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Comparative feeding ecology of the Whinchat *Saxicola rubetra* on intensively and extensively managed grassland

Diplomarbeit der Philosophisch – naturwissenschaftlichen

Fakultät der Universität Bern

vorgelegt von

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2003

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Abstract

1. The Whinchat *Saxicola rubetra* has among many other farmland birds declined steeply in western Europe since the 1950s. It has been postulated that a general decrease in insect abundance linked with intensification of agriculture may have contributed to these omnipresent declines of farmland birds. While nest losses due to earlier mowings are known to be one of the main causes for Whinchat's population decline, a potential impact of deteriorated arthropod food availability has not been investigated yet.

2. We compared studied food availability and feeding ecology of Whinchats breeding on intensively and extensively managed grassland plots in an inner-alpine valley. We used sweep-netting and pitfall traps to assess arthropod abundance and diversity, and analysed feeding ecology of pairs breeding on differently managed plots. We also studied nestling diet with cameras.

3. In the intensively managed plots, we collected a significantly lower abundance and diversity of grassland arthropods. We also found more smaller species and less chick-food invertebrates in the areas farmed more intensively.

4. Parents breeding in intensively managed plots fed their young less biomass compared to parents having their home ranges in areas farmed at low intensity. We also found the nestlings' diet in intensively managed plots to be less diverse and to be dominated by more unprofitable prey items. While feeding frequencies did not differ, foraging distances were significantly longer in home ranges farmed at high intensity.

5. We could not find any differences in clutch sizes and hatching rates depending on management intensity, but fledging success was higher in broods in extensively farmed plots. This difference arose due to a higher percentage of partial brood losses in intensively managed areas, for which the causes remain uncertain.

6. We conclude that recent changes in farming practices have led in our study area to a decrease in the availability of grassland invertebrates, in general, and of important chick-food invertebrates, in particular. This decrease in turn has negative impacts on the fitness of nestlings and adults by quantitatively and qualitatively reducing nestling food and foraging efficiency, respectively. Depending on mortality rates for fledged chicks and adults, this reduction may have partly contributed to the Whinchats decline and may hamper recovery.

7. We propose conservation measures that should both reduce nest losses caused by mowing and increase invertebrate availability at the same time so to be mostly beneficial to breeding Whinchats. Therefore, although depending heavily on overall agricultural policy, increasing the area of set-asides on a regional scale, especially in biodiversity-rich regions, would be most effective.

1. Introduction

1.1 Distribution and Population trends

The Whinchat, a ground–breeding passerine, is an indicator species of open grassland managed at low intensity. It used to be common and widespread in most parts of Europe, where extensively farmed meadows and pastures dominated the agricultural landscape (Bastian & Bastian 1996).

Today, high population densities are still present in the lowlands of Eastern– and Northern Europe, especially in parts of Sweden, Finland, Russia, Poland and Romania. In these countries, breeding densities can range up to 12 breeding pairs per 10 km^2 and stock figures seem to remain more or less constant (Bastian & Bastian 1994; Olsen 1992; Priednieks et al. 1989; Tomialojc 1992). But leaving this centre of the species distribution range heading towards West– and Middle Europe, steady population declines had been reported in many countries in the last 20 years (Bastian & Bastian 1994; Callion 1993; Melchior et al. 1987; Nicolai 1993; Oppermann 1999; Rheinwald 1993; Schwaiger & Burbach 1998; SOVON 1987; Uhl 1996; Yeatman-Berthelot & Jarry 1994).

Similar trends can be observed in Switzerland. Until the middle of the last century, the whinchat was a widespread farmland species settling in many different habitats both on the plain and in the Alps up to 2270 m asl. (Schmid et al. 1994; Studer & Fatio 1913). But since 1950, an intense decline, which was especially pronounced in broad areas of the Swiss plain, began to narrow the species distribution range in Switzerland (Anderegg et al. 1983; Fuchs 1979; Géroudet et al. 1983; Jacoby et al. 1970; Lüps et al. 1978; Müller et al. 1977; Schifferli et al. 1980). Most of the Swiss plain and the Northern Jura are abandoned meanwhile, the Whinchat having its main breeding habitats in subalpine regions of the Alps and the Jura (Schmid et al. 1994; Schmid et al. 1998). The Engadine and the Valais were still areas with considerably high population densities a few years ago (Müller 1996), but reports of recent declines indicate that these regions will not remain unaffected by the overall trend (Horch et al. 2001; Manuel & Beaud 1982; Müller et al. 2001). Thus, it is not surprising that the Whinchat is classified as "near threatened" in the "Red List 2001 of threatened and rare breeding birds of Switzerland" (Keller et al. 2001) and is one out of "50 priority birds for species action plans in Switzerland" (Bollmann et al. 2002), for whose conservation our country carries international responsibility.

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1.2 Conservational aspects – a focus on feeding ecology

The populations of many other farmland birds also declined severely across Europe during the last quarter of the 20th century (Donald et al. 2001; Fuller et al. 1995; Siriwardena et al. 1998; Tucker & Heath 1994). Within the same past 50 years, agricultural practice has changed markedly in Switzerland, as elsewhere (Blaxter & Robertson 1995). Thus, the decline in farmland bird populations has accompanied farming intensification (Chamberlain et al. 2000; Fuller et al. 1995). However, the mechanisms by which farming practice influences bird populations are still widely debated (Ackermann 1999; Bastian & Bastian 1994; Bastian et al. 1994; Campbell et al. 1997; Di Giulio et al. 2001; Freemark & Kirk 2001; Gillings & Fuller 1998; Glutz von Blotzheim & Bauer 1985; Moreby & Southway 1999; Müller et al. 2001; Oppermann 1999; Schifferli et al. 1999; Siriwardena et al. 1998; Vickery et al. 2001). There are several ways in which modern agriculture can have detrimental direct and indirect effects on birds and their insect food resources: (I) Earlier cuts, favoured by the switch from hay to silage production, result in nest destruction or make nests more visible to potential predators; (II) A management of earlier and more pronounced mowing can directly affect insects by damaging or killing individuals or removing them from the site; (III) The plant species composition and the structure of grassland vegetation are being altered (e.g. through intense mowing and herbicide application), this in turn may change the invertebrate fauna community dramatically (decline in abundance, less diverse, more smaller species); (IV) The increased application of organic and especially of inorganic fertilizers makes the sward grow taller and more dense, thus leads to a decreased visibility and accessibility of arthropods for birds.

Given the broad variety of factors that can possibly deteriorate foraging possibilities for birds on intensively managed grassland, it seems reasonable to assume that reduced food supplies may be an important reason for farming birds' decline. There are indeed recent studies suggesting reduced survival due to poor feeding conditions (Brickle et al. 2000; Laiolo & Rolando 1999; McCracken & Foster 1994; Peach et al. 1999; Wilson et al. 1997; Wilson et al. 1999). A link between arthropod availability and population size is for example known for the Grey Partridge (Potts & Aebischer 1995; Southwood & Cross 1969) and suspected to exist in several species, but for other farmland passerines, results are contradictory (Bradbury et al. 2003).

1.3 Background knowledge – nestling diet and feeding behaviour

The Whinchat depends on a high variety of arthropods within its home range making it possible to switch between different prey items according to their availability. Adult birds feeding their young preferentially forage on few, but relatively large arthropods with body sizes from 8 – 16 mm, leaving up to 75 % of the potential food resources untouched (Bastian & Bastian 1994; Labhardt 1988; Oppermann 1992). The diet of adults and young mainly consists of the following taxa: *Coleoptera, Diptera, Hymenopera, Lepidoptera* and *Araneae*. *Saltatoria, Hemiptera, Lumbricidae* and *Gastropoda* are also occasionally included. Larvae of *Hymenoptera* and *Lepidoptera* are being fed in much higher proportions than expected considering their abundance (Labhardt 1988; Müller 1985; Steinfatt 1937). This widespread preference for caterpillars has several reasons: (I) They are relatively easily detectable and move slowly through the vegetation, thus being a prey with short handling - time; (II) Their physiological usability is high (high body mass, few chitin compared to *Coleoptera* and *Saltatoria*); (III) Their clumped distribution makes it possible for adults to repeatedly exploit this profitable food resource (Bastian & Bastian 1996; Müller 1985). The arthropod composition representing the whinchats nestling diet still shows considerable variation among different breeding pairs. This circumstance is likely to reflect differences in habitat and territory quality (Smart et al. 2000), in number and constitution of young (Flinks & Pfeifer 1988; Royama 1966), in the foraging skills of adult birds (Lemon 1993; Müller 1985; Siikamaki 1996) and in weather conditions (Labhardt 1988; Schaad 2002). For example, particularly Butterflies and grasshoppers strongly reduce their activity during periods of cold weather and hide in the vegetation, the same is true for other flying insects (*Diptera, Hymenoptera*) (Boness 1953; Taylor 1963). The Whinchat exhibits different kinds of foraging tactics ("fly catching", "hovering", "hawking", "flush–pursue", for further explanations see Remsen & Robinson 1990), all of them having in common that they start and end from a perch. It opportunistically changes its hunting techniques according to food availability (Andersson 1981), thus "fly catching" e. g. being a quite energy–consuming tactic is only profitable when weather conditions are good (Bastian & Bastian 1996; Rebstock & Maulbetsch 1988).

1.4 Aims and hypothesis

The aim of this study was to investigate whether differences in feeding ecology of pairs breeding on intensively managed plots compared with extensively managed areas can partly explain the widespread decline of this farmland species. Nest losses due to mowing events have been shown in previous studies to be a key factor affecting the reproductive output of our study populations (Müller 1996; Müller et al. 2001). Yet, current data on the feeding ecology of the whinchat is rare (Labhardt 1988; Müller 1985; Oppermann 1999), and, to our knowledge, studies using a comparing approach are entirely lacking up to now. But in view of the widespread changes in agriculture in the last 20 years reshaping the whinchats breeding habitats, such an approach is of basic necessity when it comes to implementing any future conservation measures.

In a first step, an assessment of the arthropod abundance on the differently managed grassland plots was performed to check if patterns of impoverishment of insect food as found in other studies (Aebischer 1991; Sotherton & Self 2000; Wilson et al. 1999; Woiwod 1991) could be confirmed. Given the fact that our study area was a subalpine Swiss valley, which has been managed in an intensive way for only a relatively short period of time, we expected to find only slight differences in the invertebrate species composition and in the sampled biomasses.

Further, we studied nestlings diet and feeding behaviour of 18 breeding pairs having their home ranges on differently managed plots. We also took measurements of breeding success of the pairs followed. Given reductions in their food resources, it is plausible that Whinchats breeding on intensively managed plots may be suffering smaller clutch sizes or reduced nestling condition, as a result of either lowered intake rates or a diet dominated by less profitable food items (Borg & Toft 2000; Bradbury et al. 2003). Furthermore, poor nestling condition can also lead to increased begging (Cotton et al. 1996) which could attract predators, which in turn can increase the risk of state–dependent predation (Evans et al. 1997). If food supplies are very poor, chicks can of course also die of starvation (Poulsen et al. 1998). We would therefore predict to find differences in biomass and in species composition of the arthropods fed depending on which kind of agricultural practice is dominating the foraging habitat. We would also expect clutch sizes and / or fledging rates to be lower on intensively managed plots if contrasts in the nestlings diet were really pronounced.

On the other hand, parent birds may also absorb the impacts of a deteriorating environment by working harder to get the same or a reduced amount of food for their young (Brickle et al. 2000; Morris et al. 2001). In this way, they maintain the reproductive output but have to bear the possible cost of a reduction in their own survival (Richner & Tripet 1999). In our study, if

the parent Whinchats raising their young on intensively managed plots followed this reproductive strategy, it would show up in at least two ways. As way to compensate for low food quality, parents could firstly deliver food at a faster rate (Siikamaki et al. 1998; Tolonen & Korpimaki 1994) or secondly bring bigger loads. According to optimal foraging theory, these heavier loads should be connected to longer foraging trips and thus to a lower delivery rate (Andersson 1981; Stephens & Krebs 1986). Analysing the variables, which describe feeding behaviour of the adults (feeding frequency, size of loads, foraging distances), should enable us to discriminate between the two possible mechanisms.

2. Methods

2.1 Study area

The study was conducted from May - July 2002 in an inner–alpine valley in Switzerland (lower part of the Engadine valley) with a warm and dry summer climate. Total precipitation during June and July 2002 was 271 mm, the mean temperature 15 °C. Six sampling plots were chosen for the assessment of food availability, three of them being intensively managed located at the bottom of the valley, three of them being extensively managed located on the slope (SSE-SSW exposed) (Fig. 1 and Table 1). Agricultural areas at the bottom of the valley consist mainly of open, fairly flat meadows, dispersed small plots of spring sown cereals (oat and wheat) on river sediments and few embankments with bushes and hedgerows. Two of the extensively managed plots on the slope at a mean altitude of 1590 m (Vnà, Tschlin) asl. are composed of artificial terraces which are separated by borders with bushes of the *Berberido vulgaris-Rosetum* community. The terraces were formerly arable land, now mainly grassland (70% hay meadows, 20% pastures). The third plot located on the slope at 1750 m asl, Chantata, used to be an upland moor, today it consists mainly of extensively managed hay meadows (80%). For analyses of nestlings diet and feeding behaviour (see below), breeding pairs on four additional plots were followed (Fig. 1 and Table 1). The discrimination of the study plots in two agricultural practices (INT[1] vs. EXT[2]) was based upon three management variables (Di Giulio et al. 2001; Oppermann 1991 / 92), which were enough to clearly separate the plots (Table 1): (I) number of cuts per year; (II) date, when 50% of the area was mown; (III) average flower diversity. This last vegetation parameter was recorded by randomly choosing three 100 m^2 plots on each sampling site, where all flowering plant species were counted by the end of May. These three counts were then assigned to four frequency classes and the average flower diversity was calculated for each plot.

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[1] intensively managed plots
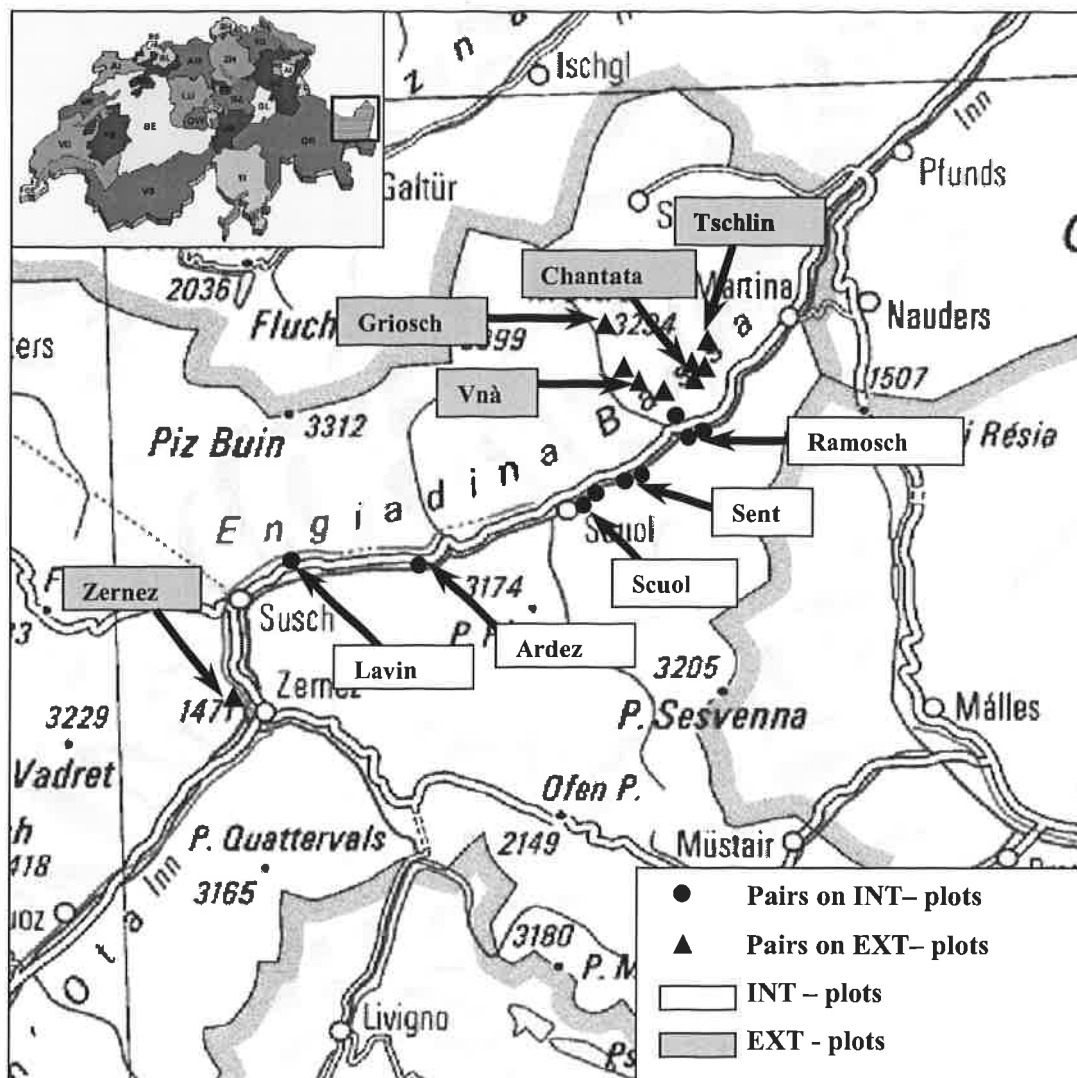[2] extensively managed plots

Fig. 1. Locations of the 18 breeding pairs followed and of the 6 study plots chosen for the arthropod sampling (Scuol, Sent, Ramosch, Vnà, Chantata, Tschlin). The four additional plots are also shown (Ardez, Lavin, Zernez, Griosch). For characteristics of the sampling plots see Table 1.

Table 1. Characteristics and management variables of the six study plots, where arthropod sampling was conducted throughout the season, and of the four additional plots, where breeding pairs were followed. Legend for the average flower diversity: 1 = 0-2 flowering species, 2 = 3-5 flowering species, 3 = 5-8 flowering species, 4 = >8 flowering species / 100 m^2. Means are shown (n=3).

Plot	Agricultural practice	Altitude (m asl)	Surface area (ha)	Coordinates	No. of cuts / year	50% of area mown	Flower diversity
Scuol	intensively	1243	35	46°48'N, 10°18'E	2 - 3	13.6.	1.3
Sent	intensively	1150	39	46°48'N, 10°20'E	2 - 3	13.6.	1.3
Ramosch	intensively	1160	48.5	46°49'N, 10°23'E	2	14.6.	1.6
Vnà	extensively	1540	45	46°50'N, 10°21'E	1 - 2	7.7.	2.3
Chantata	extensively	1680	50	46°48'N, 10°18'E	1	10.7.	3.3
Tschlin	extensively	1580	44	46°51'N, 10°25'E	1 - 2	8.7.	2.3
Lavin	intensively	1430	24	46°46'N, 10°06'E	2	15.6.	1.6
Ardez	intensively	1464	26	46°46'N, 10°11'E	2 - 3	16.6.	1.6
Zernez	extensively	1473	18	46°42'N, 10°05'E	1 - 2	3.7.	2.3
Griosch	extensively	1711	19	46°52'N, 10°19'E	1 - 2	12.7.	2.3

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2.2 Arthropod availability

To estimate arthropod abundance and species richness on the six grassland study plots, pitfall traps and sweep–net sampling were used. A combination of the two collecting techniques is needed to accurately describe the total arthropod fauna inhabiting grassland plots (Standen 2000). On each of the study plots, three collecting points were chosen randomly, taking care that they would properly reflect the composition of the different agricultural parcels present. On every collecting point, 4 plastic cups with a diameter of 7 cm were set without covers 3 m apart in a row. Ethylene glycol was used as a preservative rather than Formalin 4%, because the latter is suspected to produce biases through differentially attracting arthropod species (Nentwig, pers. comm.). The traps were set every ten days for a period of 72 hours. The collecting started on the 23.5. and lasted until the 24.7., thus 7 sampling periods were conducted. This technique focuses on collecting mostly epigeal fauna, while sweep-netting was used to catch mostly epiphytic fauna living amongst the grass sward. Sweep-net samples were taken at the same collecting points mentioned above every ten days (starting at the 23.5., ending by the 24.7.), from 10 – 17 pm when weather conditions were good (i.e. a minimum of 16 °C, sunshine, <2 Beaufort). The sampling order of the plots was varied between sampling periods. One sample unit was defined to be 20 strokes performed at equal intensity through the sward or in case of mown meadows straight over the ground, respectively (standardized sweep-net method according to Oppermann 1999; Di Gulio et al. 2001). Per collecting point and sampling period, three such sub samples were taken and pooled later on. This design hence produced two samples (one pitfall trap sample, one sweep–net sample) per collecting point and sampling period.

Furthermore, sweep–netting was also performed on the home ranges of the breeding pairs followed. Sample units were taken at four different points where the adults preferentially foraged on the days the nestlings diet was assessed. The data recorded like this was used for an analysis of prey selection, which was performed to check for preferences the adults might show while foraging for arthropods making up the nestlings diet. Only the sweep-net sampling technique was applied this time, because pitfall traps would not have provided instantaneous information about the food availability.

All the arthropods collected were conserved in 70% Ethanol in small vacuum plastic bags. In the laboratory, the content of each sample was identified separately down to suborder or family level using reference guides (Chinery 1993; Reichholf 2001; Zettel 1999) and a microscope (Leica MZ95), if necessary. Then, the arthropods were dried in an oven for 72

hours at 60°C according to Southwood (1978) and their biomasses were determined to the nearest 0.001 g with a Mettler precision balance. According to their body lengths, the arthropods were also assigned to three size classes (< 6 mm, 6 – 14 mm, > 14 mm). A total of 123 taxa- and size-classes resulted.

2.3 Nestling diet

The assessment of the nestlings diet of 18 breeding pairs was performed by filming prey items delivered to the nest with an observation video camera (Videotronic, CCD-7012P, Neumünster, Germany) placed on a tripode. Adults feeding their young were recorded two following mornings from 6 – 12 a.m. when nestlings had reached an age of 8 – 11 days and weather conditions were good (i.e. sunshine during 75 % of recording time). For 8 out of the 9 pairs breeding on intensively managed plots, it was necessary to set aside their nests and the close surrounding vegetation (about 6 m in diameter) from mowing events. This was done by searching the nests early in the season and marking them with a wooden stick of 1.20 m height, which the adults readily accepted as a nest perch. Such nest perches were also offered to the other 10 pairs to be recorded, as to force the adults to always be in focus of the camera when delivering prey items to their nestlings. In 94 % of all feeding events birds used these artificial nest perches prior to entering the nest. A similar method had been applied before successfully (Labhardt 1988). The whole setup, which consisted out of the observation camera and a time lapse video recorder (Sanyo, SRT 7168P, Osaka, Japan) protected by specially designed cases, were hidden with camouflage nets and placed the evening before recording started in a distance of 3–5 m from the nest. Power supply came from a generator (Honda EU 10l, Tokyo), which was set 40-50 m further away. Focus and sharpness of the images were controlled with a small portable monitor (Sony, GV-D800, Tokyo, Japan). Two such video systems were used and mostly simultaneously running at two different nest locations.

Video tapes were then analysed using frame by frame and freeze facilities on the video cassette recorder. The two mornings of filming were pooled resulting in a period of 12 hours of feeding for each pair. Arthropods were identified to order or to family level if possible and their body sizes were estimated by comparing them to the length of the bird's beak. Based on the sizes and biomasses of the arthropods collected on the home ranges of the videotaped pairs (see "Arthropod sampling"), biomasses delivered to the nest were calculated. About 15% of prey items turned out to be not identifiable (see also Table 5). This was not due to their small sizes, but because the feeding bird was in some cases not in focus of the camera

when sitting on the perch. Still, these items could be size-classified and their biomasses were estimated. A total of 26 classes, to which the prey items had been assigned, were used for the calculations of the Shannon-indices of diversity (Shannon & Weaver 1949).

2.4 Feeding behaviour

Feeding frequencies per young and hour and the number of prey items delivered to the nest per feeding event (load size) were calculated from 11 hours of filming material available for each pair. The first 30 minutes following the start of videotaping in the mornings were excluded from the analysis to make sure birds' feeding behaviour was not influenced by the former presence of the person installing the video camera system.

Foraging distances were measured from 8 – 12 a.m. during two hours for each pair using a laser rangefinder (LEICA Geovid Binocular 7 x 42) and a dictaphone. If an adult visited multiple locations prior to returning to the nest, the total distances flown between capture sites and the nest were calculated. Position of the observer was outside the home ranges, at a minimum distance of 130 m from the nest.

2.5 Breeding success

For each of the 18 nests, the clutch size, hatching rate and number of nestlings having reached the age of 12 days were recorded. Young are leaving their nests at the age of 12-14 days and live well hidden in the sward for some more days afterwards, which makes them very difficult to count. That was the reason to define young aged 12 days as "fledged young" in this study. Broods were visited the least often necessary (3-4 times) and care was taken not to leave obvious trails indicating nest location to potential predators. If a brood was robbed, it was decided to exclude it from the analysis for the aim of the study was to determine mortality rates of nestlings without the factors "mowing" and "predation", as far as feasible.

2.6 Weather data

Data on mean temperature, relative humidity, wind direction and strength, precipitation, cloud coverage and hours of sunshine came from the weather station Scuol (Federal Office of Meteorology and Climatology, MeteoSwiss 2002). Additionally, temperatures were measured at 6 and 12 a.m. on each of the mornings when filming took place at the site of recording. The

mean temperatures for the whole period of videotaping (12 hours per pair) were then calculated.

2.7 Statistical analysis

All variables were tested for homogeneity and normality prior to running ANOVAs.

For the multiway analysis of food availability, both the biomass variables (sampled with pitfall traps and sweep-net) and the proportions of arthropods < 6 mm were root transformed (Zar 1999). A multiway ANOVA was performed to highlight significant differences between agricultural practices, multiple comparisons were made using post hoc Tukey's tests. For the calculations of the Shannon-indices of diversity (Shannon & Weaver 1949), the 126 size- and taxa-classes were pooled to produce 53 groups of arthropod frequency. This was done due to an overdispersion of data among too many categories. Data from both trap types was also pooled, because overall diversity of grassland arthropods was of interest. A multiway ANOVA was performed on the resulting dataset to test for significant influence of agricultural practice, and other factors, on the arthropod diversity. Regarding the nestling diet, the Shannon-indices of diversity were calculated using the 26 groups mentioned earlier (see 2.3 "Nestling diet"). To check for differences in the Shannon-indices and in the proportions of arthropods fed < 9 mm, Mann-Whitney U tests were applied (Zar 1999). The same was true for other variables, which were not normally distributed (feeding frequencies per young and hour, number of arthropods per feeding event, clutch size, hatching rate, fledging rate). The variables "biomass fed per young and hour" and "mean foraging distances" were both normally distributed and thus compared by running a multiway ANOVA. For analyses of prey selection, significances of deviation from the line of no selection were assessed using sign-tests (Zar 1999).

For all data analyses performed, the program JMP4 (SAS Institute Inc. 2001, Cary, NC, USA) was used.

3. Results

3.1 Arthropod availability

During the seven sampling periods from May till July, which sum up to 21 days of collecting, an overall number of 25'666 arthropods (303.5 g dry biomass) were caught with both trap-types. Out of these, 10'098 (39.3 % of total frequency, 2.7 % of total dry biomass) arthropods, mainly Diptera, were smaller than 6 mm, thus not considered as being part of the whinchat's nestling diet (see 3.2, "Nestling diet"). The composition of the remaining, for the nestling diet relevant 15'568 (60.7 % of total frequency, 97.3 % of total dry biomass) arthropods was dominated by three most abundant orders: Coleoptera (38.5 % of frequency, 46.9 % of dry biomass), Arachnida (35.9 % of frequency, 20.8 % of dry biomass) and Diptera (9.6 % of frequency, 1.8 % of dry biomass) (Appendix 1).

The total biomass of arthropods collected with pitfall traps and sweep–net sampling was significantly lower almost over the whole season on the three intensively managed plots (INT) compared with the three extensively managed plots (EXT) (Table 2 and Fig. 2). Concerning the pitfall traps, a multiway analysis of variance (ANOVA) produced significant values for the factor "Agricultural practice" ($P < 0.0001$) and the interaction of the factors "agricultural practice" and "season" ($P = 0.0001$). Yet, the factor "season" alone could not explain a significant percentage of variance ($P = 0.0784$). Looking at the sweep–net sampling, the differences in biomass on INT and EXT– plots were significantly explained by the factor "agricultural practice" ($P < 0.0001$) and "season" ($P < 0.0001$), the interaction between the two not being significant ($P = 0.0019$). The following factors and all possible double and triple interactions with and among them were dropped during the backward elimination procedure of both analysis, because they were not explaining significant percentages of variance: "Sampling plot", "Mean temperature" and "Mean rainfall" (Table 2).

To check for differences in the arthropod biomass collected within sampling periods, a post–hoc Tukey–test was conducted. Concerning the pitfall traps, the extensively managed plots yielded significantly more biomass on the 13.6. and the 23.6. (post–hoc Tukey–Test, n = 6, $P < 0.05$), the rest of the sampling periods showed no significant differences. The arthropod biomass caught with sweep-net was significantly higher during five out of seven sampling periods (on the 3.6., 13.6., 23.6., 3.7., 13.7.; post–hoc Tukey–Test, n = 6, $P < 0.05$) (Fig. 2, for test–table see Appendix 2).

Table 2. Effects of the two factors "Agricultural practice" (intensively vs. extensively managed) and "season" on the availability of arthropods caught with pitfall traps and by sweep–net sampling, respectively. A multiway analysis of variance (ANOVA) was performed. The final model is shown, not significant factors and interactions dropped out in the backward elimination procedure were: "Study plot", "Mean temperature", "Mean rainfall". df = degrees of freedom, F = F statistics, P = rejection probability. Significant values in bold letters.

Source of variation	Sum of squares	df	Variance	F Ratio	P
Total Biomass pitfall traps					
Agricultural practice	7208.699	1	7208.699	32.9823	**< 0.0001**
Season	2824.070	6	470.678	2.1535	0.0784
Agricultural practice x Season	9407.320	6	1567.887	7.1736	**0.0001**
Error	6119.756	28	218.563		
Total Biomass sweep-net					
Agricultural practice	1486.858	1	1486.858	186.443	**< 0.0001**
Season	517.179	6	86.196	10.808	**< 0.0001**
Agricultural practice x Season	227.348	6	37.891	4.751	0.0019
Error	223.296	28	7.975		

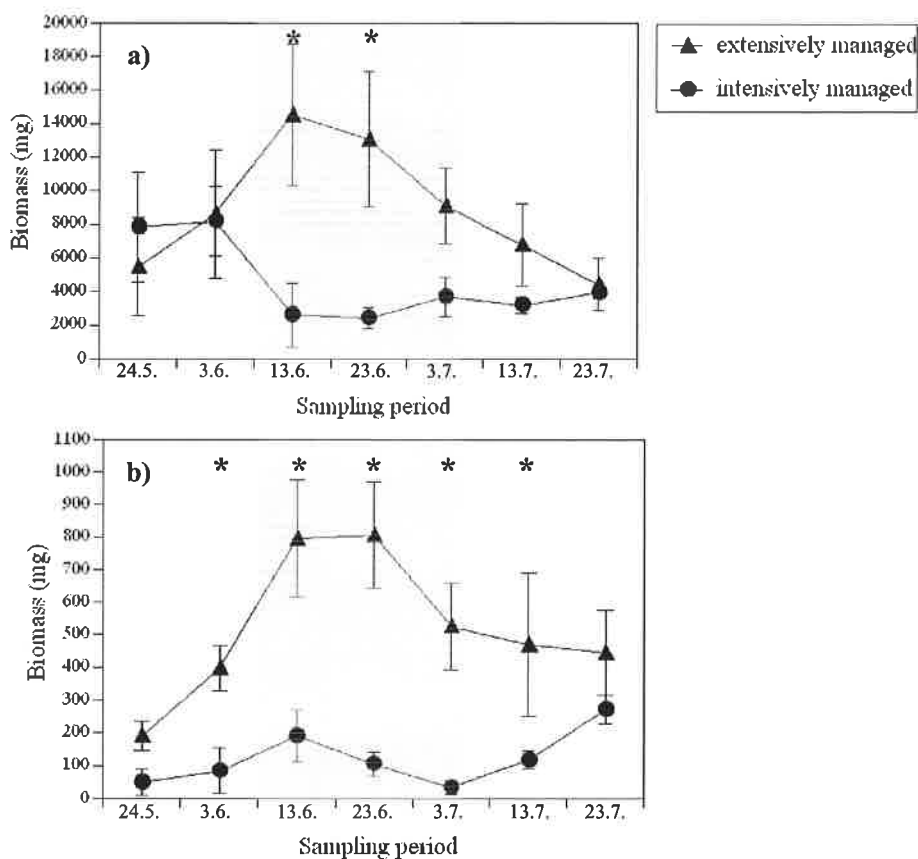**Fig. 2.** Seasonal trends in the overall biomass of the collected arthropods (means ± SD) on the six sampled plots (3 INT vs. 3EXT). The overlay indicates nestling period of the 18 Whinchat pairs followed. **(a)** Arthropods in pitfall traps; **(b)** arthropods in sweep net. Significant differences within sampling periods are depicted by a star (post–hoc Tukey–Test, n = 6, P < 0.05; for test–tables see Appendix 2).

On the intensively managed plots, the relative frequency of arthropods smaller than 6 mm tended to be higher over the season. For the pitfall traps, the factors "agricultural practice" (P < 0.0001), "season" (P = 0.0002) and the interaction between the two explained a significant part of the overall variance (P = 0.0231). Regarding the arthropods caught with sweep – net, the factor "agricultural practice" (P < 0.0001) and the interaction "agricultural practice" x "season" (P = 0.0134) turned out to be significant, the factor "season" alone was not (P = 0.8754). Again, three not significant factors along with their interactions were dropped during the backward elimination procedure of the analysis: "Sampling plot", "Mean temperature" and "Mean rainfall" (Table 3 and Fig. 3.).

Table 3. Effects of the factors "agriculture" and "sampling period" on the percentage of arthropods smaller than 6 mm caught with pitfall traps and by sweep – net sampling, respectively. A multiway analysis of variance (ANOVA) was performed. The final model is shown, not significant factors and interactions dropped out in the backward elimination procedure were: "Sampling plot", "Mean temperature", "Mean rainfall". df = degrees of freedom, F = F statistics, P = rejection probability. Significant values in bold letters.

| Source of variation	Sum of squares	df	Variance	F Ratio	P
% of arthropods < 6 mm, pitfall traps					
Agricultural practice	1660.655	1	1660.655	30.6526	**< 0.0001**
Season	2102.856	6	350.476	6.4691	**0.0002**
Agricultural practice x Season	960.299	6	254.491	0.0231	**0.0231**
Error	1516.946	28	34.296		
% of arthropods < 6 mm, sweep-net					
Agricultural practice	25.3291	1	25.329	150.728	**< 0.0001**
Season	0.3991	6	0.067	0.396	0.8754
Agricultural practice x Season	3.3538	6	0.559	3.326	**0.0134**
Error	4.7053	28	0.168		
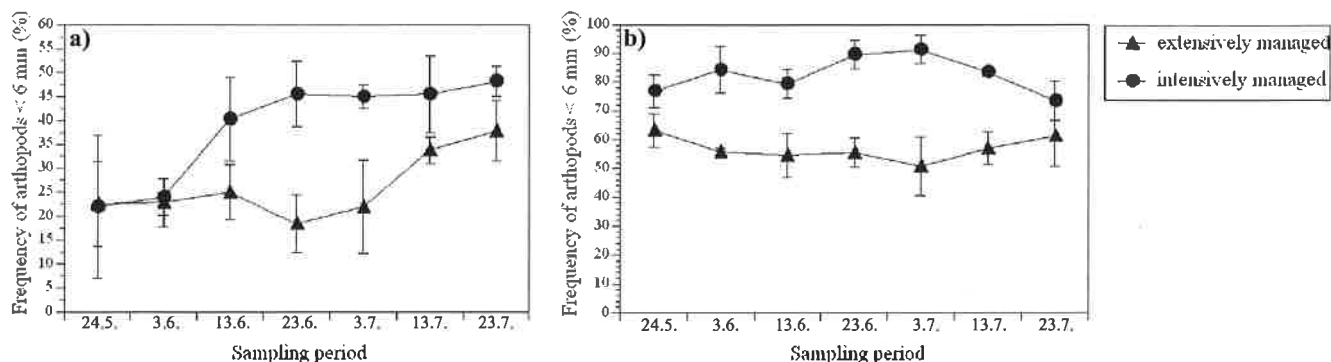
Fig. 3. Seasonal trends in the abundance (relative frequency in %, means ± SD) of arthropods smaller than 6 mm on the six sampled plots (3 INT vs. 3 EXT). **(a)** Arthropods caught with pitfall traps; **(b)** Arthropods caught with sweep–net.

The proportions of the different groups of arthropods collected differed slightly between the intensively and extensively managed plots (Fig. 3). On INT–plots, the orders *Coleoptera* and *Arachnida* mainly dominated at the beginning of the season with proportions of 41% and 47% respectively. After the 13.6., less abundant orders and groups (*Hymenoptera, Diptera, Heteroptera, Gastropoda*, Larvae and Other) increased in proportions achieving between 1% till 4% of the overall frequency of caught arthropods. At the end of the season, *Coleoptera* was with 64% the most abundant order and *Arachnida* had decreased gradually to a proportion of 9%. The orders *Saltatoria* and *Lepidoptera* did not exceed 1 % in proportions throughout the season (Fig. 4a.)

On the EXT–plots, the proportions of the different orders caught did not change much throughout the season. *Coleoptera* (36%, almost constant) and *Arachnida* (17% - 35%) were also dominating in abundance. The next following less abundant orders and groups of arthropods were: *Diptera* (7% - 15%), *Gastropoda* (5% - 7%), *Hymenoptera* (2% - 5%), Others (2% - 5%), Larvae (2% - 4%), and *Heteroptera* (1% - 3%). *Saltatoria* and *Lepidoptera* were most abundant at the end of the season with 3 % and 1% - 2%, respectively (Fig. 4b.).

The group "Others" consisted mainly of *Lumbricidae, Diplopoda, Glomeridae* and *Isopoda* which were pooled due to their small abundances. The group "Larvae" included *Symphyta*–larvae, *Lepidoptera*–larvae, *Diptera*-larvae and some *Coleoptera*–larvae.
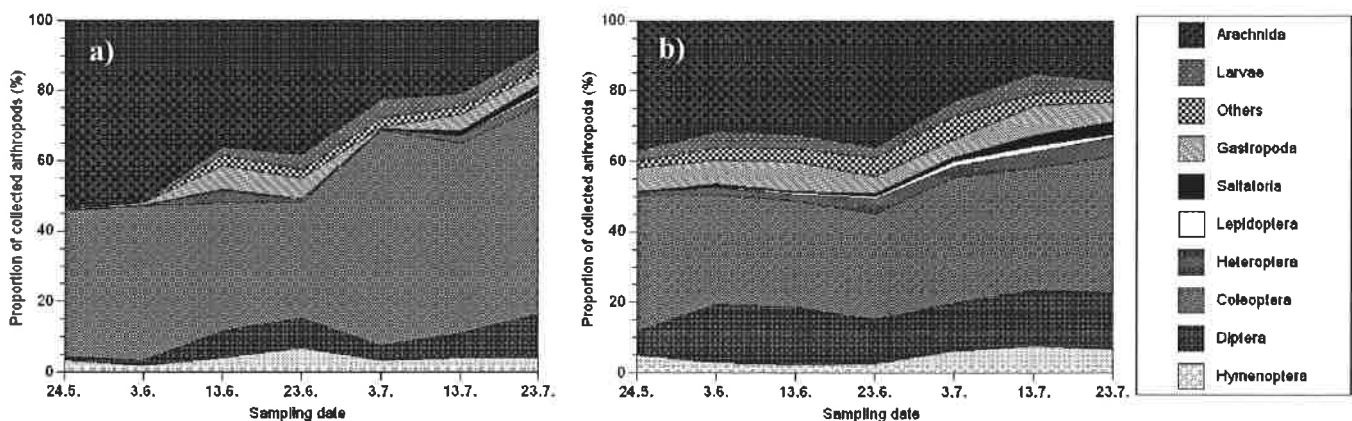
Fig. 4. Changes in the proportion of 10 classes of arthropods over the season, for explanations see text. **(a)** For arthropods collected on the 3 intensively managed plots, n = 6677; **(b)** For arthropods collected on the 3 extensively managed plots, n = 8625.

To check for differences in the overall arthropod diversity between the plots of different agricultural practices, a multiway ANOVA was performed on the Shannon–indices of diversity (Table 4). The calculation of these indices was based on the frequencies of 53 different size–classes and taxa to which the collected arthropods had been assigned (see Methods). The factors "Agricultural practice" and "Season" turned out to have significant

effects on the Shannon–indices (P < 0.0001). Thus, the diversity of arthropods throughout the season was significantly higher on extensively managed study plots (Table 4 and Fig. 5). The interaction of the two factors mentioned above showed a tendency (P = 0.0567), but no significance.

Table 4. Effects of the two factors "Agriculture" and "Sampling period" on the diversity of arthropods caught with both trap types throughout the season. A multiway analysis of variance (ANOVA) was performed. The final model is shown, not significant factors and interactions dropped out in the backward elimination procedure were: "Sampling plot", "Mean temperature", "Mean rainfall" df = Degrees of freedom, F = F Statistics, P = rejection probability. Significant values in bold letters.

Source of variation	Sum of squares	df	Variance	F Ratio	P
Shannon - Index of diversity					
Agricultural practice	2.1880	1	2.188	179.721	**< 0.0001**
Season	1.1537	6	0.192	15.704	**< 0.0001**
Agricultural practice x Season	0.1727	6	0.029	2.364	0.0567
Error	0.3409	28	0.012		
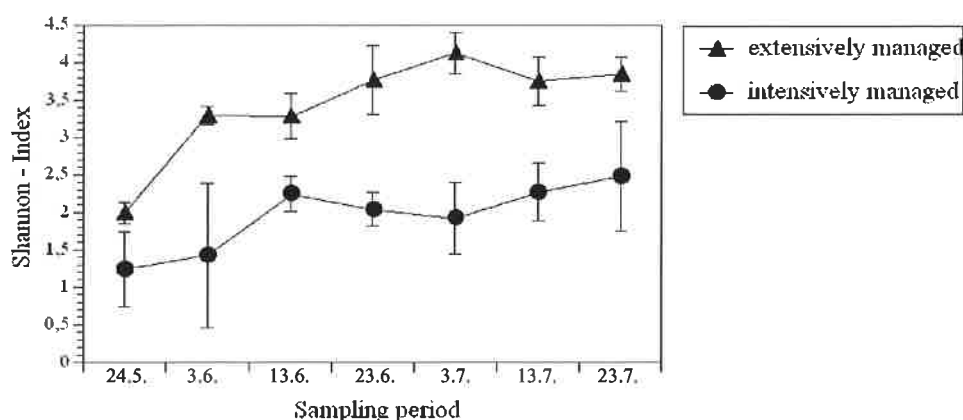
Fig. 5. Seasonal changes of the Shannon – index of diversity (means ± SD) on the six sampled plots (3 INT vs. 3 EXT).

The seasonal changes of the arthropod fauna in abundance and composition were strongly influenced by mowing events. How the parameters "overall frequency of arthropods" and "Shannon–index of diversity" reacted to the first mowing in the season demonstrates Fig. 6. On the intensively managed plots (Fig. 6a, b, c), 50 % of the agricultural area was mown around the 13.6. and the 14.6. (indicated by arrows, see Table 1). The frequency of arthropods collected with both traptypes showed a consistent reaction in all three plots with a drop in abundance. This decrease was very pronounced on the plots Scuol (Fig. 6a) and Sent (Fig. 6b), where traptypes caught about a quarter of the arthropod frequency on the 13.6. compared to the sampling period 10 days earlier. The Shannon–indices of diversity slightly increased during the season on all three plots, but they never reached values higher than 3.

Concerning the extensively managed sites, 50 % of the first plot, Vnà, has been mown on the 7.7. (Fig. 6e). The drops in the overall frequency of arthropods were not as pronounced and happened later in the season compared to the INT–plots. They did not seem to coincide strongly with mowing events, either. The Shannon–indices showed an increase at the beginning of the season and reached values between 3.6 and 4 on the last sampling period around the 23.7.
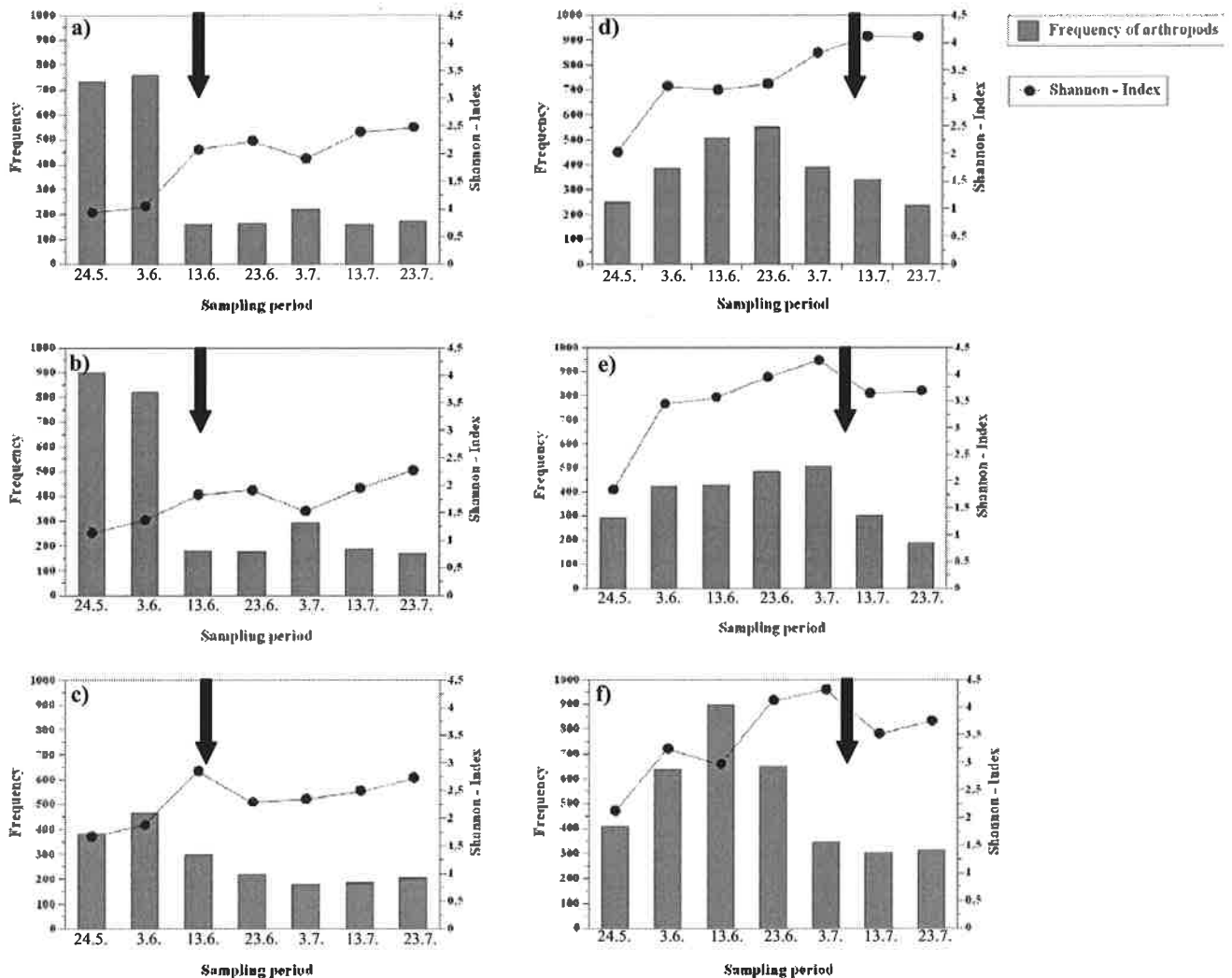
Fig. 6. Seasonal trends of the overall frequency of arthropods caught with both traptypes and of the Shannon–index of diversity. Arrows indicate when 50 % of sampled plots are mown. **(a) – (c)** INT–plots Scuol, Sent, Ramosch; **(d) – (f)** EXT–plots Chantata, Vnà, Tschlin.

3.2 Nestling diet

Muscidae and *Calliphoridae* were in terms of frequency the most important insects for broods on intensively managed plots, they accounted for almost a fifth of the prey (Table 5.). In EXT-broods, they were fed less often making up around 7.5 % of the diet. Regarding

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Coleoptera, dung beetles (*Scarabaeidae*) were most abundant with a proportion of nearly 15% in INT-broods while in EXT-broods, they were fed less than half as often (6 %). *Hymenoptera*-Larvae were a favoured prey in all 18 broods. They accounted for more than 16 % in EXT-broods, thus being the main prey type, and for about 11 % in INT-broods. *Lepidoptera* made up about 5.5 % of all arthropods in the diet in EXT-broods, while in INT-broods their proportion was much lower with about 0.5 %.

Table 5. Main invertebrate groups in Whinchat nestling diet with proportions per brood (means ± SD) and the mean biomass per prey item. The 7 most abundant groups are in bold letters.

Invertebrate group	Proportion per INT-brood (n=9) in %		Proportion per EXT-brood (n=9) in %		Mean biomass per item (mg)
Aranaeidae	1.830	± 1.448	2.099	± 0.468	10.6 (n=98)
Thomisidae	0.235	± 0.705	1.323	± 0.747	9.8 (n=45)
Coleoptera (Cantharidae)	1.041	± 1.084	3.948	± 3.305	13.3 (n=36)
Coleoptera (Elateridae)	1.954	± 2.356	4.362	± 1.810	16.4 (n=31)
Coleoptera (Scarabaeidae)	**14.849**	± 11.006	**6.084**	± 3.274	**13.4** (n=109)
Coleoptera-Larvae	0.771	± 1.576	0.182	± 0.249	14.1 (n=22)
Coleoptera (other)	1.296	± 1.912	3.240	± 1.472	14.6 (n=39)
Diptera (Muscidae, Calliphoridae)	**18.466**	± 8.167	**7.316**	± 1.164	**13.2** (n=337)
Diptera (Rhagionidae, Empididae)	**9.228**	± 4.626	**4.758**	± 1.506	**11.4** (n=35)
Diptera (Syrphidae)	0.786	± 0.881	3.883	± 1.008	9.7 (n=27)
Diptera (Syrphidae-Larvae)	0.243	± 0.729	1.496	± 0.825	21.1 (n=11)
Diptera (Tipulidae)	**5.688**	± 5.190	**4.710**	± 2.162	**9.1** (n=36)
Diptera (other)	0.398	± 0.497	2.300	± 1.129	9.9 (n=103)
Gastropoda (shell)	0.920	± 0.824	0.794	± 0.672	19.3 (n=24)
Gastropoda	0.222	± 0.386	0.496	± 0.485	12.4 (n=18)
Hymenoptera-Larvae	**10.894**	± 5.666	**16.640**	± 3.844	**25.3** (n=22)
Hymenoptera (Formicidae)	0.326	± 0.256	1.655	± 1.164	4.7 (n=113)
Hymenoptera (Ichneumonidae)	0.000	± 0.000	0.922	± 0.636	6.9 (n=62)
Hymenoptera (Apoidea)	0.163	± 0.152	0.310	± 0.198	20.1(n=34)
Hymenoptera (Vespidae)	0.102	± 0.090	0.130	± 0.926	18.2 (n=21)
Lepidoptera	**0.626**	± 0.259	**5.483**	± 2.316	**17.5** (n=52)
Lepidoptera-Larvae	1.879	± 0.609	5.181	± 1.524	32.3 (n=27)
Saltatoria	**10.804**	± 13.023	**7.455**	± 4.732	**26.7** (n=69)
Lumbricidae, Diplopoda	0.703	± 0.622	0.561	± 0.366	27.3 (n=98)
Others	0.195	± 0.267	0.057	± 0.112	17.1 (n=108)
Undefined	15.342	± 5.777	15.063	± 4.564	10.8 (estimated)

Nestlings of pairs breeding on extensively managed plots (EXT–pairs) were fed on average a significantly higher arthropod biomass (mean: 129.8 mg / young*hour) in comparison with Nestlings of INT–pairs (mean: 101.7 mg / young*hour) (Fig. 7.). In the multiway analysis of variance performed, the factor "agricultural practice" had a significant effect on the biomass fed per nestling and hour ($P = 0.0054$) (Table 6), the not significant factors "Age of young", "No. of young", "Time period", "Mean temperature", "Mean rainfall" and all possible interactions were dropped during the backward elimination procedure.

Table 6. Effects of different factors on the Biomass the adults fed their young per hour. A multiway analysis of variance (ANOVA) was performed. The final model is shown, not significant factors and interactions dropped out in the backward elimination procedure were: "Age of young", "No. of young", "Time period", "Mean temperature", "Mean rainfall". df = Degrees of freedom, F = F Statistics, P = rejection probability. Significant values in bold letters.

Source of variation	Sum of squares	Df	Variance	F Ratio	P
Biomass fed / young*hour					
Agricultural practice	1584.853	1	1122.918	10.368	**0.0054**
Error	2447.429	16	138.295		
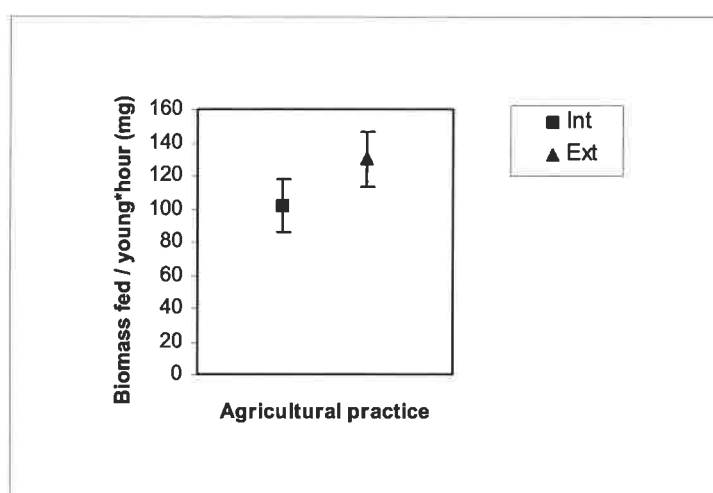
Fig. 7. Among brood-means ± SD of the biomass' the adults fed their young. For both agricultural practices, n = 9,9 pairs were observed.

The arthropods fed to EXT–young were more diverse than the ones fed to INT–young. This is demonstrated by the higher mean of the Shannon–index which was 2.8 for EXT–nestling food vs. 2.27 for INT–nestling food (Fig. 8a). This difference was significant (Mann–Whitney U test, n = 18, Z = -3.53, P = 0.0004). Calculations of the Shannon–indices were based on the frequencies of the 26 groups arthropods were assigned to during the video–analyses (see Table 5).

Over 85 % of the arthropods fed ranged in size from 9 – 16 mm, thus reflecting the main prey spectrum. The smallest prey items occasionally 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 (mean: 8.1 %) than they were in EXT–broods (mean: 3.6 %; Mann–Whitney U test, n = 18, P = 0.0005; Fig. 8b).
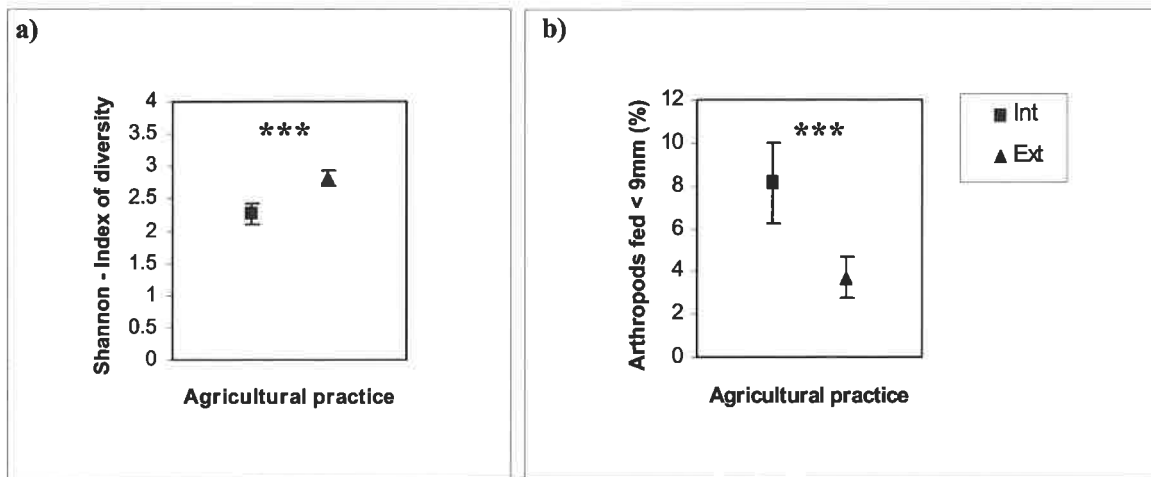
Fig. 8. Two measures (among brood-means ± SD) of nestlings food in the 18 broods observed (9 INT vs. 9 EXT). **(a)** The Shannon – index of diversity of the arthropods fed (Mann-Whitney U test, n = 18, Z = - 3.53, P = 0.0004); **(b)** The Proportions of arthropods fed smaller than 9 mm (Mann-Whitney U test, n = 18, Z = 3.45, P = 0.0006).

3.3 Feeding behaviour

The three parameters reflecting the adults' feeding behaviour analysed were the feeding frequency per young and hour, the number of arthropods the adults brought to the nest per feeding event and the mean foraging distances of adults.

The feeding frequencies did not differ significantly between INT– and EXT–adults (mean of INT: 7.4, mean of EXT 7.9, Mann-Whitney U test, Z = -1.15, P = 0.251, Fig. 8a). In EXT – broods, the average number of arthropods brought to the nest per feeding was 1.701. This number was significantly higher than the one measured in INT–broods (mean: 1.2, Mann-Whitney U test, Z = -3.54, P = 0.0004, Fig. 8b).

Adults on INT–plots had longer foraging distances (mean: 54.7 m) than adults breeding and hunting on EXT – plots (mean: 42.2 m; Table 5 and Fig. 9). In the ANOVA performed on the mean foraging distances, the factor "agricultural practice" explained a significant proportion of the overall variance (P = 0.0131). Not significant factors and interactions eliminated were: "Age of young", "No. of young", "Time period", "Mean temperature" and "Mean rainfall".
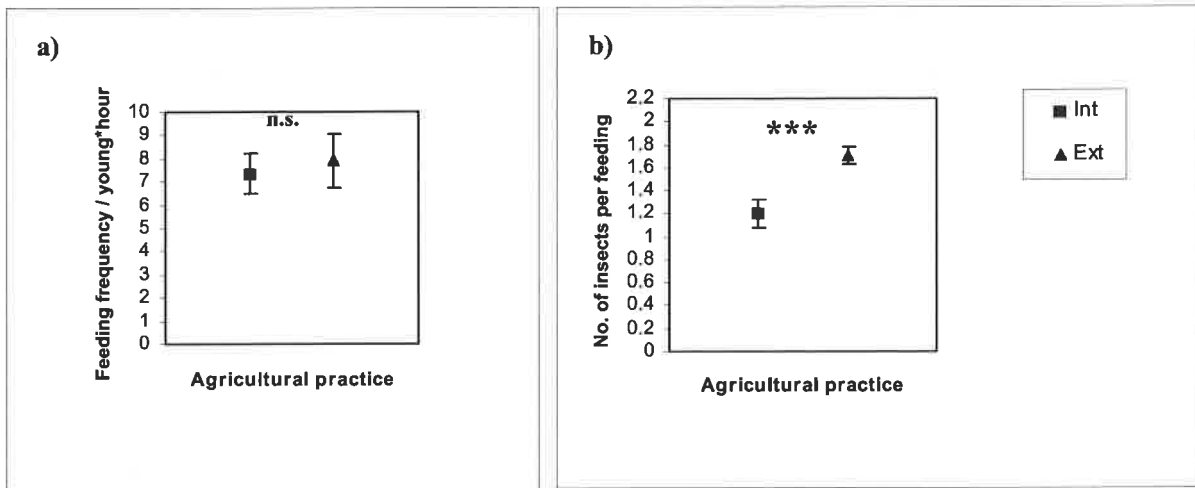
Fig. 8. Two measures (among brood-means ± SD) of the adults feeding behaviour. **(a)** The feeding frequencies per young and hour (Mann–Whitney U test, n = 18, Z = -1.15, P = 0.251); **(b)** The number of arthropods per feeding event (Mann–Whitney U test, n = 18, Z = -3.54, P = 0.0004).

Table 5. Effects of the factor "agriculture" (INT vs. EXT) on the mean foraging distances of the pairs followed. A multiway analysis of variance (ANOVA) was performed, the full model originally also included the not significant factors "Mean Temperature", "Mean rainfall", "Age of young", "No. of young" and "Time period". df = Degrees of freedom, F = F Statistics, P = rejection probability. Significant values in bold

Source of variation	Sum of squares	df	Variance	F Ratio	P
Mean foraging distance					
Agricultural practice	326.609	1	326.609	7.7803	**0.0131**
Error	671.660	16	41.979		
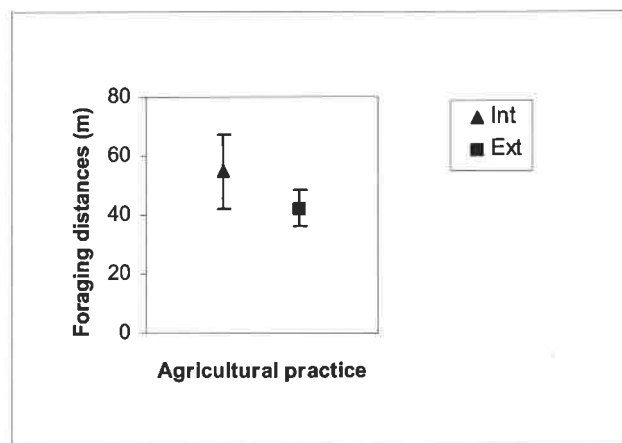
Fig. 9. The foraging distances (among brood-means ± SD) of the 18 pairs breeding either on INT– or on EXT–plots (9 vs. 9).

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3.4 Prey selection

On five main insect orders, an analysis of prey selection was performed to investigate how the adults would exploit the abundances of the different taxa within their home ranges. Scatter plots of the incorporation of *Coleoptera, Diptera, Hymenoptera, Lepidoptera* and *Symphyta*–larvae in the diet in relation to their abundances assessed with both trap types are shown in Fig. 10a – e. The presence of points below or above the line of no selection indicates whether a prey category was consistently under– or over–represented in the diet. *Coleoptera* were found to be clearly over–represented in the diet of nestlings (P = 0.005), as well as *Symphyta*–larvae (P = 0.001). Also *Lepidoptera* were slightly over–represented (P = 0.045). The taxa *Diptera* and *Hymenoptera* were both found to be significantly under–represented in the whinchats nestlings food (P < 0.001).
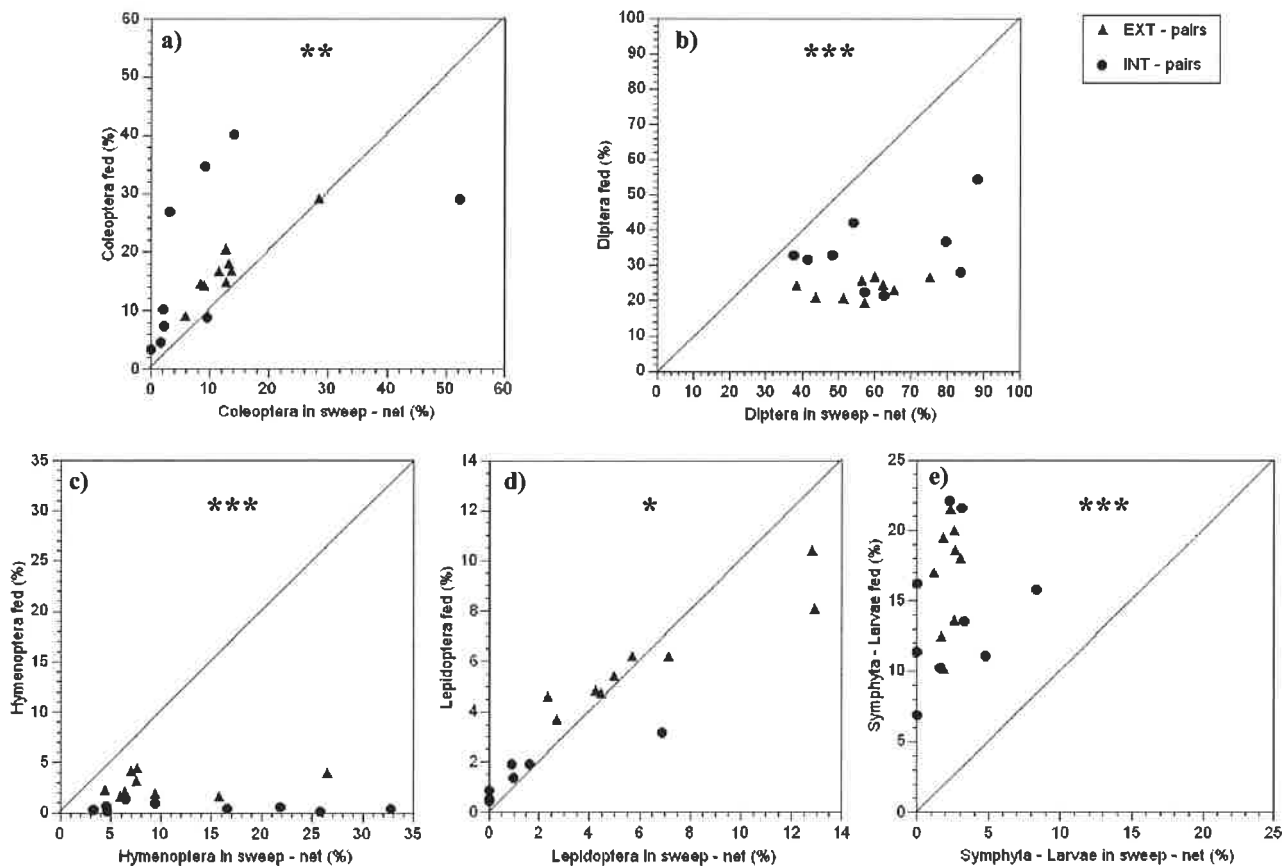
Fig. 10. Proportion of arthropod biomass fed to the young of 18 pairs (9 INT, 9 EXT) in relation to arthropod availability in sweep–net samples. Line of no selection is drawn. **(a)** Percentage of *Coleoptera* fed in relation to *Coleoptera* abundance, over–represented (Sign–Test: n = 18, P = 0.005); **(b)** Percentage of *Diptera* fed in relation to *Diptera* abundance, under-represented (Sign–Test: n = 18, P < 0.001); **(c)** Percentage of Hymenoptera fed in relation to *Hymenoptera* abundance, under–represented (Sign Test: n = 18, P < 0.001); **(d)** Percentage of *Lepidoptera* fed in relation to *Lepidoptera* abundance, over–represented (Sign–Test, n = 18, P = 0.045); **(e)** Percentage of *Symphyta*–Larvae fed in relation to *Symphyta*–Larvae abundance, over–represented (Sign–Test, n = 18, P < 0.001).

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3.5 Breeding success

Three parameters determining breeding success of the 18 pairs followed were analysed for significant differences (Fig. 11). In terms of clutch size, INT- and EXT- broods turned out to be similar: the mean clutch size for INT–broods was 5.6, the one of EXT–broods 5.3 (Mann-Whitney U test, n = 18, Z = -1.01, P = 0.3149). The differences in hatching rate were also negligible (mean for INT: 0.98, mean for EXT: 0.92, Mann-Whitney U test, n = 18, Z = -1.57, P = 0.1162). The only parameter, which turned out to show a significant difference between the groups compared, was fledging rate (mean for INT: 0.87, mean for EXT: 0.98, Mann-Whitney U test, n = 17, Z = -2.14, P = 0.0279). The number of broods compared in the test for fledging rate was only 17, because one INT-brood was robbed entirely and therefore excluded from the analysis (see chapter 2.5 Breeding success).
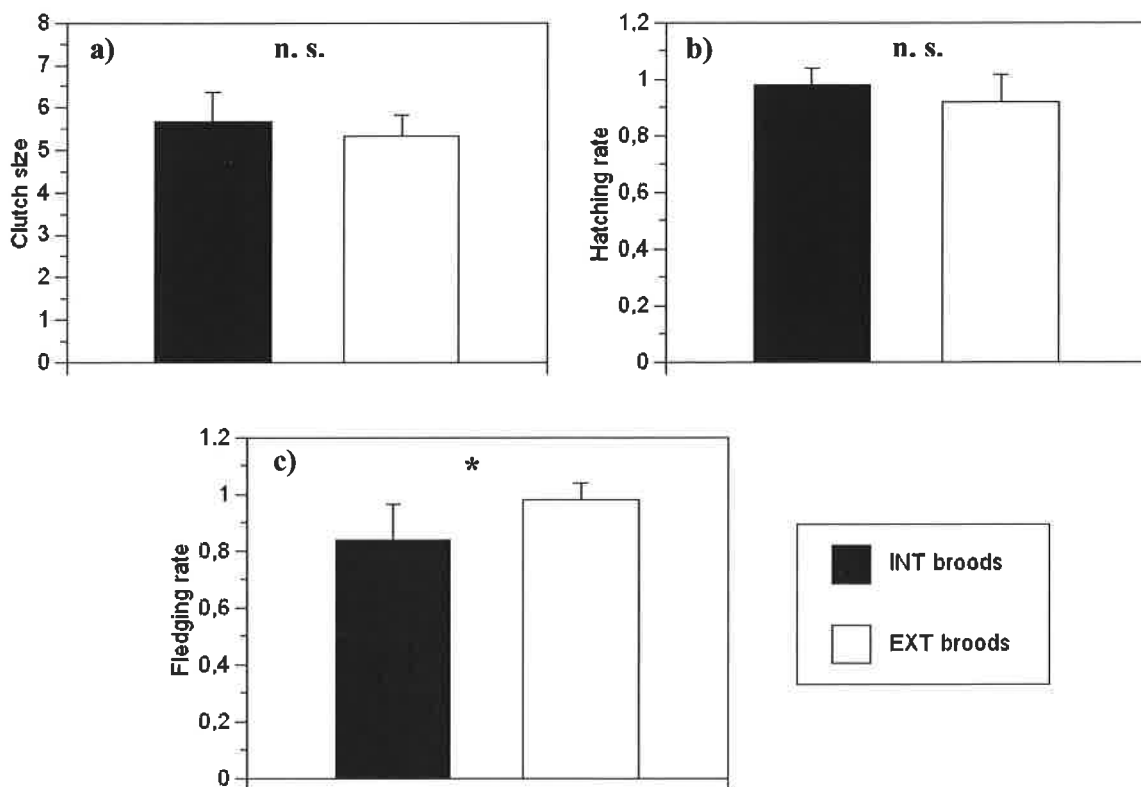
Fig. 11. Three parameters (means ± SD) determining the breeding success of the 18 broods observed. **(a)** Clutch size (Mann-Whitney U test, n = 18, Z = -1.01, P = 0.3149); **(b)** Hatching rate (Mann-Whitney U test, n = 18, Z = -1.57, P = 0.1162); **(c)** Fledging rate (Mann-Whitney U test, n = 17, Z = -2.14, P = 0.0279).

4. Discussion

4.1 Availability of arthropod food

A first goal of this study was to qualitatively and quantitatively compare arthropod abundance and diversity on agricultural plots reflecting two different kinds of management practice. For an assessment of the total number of arthropod species present, all microhabitats within the grassland have to be adequately sampled, hence such an estimation of arthropod food is strongly influenced by the methods applied. We decided to use the readily available techniques of pitfall trap sampling and sweep-netting, as they have been confirmed suitable for accurately sampling both the epigeal and the epiphytic fraction of the grassland arthropod fauna (Standen 2000). Sweep-netting e.g. has been widely used in dietary studies of grassland birds (Robel et al. 1995). Still, there are some studies proposing sampling bias' being associated with the two methods. The collecting efficiency of pitfall traps relies on the animals' behaviour. Pitfall trapping is said to over-represent larger arthropod species (e.g. *Carabidae*) (Spence & Niemela 1994; Ulber & Wolf-Schwerin 1995), to catch the same species differentially on different sites (Briggs 1960) and to catch different species differentially on the same site (Halsall & Wratten 1988). As regards sweep-netting, its efficiency also seems to vary between habitats (Southwood 1978). Especially arthropods occurring in clumped distributions, as it is the case for *Symphyta*- and *Lepidoptera*-larvae, are probably only poorly represented in sweep-net samples (Bastian et al. 1994). But besides this bias against larvae, we believe due to the great similarity of all the habitats sampled, that abundances and species richness' of the other arthropod taxa present were accurately estimated. By all means, since our sampling design assures all habitats being sampled at the same time with an equal number of traps and sweep-net strokes, respectively, a potential systematic error in assessing arthropod availability would not falsify comparisons made between the different study plots.

We found a strong seasonal variation in the overall arthropod abundance, which was more pronounced in the extensively managed plots. Biomasses sampled with pitfall traps and sweep-net showed a clear peak from the middle till the end of June (Fig. 2.). This pattern did not emerge in the intensively managed plots, where arthropod biomasses at the very beginning of the season were not significantly different from the ones collected on extensively managed plots, but then dropped to a level 7-8 fold lower compared to arthropod biomasses on EXT-plots. These declines in abundance occurred around the period of the 3.6. – 23.6.,

thus they seem to correlate well with time of the first cuts taking place on these plots. Looking at the reactions of the overall frequency of arthropods to mowing events for each study plot separately, this simultaneous occurrence of drops in abundance and timing of first cuts becomes even more obvious (Fig. 6a-c). We suppose therefore that a reason for these declines being so pronounced on all three INT-plots could be the early and fast mowing. Within the 2-3 days around the 10.–13.6., all areas had been completely mown in 2003 and grassland arthropods normally having their peaks in abundances around the middle of June were presumably eliminated or migrated to adjacent not mown sites (Curry 1994). On the EXT-plots, where mowing happened at least 20 days later and over a period of several weeks, arthropod abundances also decreased gradually after the 23.6. But these declines are within the limits that can be expected for "normal", natural situations where arthropods slowly reduce in numbers after having reached a peak in the middle of the season.

Besides holding a significantly smaller arthropod community in terms of biomass, the intensively managed plots were also characterised by higher percentages of insects with body sizes less than 6 mm and lower arthropod diversity-indices throughout the season. The Shannon-indices showed a slight increase in both groups of differently managed study plots at the beginning of the season and reached plateaus around the fifth and sixth sampling period at the beginning / middle of July (Fig. 5.). Hence the overall pattern was similar, but diversity on extensively managed plots was throughout the season at least twice as high. Spiders (*Arachnida*) and beetles (*Coleoptera*) were in terms of frequency the most abundant orders on INT-plots by far; other groups and orders were only present in very small numbers (Fig. 4a.). The same two orders also dominated the arthropod community on EXT-plots, but the distribution of all groups and orders was still more evenly over the whole season (Fig. 4b.). Taxa being collected very rarely on INT-plots were more abundant on EXT-plots, and these taxa making up only some percents of all arthropods sampled and analysed are of considerable importance for the whinchats nestling diet. We will discuss this issue more thoroughly later on.

Hence, we found our hypothesis proposing a deteriorating effect of an intensive grassland management on abundances and diversity of arthropods supported. Moreover, the contrasts in the parameters measured were more pronounced than we expected with the factor "agricultural practice" being highly significant in all analyses performed (P < 0.0001). The intensively managed pre-alpine areas investigated for this study can best be described as "moderate intensively managed", since silage meadows and the use of inorganic fertilizers are by far not as widespread as they are in lowland agricultural areas of Europe. Regarding the time span these techniques have been applied, the earliest switches from hay to silage

occurred only about 15 years ago. Thus the arthropod communities inhabiting these meadows seem to be very susceptible to changes in management practices and moreover, they seem to react within a few years to them. Litzbarski (1995) and Block et al. (1993) found in their studies, which investigated effects of extensification on arthropod biomasses, responses of similar speed: Within 8 years, biomasses increased twice to threefold in the formerly intensively managed study plots.

Comparing the amount of difference in arthropod abundance we found in our sampling plots with the ones detected in other studies, we come to the conclusion that differences in this study are of considerable extent. As mentioned above, while having their peak in abundance around the middle till the end of June, arthropods sampled on EXT-plots reached biomass' 7-8 times heavier (in both trap types) and frequencies were 2.5 and 6.5 times higher (in pitfall traps and sweep-net, respectively). Litzbarski et al. (1988) found in their comparison of a semi-natural grassland plot with a for nine years intensively managed meadow "only" up to 3.5-fold differences in biomass. More pronounced, but still not as marked as in this study, were the contrasts Bastian et al. (1994) found in their arthropod assessment on extensively and highly intensively managed plots in Germany. Sweep netting on the traditionally managed areas collected the 5-fold of invertebrate biomass sampled on the modern intensively managed sites. Oppermann (1999) compared 24 German study sites and found with sweep-netting a 6-fold difference in arthropod frequency, Brickle et al. (2000) assessed invertebrate abundances around the nests of corn buntings (*Miliaria calandra*) in west Sussex and collected at least 8 times as many individuals in unintensified grassland as on intensively managed plots. Thus, the latter two studies yielded differences of a comparable degree as found in this study (6.5x), but one has to know that study sites chosen have been intensively managed in both cases for over 20 years, are cut three times a year and are being intensely fertilized.

We found evidence to suggest that management intensity influences not only abundance, but also the size and diversity of invertebrates. These findings are in accordance with results from Bastian et al. (1994), who collected significantly more smaller and lighter species on intensively managed and hence by the whinchat unsettled plots compared to settled ones. That mowing may be indeed particularly detrimental to larger insect species showed Beintema et al. (1990) and Blake et al. (1994, 1996) in their studies as well. Although beetle numbers slightly increased with increasing intensity of grassland management, size declined. As regards arthropod diversity, there have been several studies proposing that intense grassland management is turning insect communities more uniform (e.g. Bastian et al. 1994; Di Gulio et al. 2001; Wettstein & Schnidt 1999; for an overview see Curry 1994; Vickery et al. 2001).

Hence our results are in consistence with trends observed on agricultural areas all over Europe. Unfortunately, the quantitative differences of the Shannon-indices of diversity we found cannot be compared with the ones estimated by other researchers. This is because, depending on the study, calculations of the diversity-indices are based on highly varying taxonomic levels (insect orders, families, species, size groups).

Oppermann (1999) emphasizes in his study on the habitat choice of the whinchat the synchronization between the development of the arthropod fauna and the beginning of breeding. Such a synchronization will ensure the adult birds to find enough insect food supply when their young have hatched. Also in our study, whinchats breeding on EXT-plots were in the comfortable situation to forage on the peak of insect abundance while feeding their nestlings (see Fig. 2., overlay). Since there was due to the intense mowing no such peak in the INT-plots sampled, pairs breeding in these areas most probably faced much harsher conditions during nestling period.

4.2 Nestling diet and feeding behaviour

The composition of prey items fed to nestlings is influenced by many external factors, as mentioned earlier. To account for the considerable between- and within-brood variation that can be expected, assessment of a large dataset is essential. Furthermore, given the conservation status of our study species, a method with minimal disturbance effects should be chosen for the determination of nestling diet. Analysis of faecal samples would have been one possibility, as they can be collected with very little distress to young chicks (Jenni et al. 1990). This method has been applied in numerous studies of birds, but there are many disadvantages to using feces in dietary analysis. Abundance levels, in particular, may be biased in favour of invertebrates with hard body parts such as beetles and grasshoppers and biased against soft-bodied prey such as aphids, flies or caterpillars (Cummins & O'Halloran 2002; Moreby & Stoate 2000). Differential digestibility of prey items is therefore an important factor to consider with faecal analysis (Jenni et al. 1990; Poulsen et al. 1998). In addition, identification of fragments from faecal samples can be very time-consuming. Alternatively, neck-collars (ligature method) are also often applied in dietary bird studies. Though this method delivers readily identifiable arthropods, which can be used for further analysis (e.g. biomass determination), it is certainly more harmful to the nestling (Jenni et al. 1990; Poulsen & Aebischer 1995). Besides that, it is often limited to only a short time window and hence results in only few items available for identification. Furthermore, biases seem to be associated with the use of neck-collars, as well. Johnson et al. (1980) found in

their study that food samples collected with the "ligature method" did not accurately represent the diet due to behavioural changes of nestlings.

As neither of the two methods met all our demands, we decided to use a combination of the techniques Schaad (2002) and Labhardt (1988) applied in their studies. Filming the adults and prey items provisioned to chicks during 12 hours per pair not only delivered large amounts of data, it also kept the level of disturbance as low as possible and enabled us to calculate feeding frequencies at the same time. Biases against small arthropods and multiple prey loads, which are said to be associated with methods of direct observation (Johnson et al. 1980; Moreby & Stoate 2001), were not obvious in our study (see Methods).

Nestlings of pairs breeding on EXT-plots were fed on average about 20 % more arthropod biomass than nestlings on INT-plots. Such differences between broods of diverse habitats can of course arise for many reasons, weather conditions and age and constitution of young being the most probable ones. Like that, Labhardt (1988) found in his study, where he compared feeding ecology of two whinchat populations at different altitudes, a difference in the biomass fed per young and hour of more than 25 %. He could explain this variation with the mean temperatures being 5 degrees lower in the pre-alpine population, which led to a higher energy demand of the nestlings investigated, hence they were fed significantly more biomass. As 8 of our EXT-nests were situated on the slope of the valley, on average about 300 m higher than the INT-nests followed, one could argue that the differences in fed biomass we found have to be attributed to lower temperatures, as well. But since the mean temperatures during the two months of observed nestling period did not differ more than 1.3 degrees between the two altitudes, we do not think that EXT-nestlings suffered a significantly higher energy demand. Furthermore, we tried in our study to keep other external factors constant by filming feeding adults when their young had the same age and weather conditions were as comparable as possible. We also paid attention to an even distribution of filmed breeding pairs over the season, as to take seasonal variation in insect abundance into account. Like this, we detected in our model "agricultural practice" being the only factor significantly explaining this considerable difference in the biomass fed.

Also diversity of the nestlings food and sizes of prey items in INT-pairs seem to reflect the sub optimal feeding conditions we found in assessing food availability on the intensively managed plots. Yet, some authors might consider a diet that is higher in diversity, like the one we found in nestlings of EXT-pairs, as a sign that adults have difficulty in obtaining sufficient food for their young (Blondel et al. 1991). Concerning the present study, we do not share this opinion for several reasons. Bastian et al. (1994) showed that in areas occupied by breeding Whinchats species richness was greater, and this higher arthropod diversity was even the best

factor separating occupied from unoccupied areas. Moreover, Borg & Toft (2000) came with her nice self-selection experiment to the conclusion that partridge chicks benefit from eating a mixed insect diet. The same is true for bee-eater chicks (Krebs & Avery 1984). For an insectivorous bird species like the Whinchat, which is not specialized to only one or a few prey taxa and employs different foraging techniques, a broad variety of arthropods in its habitat will always positively influence its feeding capacity.

The fact that nestlings of INT-pairs were fed significantly more small prey items and single-prey-loads has to be interpreted against the background of optimal foraging theory (Andersson 1981; Stephens & Krebs 1986). Naef-Daenzer et al. (2000) showed in their study that Great tits preferred larger prey to smaller and much more frequent arthropods, many authors have described this selection for large size of prey in nestling diet as well (Bastian & Bastian 1996; Davies 1977; Grieco 2001). Reasons for this preference are the reduced searching time and the higher energy gain per feeding trip (Naef-Daenzer & Keller 1999).

To conclude so far, parents on intensively managed plots are delivering their nestlings smaller prey items and fewer per feeding event, this obviously results in less biomass being fed. Still, we would expect to find indications for a higher feeding or searching effort in pairs breeding on INT-plots if they were trying, though vainly, to compensate for their lower habitat quality. One possibility parents have to balance for smaller prey items is to increase their feeding rate (Siikamaki et al. 1998). This was not the case in our study, breeding pairs on both INT- and EXT- plots fed at similar frequencies of 7.4 and 7.9 feedings per young and hour, respectively. Comparing these figures to delivery rates found in other studies (Labhardt (1988): 4.5, 5.3; Müller (1985) 6.1; Bastian & Bastian (1996): 6-8), they appear to be relatively high; hence a further increase might have been difficult to obtain for the adults. So INT-breeding pairs did not feed at a faster rate, but they seemed to increase their searching effort: Foraging distances were significantly longer. This was maybe due to a higher proportion of multiple location foraging trips and more unsuccessful hunting trials (pers. observ.). It has been shown in other studies that a more intense management practice can negatively influence the foraging efficiency of farmland birds either through making important prey items less accessible in the tall and dense swards (Vickery et al. 2001) or through shifting the size structure of invertebrate populations towards smaller species (Blake & Foster 1998; Blake et al. 1994). Poulsen et al. (1998) showed for skylarks that abundance of nestling food was much greater in set-aside and distances traveled by parents during feeding trips in the same habitat were significantly shorter compared to silage grass plots. Interestingly, they did not find differences in feeding frequencies, either, and suggested in consistence with our hypothesis, that parents may have fed their young as often and as much

as possible. Such a strategy is likely to result in fitness costs for parents in INT-plots, since they have less time available caring for themselves (Martin 1987).

As shown for other bird species, food items are not only selected to maximize amount of food brought to nestlings but also its quality (Krebs & 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 (little chitin, thus up to 63 % of usable protein according to Bierman & Sealy 1982) and easy to handle and swallow (Banbura et al. 1999). That feeding Whinchats absolutely share this preference show results of Labhardt (1988): Proportions of lepidopteran and sawfly larvae accounted for 35 % - 70 % of arthropods fed. Also in the prey selection analysis we performed, sawfly larvae (*Symphyta, Hymenoptera*) turned out to be highly over-represented in the nestling diet. This result has to be interpreted with caution, though, due to the probable under-representation of larvae in the sweep-net samples. The mean proportion of this profitable prey item was with 16.5 % considerably higher in EXT-nestling food than in the diet of INT-nestlings, where it accounted for only about 11 %. The same was true for butterfly (*Lepidoptera*) imago and larvae, which were according to the prey selection analysis preferentially fed arthropods, as well. On the other hand, flies (*Diptera*), beetles (*Coleoptera*) and partly also grasshoppers (*Saltatoria*) were fed in much higher proportions to INT-nestlings compared to EXT-nestlings. We consider these arthropods due to their high amount of chitin (*Coleoptera, Saltatoria*) or their relatively small biomass and high activity (*Diptera*), respectively, being much less profitable prey items (see also Bastian & Bastian 1996). Hence, they are most probably used as a supplement in the diet of INT-nestlings to replace for missing larval and lepidopteran food, as it has been shown for *Diptera* in a study of Great Tits (Naef-Daenzer et al. 2000) and for spiders in the nestling diet of skylarks (Poulsen et al. 1998).

4.3 Breeding success

There are several mechanisms through which poor food availability can deteriorate breeding success or fitness of young and adults. We will now discuss these mechanisms, which are not mutually exclusive, concerning the presence or absence of evidence in this study:

(I) Poor food availability can be absorbed by the feeding parents, which will risk reductions in their own survival by more investing in their reproductive output (Richner & Tripet 1999). Like that, Morris et al. (2001) and Poulsen et al. (1998) found in their studies longer foraging distances being the reactions to low chick food abundance. We found similar results for the

Whinchats breeding in silage grass habitats. Since it was beyond the scope of this study, we did not try to detect any fitness costs such a behaviour would presumably impose on the parents.

(II) Females can react to poor food conditions by reducing their clutch sizes. This has been shown in natural situations and experimentally by several studies, for a review see Martin (1987). We could not find any differences in clutch sizes in our study, thus females do not seem to follow this strategy. There is a possible reason for this: Such a reaction would have requested the females to assess insufficient availability of insect food prior to laying (mean laying date: 26.5. acc. to Müller 2001), hence at a period of time when mowing has not been conducted and arthropod abundance was not significantly lower on intensively managed plots yet.

(III) Reductions in food resources can result in nestlings suffering reduced condition or lower growth rates, which has been shown for corn buntings by Brickle et al. (2000). Low chick weights in turn may contribute to increased predation risk, because hungry broods often beg more loudly or for longer than well-fed broods (state-dependent predation, Evans et al. 1997). Since we did not measure chick weights in our broods due to the potential danger of increasing predation risk by visiting the nests too often, we can give no conclusive answer to the first hypothesis. Regarding state-dependent predation, one out of nine INT-broods was robbed by corvids and no predation was found in EXT-broods. But firstly sample size is too small to draw any conclusion and secondly, we did not investigate begging rate in our study because the extra disturbance was considered too intrusive.

(IV) Low food supplies at the chick stage can increase mortality of young through starvation (Poulsen et al. 1998), or can result in a higher mortality at the postfledging stage (Martin 1987). We detected partial losses of nestlings at the age of 2 – 5 days in six out of nine INT-broods and in one EXT-brood only; this difference in fledging success was significant. We could not determine any obvious causes of death, but suspect starvation to be the main mortality factor, since it is the most probable reason for partial brood losses (O'Connor 1984).

4.4 Conclusions and implications for conservation

Current farming practices within grassland and arable fields are likely to affect the arthropod fauna and chick-food resources for farmland birds. Especially important chick-food items like sawfly and lepidopteran larvae are typically found 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 numbers and range of farmland passerines (e.g.

Benton et al. 2002; Campbell et al 1997; Fuller et al. 1995, Vickery et al. 2001). But do these correlative patterns between birds and arthropods represent an underlying causality?

That poor arthropod abundance and availability can to some extent made responsible for a reduced breeding success has been shown for at least five farmland passerines so far. The Grey Partridge (*Perdix perdix*) has declined in part because of the effect of pesticides on the availability of chick-food invertebrates (Potts & Aebischer 1995). Skylark (*Alauda arvensis*) broods have been shown to be more likely to starve in intensively managed fields (Poulsen et al. 1998; Wilson et al. 1997). A study on the Corn bunting (*Miliaria calandra*) suggests that agricultural intensification can reduce its breeding success through deteriorating food availability and could therefore have contributed to its decline (Brickle et al. 2000). Yellowhammers (*Emberiza citrinella*) providing food for nestlings forage in a patchy habitat: if insect patches become rarer, supply rates to young will decrease, leading to reduced productivity (Hinsley 2000; Morris et al. 2001). Finally, reductions in chick food seem also likely to hamper population recovery as suggested for cirl buntings (*Emberiza cirlus*) (Evans et al. 1997).

The results of this study confirm for the first time that also for the Whinchat, a link between management practices, arthropod abundance, feeding behaviour, nestling diet and reduced breeding success is likely to be present. Hence, these findings are in consistence with what several studies have shown for other farmland birds. Differences in biomass, diversity and sizes of available arthropods we sampled in intensively vs. extensively managed plots were all quite precisely mirrored in the nestling diet of investigated broods. Thus it seems as if birds facing highly limited food resources were no longer able to compensate for these constraints. This is somewhat surprising, since our study was conducted in an area, where traditionally cultivated landscapes are still widely available and which is considered being the last stronghold for many once widespread farmland birds (Schifferli et al. 1999).

Yet, to conclusively determine if poor food availability significantly contributed to the Whinchats population decline in Europe, further studies at a wider scale would be necessary. The comprehensive assay we used by gathering information about arthropod abundance, nestling diet and feeding behaviour gave important insights into which processes could possibly influence breeding success. But measurements taken on breeding success itself might not have been precisely enough and based on too small sample sizes to give final answers. Furthermore, estimates of over winter and postfledging survival would allow us to test whether fitness costs imposed on parents and young during the breeding season have a measurable negative effect.

Even if reductions in availability and abundance of insect food supplies may not be the primary cause for the Whinchats population decline in Europe, we would still conclude that they seem very likely to hamper a possible population stability or recovery, as suggested for cirl buntings (Evans et al. 1997) and corn buntings (Brickle et al. 2000). Therefore, when it comes to propose effective conservation measures, the importance of enhancing or maintaining insect abundance and diversity in the Whinchats breeding habitat has to be considered. Yet, what is known to be a major factor having lead to dramatic population declines in the central European lowlands and more recently in subalpine regions, as well, is nest destruction by mowing (Ackermann 1999; Müller et al. 2001; Schifferli et al. 1999; Schmid et al. 1998; Schuler 2003). Müller et al. (2001) showed in their study conducted in two subalpine agricultural areas, which were also parts of our study plots, that mowing advanced by 2-3 weeks in 13 years and that the Whinchat and possibly many other ground-nesting farmland birds are apparently unable to adapt to these recent and fast-occurring changes in agriculture. Similar results found Ackermann (1999), who reports a population decline of 50 % in the subalpine Doller Valley (France) between 1988 and 1998, mainly due to nest destruction by mowing. A new mowing regime tested in 2002, which aimed at drawing nesting females to small set-aside plots made attractive with artificial perches, was not successful in increasing breeding success (Schuler 2003). According to our findings, such a regime would not have enhanced arthropod abundance significantly, either, and thus a population recovery might have been difficult to achieve or only short-termed.

We would therefore propose that any future conservation measures should aim at maintaining viable bird populations and at maximizing key insect populations at the same time. Perhaps the most obvious way to achieve this is to increase the area of farmland managed at low intensity, whereas the breeding phenology of the Whinchat has to be considered (Müller et al. 2001). In Switzerland, set-asides for ecological compensation are accounting for 7 % of agricultural land on a nationwide scale. While this percentage might be effective in enhancing biodiversity in the intensively managed lowlands, it is not sufficient to maintain the much higher biodiversity in the subalpine regions. Conservation measures increasing set-aside areas on a regional scale would not only favor the Whinchat and help to conserve or restore insect abundance and diversity, but they would also be of important value to many other farmland birds suffering from similar or even greater declines.

Acknowledgements

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Appendix 1. Dataset of arthropods (absolute frequency and biomass in mg) caught with both trap - types for the seasonal sampling, split into the main arthropod orders / groups and the six sampling plots, dates of sampling respectively.

Agricultural practice	Area	Date of sampling	Hymenoptera Freq	Biomass	Diptera Freq	Biomass	Coleoptera Freq	Biomass	Heteroptera Freq	Biomass	Lepidoptera Freq	Biomass	Saltatoria Freq	Biomass	Gastropoda Freq	Biomass	Larvae Freq	Biomass	Arachnida Freq	Biomass	Others Freq	Biomass	Arthropods<6mm Freq	Biomass	Total Freq	Biomass
Extensively	Chantata	24.5.	9	52	28	63	140	2'982	1	6	0	0	0	0	1	146	8	36	61	442	5	374	161	157	410	4262
Extensively	Chantata	3.6.	8	184	96	211	104	2'257	13	165	1	3	4	41	1	81	16	141	134	1468	15	1'189	237	180	622	5921
Extensively	Chantata	13.6.	9	50	118	297	100	2'162	18	195	5	22	4	52	1	90	45	125	237	5620	15	1591	250	175	759	10379
Extensively	Chantata	23.6.	13	154	56	147	173	4'289	43	345	2	8	4	479	1	4	9	205	231	5'514	20	2908	240	133	790	14'202
Extensively	Chantata	3.7.	15	208	43	247	167	4'141	12	125	9	104	3	67	4	131	10	153	99	1364	16	1374	228	159	617	8180
Extensively	Chantata	13.7.	23	214	46	237	123	3'725	18	127	10	74	8	346	10	2173	18	260	82	842	10	597	224	173	565	8790
Extensively	Chantata	23.7.	17	167	36	269	78	3071	11	70	5	39	10	607	9	132	5	70	59	575	4	62	202	129	437	5239
Extensively	Tschlin	24.5.	11	681	21	78	179	4'143	0	0	0	0	2	9	49	2'748	8	106	132	940	8	363	129	397	532	9465
Extensively	Tschlin	3.6.	5	19	57	150	265	6357	12	210	0	0	1	7	85	6072	32	56	161	1720	19	1'049	324	421	935	16'080
Extensively	Tschlin	13.6.	11	582	81	162	373	7'854	7	82	1	6	0	0	114	9092	13	168	251	6051	45	2894	338	294	1'224	27'185
Extensively	Tschlin	23.6.	14	157	98	265	210	5'835	9	93	4	76	5	88	53	3'531	14	77	187	4550	47	3138	289	230	930	18'065
Extensively	Tschlin	3.7.	14	123	35	144	114	4'300	12	127	8	86	5	130	31	716	24	254	60	932	32	1'789	166	96	491	8742
Extensively	Tschlin	13.7.	10	67	33	198	115	4'797	11	71	2	8	4	126	55	2351	18	200	27	280	16	532	204	139	492	8841
Extensively	Tschlin	23.7.	14	144	56	401	121	3'434	18	115	1	6	5	188	26	1081	11	49	37	470	12	454	194	123	494	6534
Extensively	Vnà	24.5.	27	248	17	40	40	926	5	67	0	0	0	0	13	1053	11	46	173	1291	6	159	121	91	404	3921
Extensively	Vnà	3.6.	28	219	78	148	73	1'700	4	91	1	7	5	73	9	471	16	156	192	1468	18	1321	205	154	621	5813
Extensively	Vnà	13.6.	22	441	98	274	77	1'828	6	77	4	23	2	22	35	3'359	16	162	155	1771	13	846	388	217	813	9038
Extensively	Vnà	23.6.	16	191	54	173	113	2'724	15	71	7	123	7	193	26	1656	26	349	196	3'298	18	940	240	148	704	9880
Extensively	Vnà	3.7.	48	503	85	259	152	4072	13	184	3	17	5	273	25	2032	17	927	101	1520	33	2'363	135	58	635	12'313
Extensively	Vnà	13.7.	38	199	65	244	80	1'739	13	85	4	38	16	401	12	737	15	123	50	528	6	362	233	142	523	4609
Extensively	Vnà	23.7.	17	134	23	126	78	1'618	8	35	1	10	11	378	4	221	2	11	25	275	9	333	231	152	412	3316
Intensively	Scuol	24.5.	2	5	7	31	191	2'439	0	0	0	0	0	0	0	0	0	0	528	3213	2	32	159	152	889	5872
Intensively	Scuol	3.6.	7	27	14	97	242	3'459	0	0	0	0	0	0	1	25	1	34	495	3056	0	0	235	315	995	7013
Intensively	Scuol	13.6.	9	30	16	66	35	455	22	121	0	0	0	0	0	0	2	24	74	526	2	34	218	164	376	1420
Intensively	Scuol	23.6.	5	31	10	37	50	1'447	1	12	0	0	0	0	13	98	13	33	64	529	3	84	353	157	505	2479
Intensively	Scuol	3.7.	1	5	6	92	144	3'220	0	0	1	42	0	0	2	16	0	0	52	361	12	533	306	150	526	4405
Intensively	Scuol	13.7.	12	70	13	43	89	2'546	0	0	0	0	1	20	2	30	6	31	26	189	5	20	262	116	416	3123
Intensively	Scuol	23.7.	5	57	21	119	100	3'435	6	13	3	13	4	49	8	182	8	10	13	98	2	31	239	103	399	4109
Intensively	Pradellas	24.5.	61	194	13	27	130	2615	2	43	0	0	1	27	4	2'341	0	0	168	1046	5	74	282	626	665	6966
Intensively	Pradellas	3.6.	32	82	7	16	211	4'252	3	59	0	0	0	0	14	1440	3	5	190	1603	1	60	272	178	734	7742
Intensively	Pradellas	13.6.	12	22	21	45	128	2'548	0	0	0	0	2	36	36	1'032	9	47	79	810	13	98	371	213	661	5007
Intensively	Pradellas	23.6.	20	24	19	44	68	1'477	1	4	1	38	1	192	12	149	9	35	76	730	10	148	281	143	491	2821
Intensively	Pradellas	3.7.	14	62	12	48	76	1'603	0	0	0	0	1	11	2	42	33	539	36	461	4	90	222	117	368	2982
Intensively	Pradellas	13.7.	6	69	13	63	90	1'863	6	18	0	0	0	0	21	589	13	132	29	291	1	25	272	139	443	3'250
Intensively	Pradellas	23.7.	10	59	34	146	93	2'982	2	7	1	9	2	32	9	302	15	131	19	182	4	95	266	146	451	4223
Intensively	Sent	24.5.	4	12	2	7	511	9'300	0	0	0	0	0	0	0	0	3	2	379	2'240	3	46	142	146	1'041	11753
Intensively	Sent	3.6.	2	160	8	63	438	7'842	0	0	0	0	0	0	0	0	0	0	371	2'442	2	35	357	937	1'178	11479
Intensively	Sent	13.6.	4	47	12	32	65	1'394	0	0	0	0	0	0	6	35	2	6	85	676	5	161	175	117	354	2468
Intensively	Sent	23.6.	12	59	16	66	61	1809	0	0	0	0	0	0	5	25	2	31	76	547	0	0	264	128	441	2706
Intensively	Sent	3.7.	7	18	10	49	183	3'132	1	35	0	0	0	0	0	0	1	31	91	748	1	67	290	209	583	4289
Intensively	Sent	13.7.	3	51	9	33	97	2'999	5	11	0	0	1	15	0	0	4	4	63	552	5	152	168	115	354	3944
Intensively	Sent	23.7.	6	159	9	54	109	3'915	6	19	1	17	5	76	1	33	11	11	29	234	1	46	219	135	386	4699
Total			603	5'980	1'496	5'310	5'986	138'686	304	2'683	76	801	125	4037	700	44'216	458	4'780	5'593	61'453	448	26'469	10'098	8'270	25'666	303'523

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Appendix 2. The Tukey-Test-Table for differences within sampling periods between arthropod biomass caught on EXT- and INT- plots. Sampling periods are numbered from 1 (24.5.) till 7 (23.7.). N = 6 study plots, significant values in bold letters (P < 0.05). CL=confidence limit. **(a)** Pitfall traps **(b)** Sweep-net (next page)

Each cell lists four statistics in order: Mean[i]-Mean[j] / Std Err Dif / Lower CL Dif / Upper CL Dif. Rows = LS Mean[i], Columns = LS Mean[j].

(a)	Ext,1	Ext,2	Ext,3	Ext,4	Ext,5	Ext,6	Ext,7	Int,1	Int,2	Int,3	Int,4	Int,5	Int,6	Int,7
Ext,1	0 0 0 0	-18.833 12.071 -63.017 25.3522	**-46.403 12.071 -90.588 -2.2187**	-40.989 12.071 -85.174 3.19546	-22.619 12.071 -66.804 21.5654	-8.9515 12.071 -53.136 35.2332	6.1417 12.071 -38.043 50.3264	-14.93 12.071 -59.115 29.2544	-17.586 12.071 -61.77 26.599	23.6512 12.071 -20.533 67.8359	23.2367 12.071 -20.948 67.4213	11.84 12.071 -32.345 56.0247	15.9684 12.071 -28.216 60.1531	9.57921 12.071 -34.605 53.7639
Ext,2	18.8325 12.071 -25.352 63.0172	0 0 0 0	-27.571 12.071 -71.756 16.6138	-22.157 12.071 -66.341 22.028	-3.7868 12.071 -47.971 40.3979	9.88107 12.071 -34.304 54.0658	24.9742 12.071 -19.21 69.1589	3.90219 12.071 -40.282 48.0869	1.24679 12.071 -42.938 45.4315	42.4838 12.071 -1.7009 86.6684	42.0692 12.071 -2.1155 86.2539	30.6726 12.071 -13.512 74.8572	34.8009 12.071 -9.3838 78.9856	28.4117 12.071 -15.773 72.5964
Ext,3	**46.4034 12.071 2.21868 90.588**	27.5708 12.071 -16.614 71.7555	0 0 0 0	5.41415 12.071 -38.771 49.5988	23.7841 12.071 -20.401 67.9688	37.4519 12.071 -6.7328 81.6366	**52.5451 12.071 8.36038 96.7297**	31.473 12.071 -12.712 75.6577	28.8176 12.071 -15.367 73.0023	**70.0546 12.071 25.8699 114.239**	**69.64 12.071 25.4553 113.825**	**58.2434 12.071 14.0587 102.428**	**62.3718 12.071 18.1871 106.556**	**55.9826 12.071 11.7979 100.167**
Ext,4	40.9892 12.071 -3.1955 85.1739	22.1567 12.071 -22.028 66.3414	-5.4141 12.071 -49.599 38.7705	0 0 0 0	18.3699 12.071 -25.815 62.5546	32.0378 12.071 -12.147 76.2224	**47.1309 12.071 2.94623 91.3156**	26.0589 12.071 -18.126 70.2436	23.4035 12.071 -20.781 67.5882	**64.6405 12.071 20.4558 108.825**	**64.2259 12.071 20.0412 108.411**	**52.8293 12.071 8.64458 97.0139**	**56.9576 12.071 12.7729 101.142**	**50.5684 12.071 6.38374 94.7531**
Ext,5	22.6193 12.071 -21.565 66.804	3.78677 12.071 -40.398 47.9714	-23.784 12.071 -67.969 20.4006	-18.37 12.071 -62.555 25.8148	0 0 0 0	13.6678 12.071 -30.517 57.8525	28.761 12.071 -15.424 72.9457	7.68896 12.071 -36.496 51.8736	5.03356 12.071 -39.151 49.2182	**46.2705 12.071 2.08585 90.4552**	**45.8559 12.071 1.67126 90.0406**	34.4593 12.071 -9.7253 78.644	38.5877 12.071 -5.597 82.7724	32.1985 12.071 -11.986 76.3832
Ext,6	8.95145 12.071 -35.233 53.1361	-9.8811 12.071 -54.066 34.3036	-37.452 12.071 -81.637 6.73277	-32.038 12.071 -76.222 12.1469	-13.668 12.071 -57.853 30.5168	0 0 0 0	15.0932 12.071 -29.092 59.2778	-5.9789 12.071 -50.164 38.2058	-8.6343 12.071 -52.819 35.5504	32.6027 12.071 -11.582 76.7874	32.1881 12.071 -11.997 76.3728	20.7915 12.071 -23.393 64.9762	24.9199 12.071 -19.265 69.1045	18.5307 12.071 -25.654 62.7153
Ext,7	-6.1417 12.071 -50.326 38.043	-24.974 12.071 -69.159 19.2105	**-52.545 12.071 -96.73 -8.3604**	**-47.131 12.071 -91.316 -2.9462**	-28.761 12.071 -72.946 15.4237	-15.093 12.071 -59.278 29.0915	0 0 0 0	-21.072 12.071 -65.257 23.1127	-23.727 12.071 -67.912 20.4573	17.5095 12.071 -26.675 61.6942	17.095 12.071 -27.09 61.2796	5.69835 12.071 -38.486 49.883	9.8267 12.071 -34.358 54.0114	3.43751 12.071 -40.747 47.6222
Int,1	14.9303 12.071 -29.254 59.115	-3.9022 12.071 -48.087 40.2825	-31.473 12.071 -75.658 12.7116	-26.059 12.071 -70.244 18.1258	-7.689 12.071 -51.874 36.4957	5.97888 12.071 -38.206 50.1636	21.072 12.071 -23.113 65.2567	0 0 0 0	-2.6554 12.071 -46.84 41.5293	38.5816 12.071 -5.6031 82.7663	38.167 12.071 -6.0177 82.3517	26.7704 12.071 -17.414 70.9551	30.8987 12.071 -13.286 75.0834	24.5095 12.071 -19.675 68.6942
Int,2	17.5857 12.071 -26.599 61.7704	-1.2468 12.071 -45.431 42.9379	-28.818 12.071 -73.002 15.367	-23.403 12.071 -67.588 20.7812	-5.0336 12.071 -49.218 39.1511	8.63428 12.071 -35.55 52.819	23.7274 12.071 -20.457 67.9121	2.6554 12.071 -41.529 46.8401	0 0 0 0	41.237 12.071 -2.9477 85.4217	40.8224 12.071 -3.3623 85.0071	29.4258 12.071 -14.759 73.6105	33.5541 12.071 -10.631 77.7388	27.1649 12.071 -17.02 71.3496
Int,3	-23.651 12.071 -67.836 20.5334	-42.484 12.071 -86.668 1.70092	**-70.055 12.071 -114.24 -25.87**	**-64.64 12.071 -108.83 -20.456**	**-46.271 12.071 -90.455 -2.0858**	-32.603 12.071 -76.787 11.582	-17.51 12.071 -61.694 26.6751	-38.582 12.071 -82.766 5.60311	-41.237 12.071 -85.422 2.94771	0 0 0 0	-0.4146 12.071 -44.599 43.7701	-11.811 12.071 -55.996 32.3735	-7.6828 12.071 -51.868 36.5018	-14.072 12.071 -58.257 30.1126
Int,4	-23.237 12.071 -67.421 20.948	-42.069 12.071 -86.254 2.1155	**-69.64 12.071 -113.82 -25.455**	**-64.226 12.071 -108.41 -20.041**	**-45.856 12.071 -90.041 -1.6713**	-32.188 12.071 -76.373 11.9966	-17.095 12.071 -61.28 27.0897	-38.167 12.071 -82.352 6.0177	-40.822 12.071 -85.007 3.3623	0.41459 12.071 -43.77 44.5993	0 0 0 0	-11.397 12.071 -55.581 32.7881	-7.2683 12.071 -51.453 36.9164	-13.657 12.071 -57.842 30.5272
Int,5	-11.84 12.071 -56.025 32.3446	-30.673 12.071 -74.857 13.5121	**-58.243 12.071 -102.43 -14.059**	**-52.829 12.071 -97.014 -8.6446**	-34.459 12.071 -78.644 9.72535	-20.791 12.071 -64.976 23.3932	-5.6983 12.071 -49.883 38.4863	-26.77 12.071 -70.955 17.4143	-29.426 12.071 -73.61 14.7589	11.8112 12.071 -32.373 55.9959	11.3966 12.071 -32.788 55.5813	0 0 0 0	4.12836 12.071 -40.056 48.313	-2.2608 12.071 -46.446 41.9238
Int,6	-15.968 12.071 -60.153 28.2163	-34.801 12.071 -78.986 9.38376	**-62.372 12.071 -106.56 -18.187**	**-56.958 12.071 -101.14 -12.773**	-38.588 12.071 -82.772 5.59699	-24.92 12.071 -69.105 19.2648	-9.8267 12.071 -54.011 34.358	-30.899 12.071 -75.083 13.2859	-33.554 12.071 -77.739 10.6305	7.68284 12.071 -36.502 51.8675	7.26825 12.071 -36.916 51.4529	-4.1284 12.071 -48.313 40.0563	0 0 0 0	-6.3892 12.071 -50.574 37.7955
Int,7	-9.5792 12.071 -53.764 34.6055	-28.412 12.071 -72.596 15.773	**-55.983 12.071 -100.17 -11.798**	**-50.568 12.071 -94.753 -6.3837**	-32.198 12.071 -76.383 11.9862	-18.531 12.071 -62.715 25.654	-3.4375 12.071 -47.622 40.7472	-24.51 12.071 -68.694 19.6751	-27.165 12.071 -71.35 17.0197	14.072 12.071 -30.113 58.2567	13.6574 12.071 -30.527 57.8421	2.26084 12.071 -41.924 46.4455	6.3892 12.071 -37.795 50.5739	0 0 0 0

II

(b)

LS Mean[i]

Mean[i]-Mean[j] / Std Err Dif / Lower CL Dif / Upper CL Dif	Ext,1	Ext,2	Ext,3	Ext,4	Ext,5	Ext,6	Ext,7	Int,1	Int,2	Int,3	Int,4	Int,5	Int,6	Int,7
Ext,1 Mean[i]-Mean[j]	0	-6.1735	-14.361	-14.56	-9.1104	-7.4789	-7.9802	7.22992	5.18351	0.08763	3.55518	8.07337	2.95223	-3.4468
Std Err Dif	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	0	-14.614	-22.801	-23	-17.55	-15.919	-16.42	-1.2101	-3.2565	-8.3524	-4.8849	-0.3667	-5.4878	-11.887
Upper CL Dif	0	2.26657	-5.9211	-6.1195	-0.6703	0.9612	0.45986	15.67	13.6236	8.52768	11.9952	16.5134	11.3923	4.99329
Ext,2 Mean[i]-Mean[j]	6.17349	0	-8.1877	-8.386	-2.9369	-1.3054	-1.8067	13.4034	11.357	6.26112	9.72867	14.2469	9.12572	2.72672
Std Err Dif	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	-2.2666	0	-16.628	-16.826	-11.377	-9.7454	-10.247	4.96335	2.91694	-2.1789	1.28861	5.80681	0.68567	-5.7133
Upper CL Dif	14.6135		0.25236	0.05404	5.50315	7.13469	6.63335	21.8435	19.7971	14.7012	18.1687	22.6869	17.5658	11.1668
Ext,3 Mean[i]-Mean[j]	14.3612	8.18769	0	-0.1983	5.25078	6.88233	6.38099	21.5911	19.5447	14.4488	17.9164	22.4346	17.3134	10.9144
Std Err Dif	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	5.92113	-0.2524	0	-8.6384	-3.1893	-1.5577	-2.0591	13.151	11.1046	6.00876	9.47631	13.9945	8.87336	2.47436
Upper CL Dif	22.8012	16.6277	0	8.24173	13.6908	15.3224	14.821	30.0312	27.9847	22.8889	26.3564	30.8746	25.7535	19.3545
Ext,4 Mean[i]-Mean[j]	14.5595	8.38602	0.19832	0	5.44911	7.08065	6.57931	21.7894	19.743	14.6471	18.1147	22.6329	17.5117	11.1127
Std Err Dif	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	6.11945	-0.054	-8.2417	0	-2.9909	-1.3594	-1.8607	13.3494	11.303	6.20708	9.67463	14.1928	9.07169	2.67268
Upper CL Dif	22.9996	16.8261	8.63838	0	13.8892	15.5207	15.0194	30.2295	28.1831	23.0872	26.5547	31.0729	25.9518	19.5528
Ext,5 Mean[i]-Mean[j]	9.1104	2.93691	-5.2508	-5.4491	0	1.63154	1.1302	16.3403	14.2939	9.19803	12.6656	17.1838	12.0626	5.66363
Std Err Dif	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	0.67034	-5.5031	-13.691	-13.889	0	-6.8085	-7.3099	7.90026	5.85385	0.75797	4.22552	8.74372	3.62258	-2.7764
Upper CL Dif	17.5505	11.377	3.18927	2.99095	0	10.0716	9.57026	24.7804	22.734	17.6381	21.1056	25.6238	20.5027	14.1037
Ext,6 Mean[i]-Mean[j]	7.47886	1.30537	-6.8823	-7.0807	-1.6315	0	-0.5013	14.7088	12.6624	7.56648	11.034	15.5522	10.4311	4.03209
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	-0.9612	-7.1347	-15.322	-15.521	-10.072	0	-8.9414	6.26872	4.22231	-0.8736	2.59398	7.11218	1.99104	-4.408
Upper CL Dif	15.9189	9.74542	1.55294	1.3594	6.80851	0	7.93872	23.1488	21.1024	16.0065	19.4741	23.9923	18.8711	12.4721
Ext,7 Mean[i]-Mean[j]	7.98019	1.80671	-6.381	-6.5793	-1.1302	0.50134	0	15.2101	13.1637	8.06782	11.5354	16.0536	10.9324	4.53342
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	-0.4599	-6.6333	-14.821	-15.019	-9.5703	-7.9387	0	6.77006	4.72365	-0.3722	3.09532	7.61351	2.49237	-3.9066
Upper CL Dif	16.4202	10.2468	2.05907	1.86074	7.30985	8.94139	0	23.6502	21.6038	16.5079	19.9754	24.4936	19.3725	12.9735
Int,1 Mean[i]-Mean[j]	-7.2299	-13.403	-21.591	-21.789	-16.34	-14.709	-15.21	0	-2.0464	-7.1423	-3.6747	0.84346	-4.2777	-10.677
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	-15.67	-21.843	-30.031	-30.229	-24.78	-23.149	-23.65	0	-10.486	-15.582	-12.115	-7.5966	-12.718	-19.117
Upper CL Dif	1.21014	-4.9633	-13.151	-13.349	-7.9003	-6.2687	-6.7701	0	6.39365	1.29777	4.76532	9.28351	4.16237	-2.2366
Int,2 Mean[i]-Mean[j]	-5.1835	-11.357	-19.545	-19.743	-14.294	-12.662	-13.164	2.04641	0	-5.0959	-1.6283	2.88986	-2.2313	-8.6303
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	-13.624	-19.797	-27.985	-28.183	-22.734	-21.102	-21.604	-6.3936	0	-13.536	-10.068	-5.5502	-10.671	-17.07
Upper CL Dif	3.25654	-2.9169	-11.105	-11.303	-5.8539	-4.2223	-4.7236	10.4865	0	3.34417	6.81172	11.3299	6.20878	-0.1902
Int,3 Mean[i]-Mean[j]	-0.0876	-6.2611	-14.449	-14.647	-9.198	-7.5665	-8.0678	7.14229	5.09588	0	3.46755	7.98575	2.86461	-3.5344
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577	2.30577
Lower CL Dif	-8.5277	-14.701	-22.889	-23.087	-17.638	-16.007	-16.508	-1.2978	-3.3442	0	-4.9725	-0.4543	-5.5754	-11.974
Upper CL Dif	8.35243	2.17894	-6.0088	-6.2071	-0.758	0.87357	0.37223	15.5823	13.5359	0	11.9076	16.4258	11.3047	4.90566
Int,4 Mean[i]-Mean[j]	-3.5552	-9.7287	-17.916	-18.115	-12.666	-11.034	-11.535	3.67474	1.62833	-3.4675	0	4.5182	-0.6029	-7.0019
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577	2.30577
Lower CL Dif	-11.995	-18.169	-26.356	-26.555	-21.106	-19.474	-19.975	-4.7653	-6.8117	-11.908	0	-3.9219	-9.043	-15.442
Upper CL Dif	4.88488	-1.2886	-9.4763	-9.6746	-4.2255	-2.594	-3.0953	12.1148	10.0684	4.97251	0	12.9583	7.83711	1.43811
Int,5 Mean[i]-Mean[j]	-8.0734	-14.247	-22.435	-22.633	-17.184	-15.552	-16.054	-0.8435	-2.8899	-7.9857	-4.5182	0	-5.1211	-11.52
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577	2.30577
Lower CL Dif	-16.513	-22.687	-30.875	-31.073	-25.624	-23.992	-24.494	-9.2835	-11.33	-16.426	-12.958	0	-13.561	-19.96
Upper CL Dif	0.36668	-5.8068	-13.995	-14.193	-8.7437	-7.1122	-7.6135	7.5966	5.55019	0.45431	3.92186	0	3.31891	-3.0801
Int,6 Mean[i]-Mean[j]	-2.9522	-9.1257	-17.313	-17.512	-12.063	-10.431	-10.932	4.27768	2.23128	-2.8646	0.60294	5.12114	0	-6.399
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0	2.30577
Lower CL Dif	-11.392	-17.566	-25.753	-25.952	-20.503	-18.871	-19.372	-4.1624	-6.2088	-11.305	-7.8371	-3.3189	0	-14.839
Upper CL Dif	5.48782	-0.6857	-8.8734	-9.0717	-3.6226	-1.991	-2.4924	12.7177	10.6713	5.57545	9.043	13.5612	0	2.04105
Int,7 Mean[i]-Mean[j]	3.44677	-2.7267	-10.914	-11.113	-5.6636	-4.0321	-4.5334	10.6767	8.63028	3.5344	7.00195	11.5201	6.399	0
Std Err Dif	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	2.30577	0
Lower CL Dif	-4.9933	-11.167	-19.354	-19.553	-14.104	-12.472	-12.973	2.23663	0.19022	-4.9057	-1.4381	3.08009	-2.0411	0
Upper CL Dif	11.8868	5.71334	-2.4744	-2.6727	2.77643	4.40797	3.90663	19.1167	17.0703	11.9745	15.442	19.9602	14.8391	0

III