher for advice about arthropod sampling, to M. Schaub for helping with statistics, and to H.-M. Stampfli for technical support. Special thanks to S. Schmied, T. Sattler, A. Valsangiacomo and A. Heitzmann for numerous advices. For valuable comments on earlier drafts of the manuscript we like to thank D.G. Dawson, C. Wedekind and an anonymous reviewer. During writing up, A.B. was financially supported by a Swiss National Science Foundation grant to C. Wedekind. Finally, we thank the numerous farmers who contributed to this study.

REFERENCES

Ackermann, L., 1999. Suivi d’une population de Tarier des prés (*Saxicola rubetra*) dans la Haute Vallée de la Doller (Haut-Rhin). *Ciconia* 23, 81–100.

Aebischer, N.J., Robertson, P.A., Kenward, R.E., 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74, 1313–1325.

Andersson, M., 1981. Central Place Foraging in the Whinchat, *Saxicola rubetra*. *Ecology* 62, 538–544.

Arlettaz, R., Perrin, N., 1995. The trophic niches of sympatric sibling *Myotis myotis* and *M. blythii*: do mouse-eared bats select prey? *Symposia of the Zoological Society of London* 67, 361–376.

Banbura, J., Lambrechts, M.M., Blondel, J., Perret, P., Cartan-Son, M., 1999. Food handling time of Blue Tit chicks: constraints and adaptation to different prey types. *Journal of Avian Biology* 30, 263–270.

Bastian, A., Bastian, H.-V., 1994. Bestände und Bestandstrends des Braunkehlchens (*Saxicola rubetra*). *Limicola* 8, 241–270.

Bastian, A., Bastian, H.-V., 1996. Das Braunkehlchen - Opfer der ausgeräumten Kulturlandschaft. AULA-Verlag, Wiesbaden.

Bastian, A., Bastian, H.-V., Sternberg, H.E., 1994. Ist das Nahrungsangebot für die Brutrevierwahl von Braunkehlchen *Saxicola rubetra* entscheidend? *Die Vogelwelt* 115, 103–114.

Beecher, N.A., Johnson, R.J., Brandle, J.R., Case, R.M., Young, L.J., 2002. Agroecology of birds in organic and nonorganic farmland. *Conservation Biology* 16, 1620–1631.

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., Bryant, D.M., Cole, L., Crick, H.Q.P., 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology* 39, 673–687.

Benton, T.G., Vickery, J.A., Wilson, J.D., 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* 18, 182–188.

Bingham, R.L., Brennan, L.A., 2004. Comparison of Type I error rates for statistical analyses of resource selection. *Journal of Wildlife Management* 68, 206–212.

Blake, S., Foster, G.N., 1998. The influence of grassland management on body size in ground beetles and its bearing on the conservation of wading birds. Wiley, Chichester.

Blake, S., Foster, G.N., Eyre, M.D., Luff, M.L., 1994. Effects of habitat type and grassland management-practices on the body-size distribution of Carabid beetles. *Pedobiologia* 38, 502–512.

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.

Bollmann, K., Keller, V., Müller, W., Zbinden, N., 2002. Prioritäre Vogelarten für Artenförderungsprogramme in der Schweiz. *Der Ornithologische Beobachter* 99, 301–320.

Borg, C., Toft, S., 2000. Importance of insect prey quality for grey partridge chicks *Perdix perdix*: a self-selection experiment. *Journal of Applied Ecology* 37, 557–563.

Bradbury, R.B., Wilson, J.D., Moorcroft, D., Morris, A.J., Perkins, A.J., 2003. Habitat and weather are weak correlates of nestling condition and growth rates of four UK farmland passerines. *Ibis* 145, 295–306.

Brickle, N.W., Harper, D.G.C., Aebischer, N.J., Cockayne, S.H., 2000. Effects of agricultural intensification on the breeding success of corn buntings *Miliaria calandra*. *Journal of Applied Ecology* 37, 742–755.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach, second ed. Springer, New York, USA.

Callion, J., 1993. Whinchat. Poyser, London.

Chamberlain, D.E., 2004. Lowland farmland birds: the road to recovery. A report on the BOU’s Annual Conference held at the University of Leicester, 2628 March 2004. *Ibis* 146, 704–706.

Chinery, M., 1993. Pareys Buch der Insekten, 2. Auflage edn. Parey, Hamburg, Berlin.

Cotton, P.A., Kacelnik, A., Wright, J., 1996. Chick begging as a signal: are nestlings honest? *Behavioral Ecology* 7, 178–182.

Curry, J.P., 1994. Grassland Invertebrates, first ed. Chapman & Hall, London.

- Davies, N.B., 1977. Prey selection and search strategy of spotted Flycatcher (*Muscicapa striata*) – field-study on optimal foraging. *Animal Behaviour* 25, 1016.
- Di Giulio, M., Edwards, P.J., Meister, E., 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* 38, 310–319.
- Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings of the Royal Society of London Series B-Biological Sciences* 268, 25–29.
- Evans, A.D., Smith, K.W., Buckingham, D.L., Evans, J., 1997. Seasonal variation in breeding performance and nestling diet of Cirl Buntings *Emberiza cirulus* in England. *Bird Study* 44, 69–79.
- Freemark, K.E., Kirk, D.A., 2001. Birds on organic and conventional farms in Ontario: partitioning effects of habitat and practices on species composition and abundance. *Biological Conservation* 101, 337–350.
- Fuller, R.J., Gregory, R.D., Gibbons, D.W., Marchant, J.H., Wilson, J.D., Baillie, S.R., Carter, N., 1995. Population declines and range contractions among lowland farmland birds in Britain. *Conservation Biology* 9, 1425–1441.
- Grieco, F., 2001. Short-term regulation of food-provisioning rate and effect on prey size in blue tits, *Parus caeruleus*. *Animal Behaviour* 62, 107–116.
- Harrell, F., 2001. *Regression Modeling Strategies*. Springer, New York, USA.
- Hinsley, S.A., 2000. The costs of multiple patch use by birds. *Landscape Ecology* 15, 765–775.
- Hole, D.G., Perkins, A.J., Wilson, J.D., Alexander, I.H., Grice, F., Evans, A.D., 2005. Does organic farming benefit biodiversity? *Biological Conservation* 122, 113–130.
- Keller, V., Zbinden, N., Schmid, H., Volet, B., 2001. Rote Liste der gefährdeten Brutvogelarten der Schweiz. Swiss Federal Office for the Environment and Swiss Ornithological Institute, Bern and Sempach.
- 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. *Conservation Biology* 18, 775–786.
- Krebs, C.J., 1989. *Ecological Methodology*. HarperCollins, New York.
- Krebs, J.R., Avery, M.I., 1984. Chick growth and prey quality in the European bee-eater (*Merops apiaster*). *Oecologia* 64, 363–368.
- Krebs, J.R., Avery, M.I., 1985. Central place foraging in the European bee-eater, *Merops-Apiaster*. *Journal of Animal Ecology* 54, 459–472.
- Labhardt, A., 1988. Zur Nahrung des Braunkehlchens (*Saxicola rubetra*) während der Jungenaufzucht. *Beih. Veröff. Natursch. & Landschaftspfl. Bad.-Württ.* 51, 179–185.
- Martin, T.E., 1987. Food as a limit on breeding birds – a life-history perspective. *Annual Review of Ecology and Systematics* 18, 453–487.
- Moreby, S.J., Stoate, C., 2001. Relative abundance of invertebrate taxa in the nestling diet of three farmland passerine species, Dunnock *Prunella modularis*, Whitethroat *Sylvia communis* and Yellowhammer *Emberiza citrinella* in Leicestershire, England. *Agriculture Ecosystems and Environment* 86, 125–134.
- Morris, A.J., Whittingham, M.J., Bradbury, R.B., Wilson, J.D., Kyrkos, A., Buckingham, D.L., Evans, A.D., 2001. Foraging habitat selection by yellowhammers (*Emberiza citrinella*) nesting in agriculturally contrasting regions in lowland England. *Biological Conservation* 101, 197–210.
- Müller, M., Spaar, R., Schifferli, L., Jenni, L., 2005. Effects of changes in farming of subalpine meadows on a grassland bird, the whinchat (*Saxicola rubetra*). *Journal of Ornithology* 146, 14–23.
- Naef-Daenzer, B., Keller, L.F., 1999. The foraging performance of great and blue tits (*Parus major* and *P. caeruleus*) in relation to caterpillar development, and its consequences for nestling growth and fledging weight. *Journal of Animal Ecology* 68, 708–718.
- Naef-Daenzer, L., Naef-Daenzer, B., Nager, R.G., 2000. Prey selection and foraging performance of breeding Great Tits *Parus major* in relation to food availability. *Journal of Avian Biology* 31, 206–214.
- Newton, I., 2004. The recent declines of farmland bird populations in Britain: an appraisal of causal factors and conservation actions. *Ibis* 146, 579–600.
- O'Connor, R.J., 1984. *The Growth and Developments of Birds*. Wiley, Chichester.
- Oppermann, R., 1999. Nahrungsökologische Grundlagen und Habitatansprüche des Braunkehlchens *Saxicola rubetra*. *Vogelwelt* 120, 7–25.
- Peach, W.J., Siriwardena, G.M., Gregory, R.D., 1999. Long-term changes in over-winter survival rates explain the decline of reed buntings *Emberiza schoeniclus* in Britain. *Journal of Applied Ecology* 36, 798–811.
- Potts, G.R., Aebischer, N.J., 1995. Population-dynamics of the grey partridge *perdix-perdix* 1793–1993 – monitoring, modeling and management. *Ibis* 137, S29–S37.
- Poulsen, J.G., Sotherton, N.W., Aebischer, N.J., 1998. Comparative nesting and feeding ecology of skylarks *Alauda arvensis* on arable farmland in southern England with special reference to set-aside. *Journal of Applied Ecology* 35, 131–147.
- Rheinwald, G., 1993. *Atlas der Verbreitung und Häufigkeit der Brutvögel Deutschlands - Kartierung um 1985*, Bonn.
- Richner, H., Tripet, F., 1999. Ectoparasitism and the trade-off between current and future reproduction. *Oikos* 86, 535–538.
- 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.
- Schmidt, M.H., Lefebvre, G., Poulin, B., Tschardtke, T., 2005. Reed cutting affects arthropod communities, potentially reducing food for passerine birds. *Biological Conservation* 121, 157–166.
- Shannon, C.E., Weaver, W., 1949. *The Mathematical Theory of Communication*, Urbana.
- Siikamäki, P., Haimi, J., Hovi, M., Ratti, O., 1998. Properties of food loads delivered to nestlings in the pied flycatcher: effects of clutch size manipulation, year, and sex. *Oecologia* 115, 579–585.
- Siriwardena, G.M., Baillie, S.R., Buckland, S.T., Fewster, R.M., Marchant, J.H., Wilson, J.D., 1998. Trends in the abundance of farmland birds: a quantitative comparison of smoothed Common Birds Census indices. *Journal of Applied Ecology* 35, 24–43.
- Sotherton, N.W., Self, M.J., 2000. Changes in plant and arthropod biodiversity on lowland farmland: an overview. In: Aebischer, N.J., Evans, A.D., Grice, P.V., Vickery, J.A. *Ecology and Conservation of Lowland Farmland Birds*. BOU, pp. 26–36.
- Southwood, T.R.E., 1978. *Ecological Methods*. Chapman and Hall, London.
- Standen, V., 2000. The adequacy of collecting techniques for estimating species richness of grassland invertebrates. *Journal of Applied Ecology* 37, 884–893.
- Stephens, D.W., Krebs, J.R., 1986. *Foraging Theory*. Princeton University Press, Princeton.
- Stephens, P.A., Freckleton, R.P., Watkinson, A.R., Sutherland, W.J., 2003. Predicting the response of farmland bird populations to changing food supplies. *Journal of Applied Ecology* 40, 970–983.
- Tucker, G.M., Heath, M.F., 1994. *Birds in Europe: Their Conservation Status*. Birdlife International, Cambridge, UK.

- Tukey, J., 1953. Multiple comparisons. *Journal of the American Statistical Association* 48, 624–625.
- 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 resources. *Journal of Applied Ecology* 38, 647–664.
- 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. *Biological Conservation* 119, 19–39.
- Wettstein, W., Schmid, B., 1999. Conservation of arthropod diversity in montane wetlands: effect of altitude, habitat quality and habitat fragmentation on butterflies and grasshoppers. *Journal of Applied Ecology* 36, 363–373.
- Wilson, J.D., Evans, J., Browne, S.J., King, J.R., 1997. Territory distribution and breeding success of skylarks *Alauda arvensis* on organic and intensive farmland in southern England. *Journal of Applied Ecology* 34, 1462–1478.
- Yeatman-Berthelot, D., Jarry, G., 1994. *Nouvel Atlas des oiseaux nicheurs de France 1985–1989*. Société Ornithologique de France, Paris.
- Zar, H.J., 1999. *Biostatistical Analysis*, fourth ed. Pearson Education, New Jersey.
- Zettel, J., 1999. *Blick in die Unterwelt: Ein illustrierter Bestimmungsschlüssel zur Bodenfauna*. Verlag Agrarökologie, Bern, Hannover.