ORIGINAL ARTICLE

Foraging ecology and reproductive biology of the Stonechat *Saxicola torquata*: comparison between a revitalized, intensively cultivated and a historical, traditionally cultivated agro-ecosystem

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Abstract An effective strategy to reintegrate biodiversity within otherwise intensively cultivated agroecosystems is to create set-aside and wildflower areas. It remains largely unknown, however, whether the ecological performance of an agroecosystem revitalized in this manner is comparable—from a species' population biology perspective—to traditionally exploited farmland. To address this question we compared, during two successive years, the trophic ecology and breeding performance of an insectivorous, indicator passerine (the Stonechat *Saxicola torquata*) in a revitalized intensively cultivated farmland (RIC) and a traditional, extensively cultivated farmland (TEC) in southern Switzerland. The chicks' diet and prey abundance did not differ between the RIC and TEC, with orthopterans, caterpillars (Lepidoptera) and coleopterans predominating (approx. 80% of diet biomass). Although Stonechat pairs initiated more broods in TEC than in the RIC, reproductive success (number of fledglings/territory × year) did not differ significantly between the TEC and RIC. The chicks' condition (body mass) was slightly better in TEC than in RIC, while no such effect could be shown for chick constitution (tarsus length) in either year. The inter-site (RIC vs. TEC) variation fell well within the inter-annual variation of breeding parameters, indicating that environmental stochasticity could be a greater determinant of reproductive output and young quality than agroecosystem type. Although in need of replication, these results suggest that incentives for setting aside farmland and creating wildflower areas within agroecosystems may not only enhance plant and invertebrate diversity, as has been demonstrated earlier, but can also support functioning populations of vertebrates situated at higher trophic levels along the food chain.

Keywords Agroecosystems · Ecological restoration · Farmland · Set-aside areas · Species conservation · Trophic niche · *Saxicola torquata*

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Introduction

Due to tremendous changes that have occurred in agricultural practices since the mid-twentieth century, plant and animal species traditionally associated with farmland have declined massively in most regions of the Western world (Andreasen et al. 1996; Benton et al. 2002; Bignal and McCraken 1996; Böhning-Gaese and Bauer 1996; Chamberlain and Fuller 2001; Chamberlain et al. 2000; Donald et al. 2001; Fewster et al. 2000; Fuller et al. 1995; Gillings and Fuller 1998; Jackson and Jackson 2002; Siriwardena et al. 1998; Smart et al. 2000; Sotherton and Self 2000; Wilson et al. 1999). Recently, there have been widespread incentives to promote cultivation methods that are less detrimental to wildlife, such as biological control and

organic farming, which have progressively enabled the ecological quality of these habitats to be improved (Chamberlain et al. 1999; Dennis et al. 1994; de Snoo 1999; Freemark and Kirk 2001; Robinson and Sutherland 2002). Among the newly introduced agricultural schemes is the policy of setting aside land, which aims at diminishing agricultural production and/or favouring biodiversity in agroecosystems (Bignal 1998; di Giulio et al. 2001; Henderson et al. 2000; Henderson and Evans 2000; Kleijn and Sutherland 2003; Sotherton 1998; Wilson and Fuller 1992). In Switzerland, agricultural subsidies have been entirely decoupled from the agricultural production system since 1999. If Swiss agriculturists want to receive subsidies, they are now obliged to conserve or convert 7% of the total area of their land into "natural and/or ecologically relevant" units. These ecological compensation areas include extensive meadowland and pastureland, hedge rows, stone fences, ditches, unpaved roads, among others (Günter et al. 2002; Jeanneret et al. 2003; Kleijn and Sutherland 2003; Koller et al. 2004). Thus, wildflower strips can be found among extensively managed land types; these strips are known as set-asides where special mixes of seeds from several indigenous flowering plants are sown (Günter et al. 2002; Koller et al. 2004). In some instances, set-asides may also result from natural vegetation growth, but this sort of management is much less frequent and restricted to a few areas, due to fears regarding spread of weeds. These ecological compensation areas often provide suitable refuges for several local plant and animal species, which may allow them to recolonize the ecosystems from which they had vanished some decades ago. Thanks to the implementation of ecological compensation areas, several rare plant, arthropod and vertebrate species have been able to recover in several regions of Switzerland within a few years (Aschwanden et al. 2007; Birrer et al. 2007; Hofer et al. 2002; Jeanneret et al. 2003; Jenny et al. 2002; Lambelet-Haueter 1995; Lugrin 1999; Peter and Walter 2001; Pfiffner et al. 2000; Spiess et al. 2002; Weibel 1998). Although populations of some endangered species are favoured by these newly created landscape features, it is still poorly understood whether these can actually provide a suitable reproductive habitat of comparable ecological quality to traditional, extensively cultivated farmland (Stephens et al. 2003; Wilson et al. 1997), in particular for insectivorous vertebrates situated higher up the food chain.

The aim of the study reported here was to evaluate whether newly engineered agroecosystems (with set-aside land, including wildflower areas) can provide suitable reproductive conditions to wildlife (Donald and Vickery 2000). We have chosen the Stonechat Saxicola torquata as a model species for its role as a bioindicator. The insectivorous Stonechat prefers open and semi-open habitats, from heatherland through to steppe and garrigue. In Switzerland, however, S. torquata colonizes only cultivated landscapes, preferring patches or verges of permanent, extensive grassy habitat. In contrast, the species is totally absent in homogenous, intensive farmland without perennial grass structures. A constant feature of its breeding habitat is the availability of vertical perches, such as tall plant stalks (often desiccated), isolated bushes, small trees and/or fences (Flinks and Pfeifer 1993).

Once widespread and abundant throughout Western Europe, Stonechat populations have declined sharply between 1940 and 1990; this trend has been particularly evident since the 1970s (Bauer and Berthold 1996; Magee 1965; Tucker and Heath 1994). However, in more recent years, this species has shown show some recovery, notably in Germany, Denmark and Poland (Bauer and Berthold 1996; Pfeifer 2000). The population trends of Stonechats in Switzerland are comparable; for example, the population size has doubled from 1978–1979 (239 pairs; Biber 1984) to 1993–1996 (Posse et al. 1998), possibly partly due to the implementation of novel farming regimes, including the newly established set-aside policy. This positive demography, however, concerns only a few regions, including our study areas.

We have compared the density, prey abundance, diet selection, foraging strategy, reproductive phenology and performance of the Stonechat population in two areas in southern Switzerland that offer contrasting patterns of agricultural use: (1) an area with intensive cultivation (canton of Geneva), but where a rich network of set-aside and wildflower areas contribute to enhance the local diversity of native plant and animal species (Birrer et al. 2007; Lambelet-Haueter 1995; Lugrin 1999); (2) a traditional, extensively cultivated area on the plain of the Rhone (canton of Valais), with a network of linear landscape elements consisting of historical irrigation canals and ditches bordered with grassy vegetation and/or isolated bushes and shrubs. The restriction to only two study areas was due to a lack of similar matrices elsewhere in the country: properly revitalized farmland occurs only at two distant places in Switzerland (Geneva and in the canton of Schaffhausen), whereas the Central Valais is the sole region still offering the remnants of the traditional cultivated landscape at lowland altitudes. Although we were aware of the problem of a lack of replication, the speed at which traditional farmland is currently shrinking in Central Europe convinced us to carry out this comparison before it was no longer feasible.

The hypothesis underlying this study is that modern, revitalized agroecosystems (i.e. farmland specifically designed for biodiversity) represent suitable breeding habitats for this insectivorous species and may thus support sustainable populations. As the Stonechat is an indicator species of open and semi-open lowland farmland, our

results might be relevant to—and have implications for— wider segments of these ecological communities.

Material and methods

Study areas and populations

The first study area is located in the surroundings of Geneva (500 ha; 46°10′N, 06°00′E), and the second area is in the Upper Valais (360 ha; 46°18′N, 07°42′E). The two study areas are situated at similar altitudes (420–450 vs. 620–630 m a.s.l., respectively) and are about 100 km apart. The mean yearly ambient temperatures are similar (approx. 9–10°C), but the Upper Valais is slightly drier than Geneva (700 vs. 900 mm rainfall per year, respectively). While cereal fields and other crops (approx. 70% altogether) predominate in Geneva, the cultivated landscape in Central Valais consists primarily of meadowland (60%). Since 1991, the study area at Geneva has benefitted from a large-scale revitalization scheme within the framework of a national conservation programme of the Grey Partridge *Perdix perdix* (Swiss Ornithological Institute and Federal Office for the Environment; Jenny et al. 2002). The revitalized habitat consisted of 83 set-aside strips (approx. 10 m wide) totaling 19 ha in 1991–1998. No similar revitalization has been implemented in the second study area in Upper Valais. We refer to the two study areas as "revitalized intensively cultivated" farmland (RIC, Geneva) and "traditional extensively cultivated" farmland (TEC, Upper Valais).

In 1999 and 2000, territorial pairs were monitored weekly from mid-March (note that very few Stonechats winter on breeding grounds in Switzerland, most of them migrate to the South) to late June and then every second week from early July to mid September (last adults provisioning chicks on 11 September). In 1999, we surveyed 17 and 25 territories in Geneva (RIC) and Valais (TEC), respectively; in 2000, this was 23 and 21 territories, respectively. The criterion for retaining a given territorial pair in our sample was that at least one breeding attempt occurred there in a given year. The number of breeding attempts was controlled for each territory throughout the reproductive season.

Trophic ecology and foraging

The diet of the nestlings was investigated using neck collars (ligature method; Kluijver 1933) placed on 7- to 10-day-old chicks (with the authorized approval of the cantonal veterinary offices) in six broods in TEC and five broods at RIC (all broods belonged to distinct territories

within a 1-year period). Nestling diet was collected over two successive days per brood. We studied two randomly chosen chicks on the first day and two others on the following day. During an experiment, the non-focal chicks were temporarily removed from the nest. Diet collection lasted for 2–4 h according to weather conditions and the number of prey items provisioned. Neck collars were checked and emptied every 20 min on average. At the end of the experiment, temporarily removed chicks were fed with crickets, and the neck-collared young were given a compensatory amount of crickets corresponding to the prey biomass collected with neck collars. In total, we retrieved food items from 47 chicks, of which none suffered apparent damage due to the method. Prey items were stored in 70% ethanol and then dried for 72 h at 65°C in an oven to measure dry biomass using a precision balance (±0.1 mg).

The abundance of ground-dwelling arthropods was estimated with Barber's pitfalls and abundance of grass-dwelling arthropods with hand netting. For each brood investigated, 15 pitfalls were placed in three lines of five pitfalls each, along an approximately 30-m-long transect within the main habitat features of the habitat (set-aside strips in RIC and irrigation canals and ditches in TEC). Within a line, pitfalls were placed 2 m apart, with lines positioned 10–20 m apart. Pitfalls were used to collect prey during seven successive days from the onset of a neck collar experiment. Hand netting was carried out along pitfall rows (i.e. 30-m-long transects, one sweep every metre) on the same day as the neck-collar collection took place. The samples collected were stored in 70% ethanol and identified down to the family or order level (40 categories recognized). The samples were dried and dry biomass measured (as described above).

To test whether Stonechats prefer certain categories and/or sizes of prey, we compared the composition of the chick diet with prey abundance. Data from all broods within a given study area were grouped together. Given that we used two different methods to sample invertebrates (hand-netting for grass-dwelling arthropods vs. pitfall trapping for ground-dwelling arthropods), two separate analyses were performed for each corresponding ecological niche.

The foraging behaviour of provisioning parents was monitored visually in some of the broods (TEC: $n = 6$; RIC: $n = 4$) already studied for diet composition; this was done for each brood on two separate days in the early morning or late afternoon (totaling 5 h of observation per brood). Using an optic telemeter, we estimated the distances from the nest for the furthest locations of prey capture and mapped a pairs' home range as a maximum convex polygon, as obtained from these locations.

Breeding parameters

The reproductive progress of the pairs under observation was checked twice weekly. Nests were located during nest building or during incubation. The breeding parameters recorded were clutch size, hatching success, number of fledglings and number of successful broods (i.e. with ≥1 fledgling) per pair/year. To estimate the physical constitution of the chick, we measured the tarsus length [average length (±0.1 mm, calliper) of the left and right tarsi at 9–11 days of age—i.e. close to the growth asymptote; Greig-Smith 1985]. The physiological condition of the chicks was estimated by measuring body mass (±0.25 g; Pesola, Baar, Switzerland) at the same age. Tarsus length (constitution) is likely to reflect genetic background to some extent, whereas body mass (condition) is probably influenced to a large extent by environmental circumstances (Hailman 1986).

Statistics

To achieve data independency—i.e. avoid pseudo-replication—statistical tests were carried out using average brood values or average territorial pair values, respectively, where applicable. We used SYSTAT (Statsoft, Tulsa, OK) to perform the statistical treatment.

Results

Density

At the TEC study plot, Stonechat density was 7.5 and 6.4 pairs/km^2, in 1999 and 2000, respectively. At RIC this reached 8 and 7.3 pairs/km^2, respectively.

Prey abundance

A total of 16,662 invertebrates were collected and classified into 40 categories, mostly taxonomic families (Appendix 1). Overall, the average (among territories) frequency and biomass of these 40 categories did not significantly differ between the two study areas in terms of ground-dwelling and grass-dwelling arthropods (Fig. 1), suggesting that prey availability in the two areas was similar.

Fig. 1 Comparison of prey category number (*n*, *left column*) and biomass (μg, *right column*) (*n* = 40 categories; Appendix 1) occurring in revitalized intensively cultivated farmland (*RIC*, Geneva; *Y*-axis) versus traditional extensively cultivated farmland (*TEC*, Valais; *X*-axis) within Stonechat (*Saxicola torquata*) habitats, as estimated by: **a** hand netting (grass-dwelling arthropods), **b** pitfall trapping (ground-dwelling arthropods). A logarithmic scale is used because distributions are strongly skewed. The outcome of Spearman's rank correlation (*r$_s$*) and sign tests (*Z*) is given
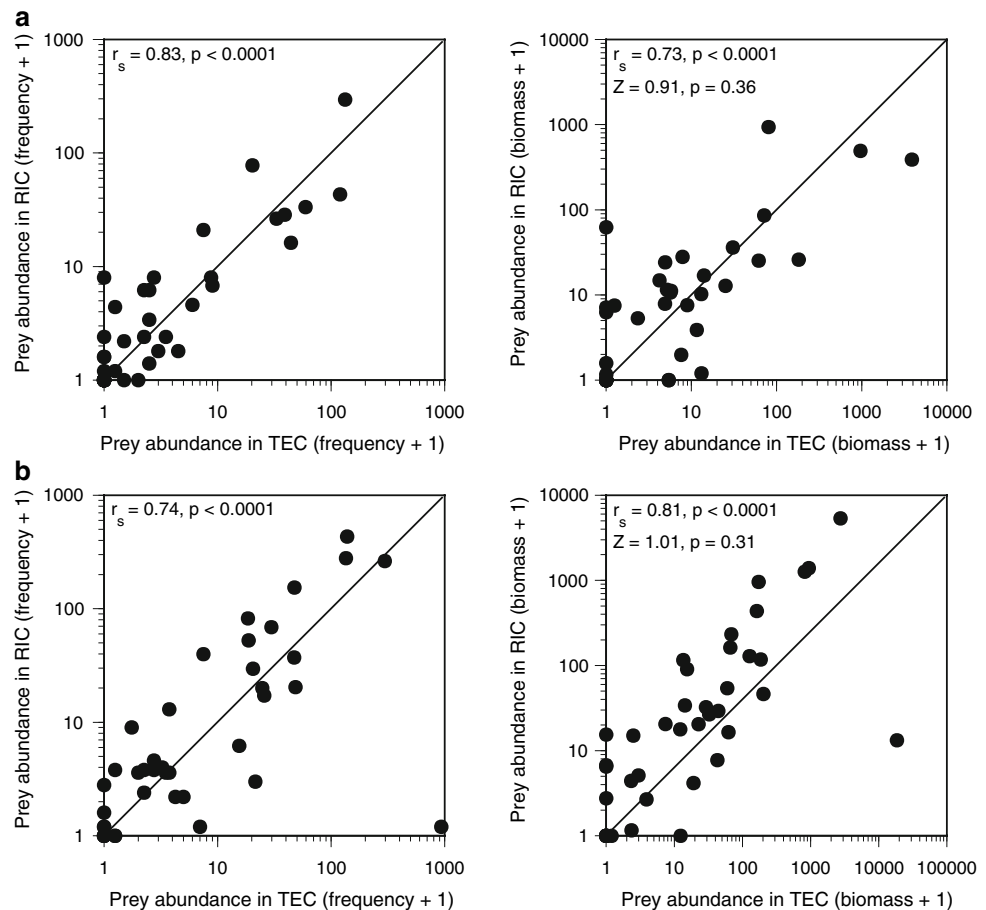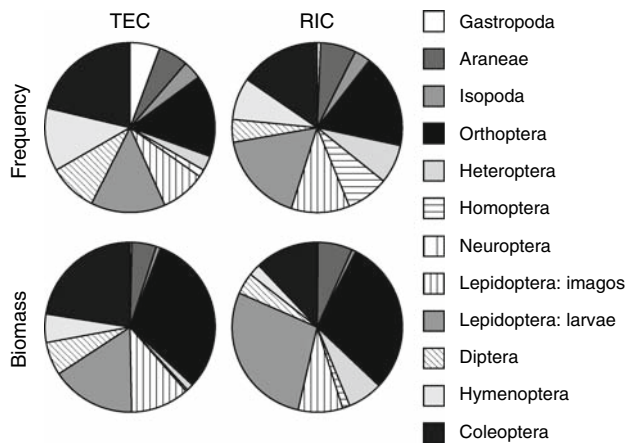
Fig. 2 Frequency and biomass proportions of the various prey categories found in chicks' diet at TEC (Valais) and the RIC (Geneva)

Table 1 Spearman's rank correlation coefficients between categories of prey delivered to nestlings (either in frequency or biomass terms) and their abundance in foraging habitats in relation to the prey abundance sampling technique (hand-netting vs. pitfall trapping)

Sampling technique	Site	Variable type	r_s	P
Hand netting	TEC	Frequency	0.36*	0.024*
		Biomass	0.32*	0.045*
	RIC	Frequency	0.46*	0.003*
		Biomass	0.52*	0.001*
Pitfalls	TEC	Frequency	0.02	0.891
		Biomass	0.14	0.399
	RIC	Frequency	0.14	0.402
		Biomass	0.15	0.367

TEC Traditional extensively cultivated farmland (Valais), *RIC* revitalized intensively cultivated farmland (Geneva)

* Significant ($P < 0.05$) coefficients occur only for hand-netting

Chick diet

Using the neck-collar technique, we collected 301 prey items from chicks ($n = 141$ in TEC, 160 in RIC, from six and five broods, respectively). These were assigned to 12 categories (mostly taxonomic orders; Fig. 2). The frequency of prey categories did not differ between TEC and RIC (contingency table, $\chi^2 = 9.514$, $df = 8$, $P = 0.301$) after the three less numerous categories with a mean item dry biomass <10 mg had been grouped together. Three prey categories dominated in the diet at the two study plots, both in numbers and biomass: Orthoptera made up 32 and 30% of the diet biomass in TEC and RIC, respectively; Lepidoptera (mostly caterpillars) made up 27 and 36%, respectively, and Coleoptera made up 23 and 12%, respectively. Combined, these three categories represented 82% of the total biomass supplied to chicks in TEC and 78% in RIC. Shannon–Weaver indices of diet diversity did not differ between TEC (0.88) and RIC (0.86; Mann–Whitney U-test $U = 14$, $n = 6$ and 5, $P = 0.86$).

Size and type of selected prey

In both study areas, there was a significant correlation between diet composition and grass-dwelling prey in terms of both prey category frequency and biomass (Spearman's rank tests, $n = 40$ categories, all P values < 0.05; Table 1). In contrast, the relationships between diet composition and ground-dwelling prey were not significant (Table 1). These results indicate that Stonechats preferred to hunt grass-dwelling prey; we therefore did not take ground-dwelling prey into consideration in subsequent analyses.

A comparison of the average prey item biomass (total biomass of a category divided by number of items in that category) in the diet with the average item biomass of available grass-dwelling invertebrates revealed that Stonechats preferred larger prey items in both study areas (sign test; Fig. 3). Outlying points on both graphs in Fig. 3 (dots under the line of equality) represent small gastropods.

Home ranges

Home ranges tended to be larger at RIC (mean 2.5 ha, range 1.8–3.6 ha; $n = 4$) than at TEC, but the difference is only marginally significant (mean 1.5 ha, range 1.0–2.0 ha; $n = 6$; Mann–Whitney U-test $U = 9.5$, $P = 0.055$).

Reproductive success

Clutch size did not differ between the two study areas or between years (Table 2). Indeed, the only factor influencing variation in clutch size was the time of year, with small clutches occurring early and late in the breeding season and larger clutches occurring from the last decade of April until mid-June (Fig. 4).

Nestlings close to fledging were significantly heavier at TEC than at the RIC (Table 2). There was also an effect of year, with 2000 producing young in better body condition (Fig. 5a). Tarsus length of the nestlings (constitution) did not differ significantly between the two agroecosystem types, but there was a distinct year effect (Table 2; Fig. 5b).

The mean number of breeding attempts per territory was significantly larger at TEC than at RIC, and larger in 2000 than in 1999 (Table 2; Fig. 5c). This parameter explains a large part of the variation in productivity among territorial pairs (ANOVA, $F = 11.366$, $df = 3$, $P < 0.0001$).

Fig. 3 Relationship between mean prey item biomass (µg) in chicks' diet and mean prey item biomass (µg) in grass-dwelling prey abundance (hand-netting) for each prey category. A logarithmic scale is used as distributions are strongly skewed. Results of the sign tests (Z) are given
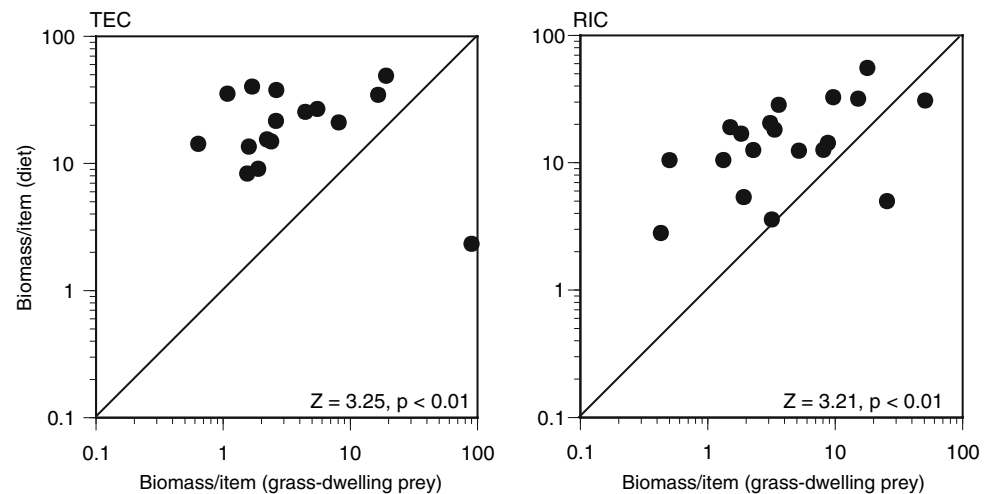

Table 2 Results of ANOVAs performed on five breeding parameters (see Appendix 2 for descriptive statistics)

Variable	Source of variation	Sum of squares	df	Variance	F	P
Clutch size	Site	0.437	1	0.437	0.881	0.3504
	Period[a]	11.340	3	3.780	7.611*	0.0001*
	Year	0.018	1	0.018	0.036	0.8506
	Site × period	2.826	3	0.942	1.896	0.1356
	Site × year	0.027	1	0.027	0.054	0.8164
	Period × year	0.888	3	0.296	0.596	0.619
	Error	46.221	93	0.497		
Chick mass	Site	13.296	1	13.296	17.123*	0.0001*
	Year	8.308	1	8.308	10.699*	0.0019*
	Site × year	1.603	1	1.603	2.064	0.1565
	Error	42.12	54	0.78		
Chick tarsus	Site	0.362	1	0.362	0.875	0.3537
	Year	2.593	1	2.593	6.272*	0.0152*
	Site × year	0.041	1	0.041	0.100	0.7529
	Error	23.151	56	0.413		
Breeding attempts/territory	Site	4.725	1	4.725	9.014*	0.0036*
	Year	6.538	1	6.538	12.471*	0.0007*
	Site × year	0.234	1	0.234	0.446	0.5060
	Error	42.987	82	0.524		
Fledglings/territory	Site	8.052	1	8.052	1.163	0.2839
	Year	22.290	1	22.290	3.221	0.0764
	Site × year	1.330	1	1.330	0.192	0.6623
	Error	567.531	82	6.921		

The explanatory variables were site (farming regime, i.e. RIC vs. TEC), year and season

* Significant at $P < 0.05$

[a] See periods in Fig. 4

The mean number of fledglings per territory (Fig. 5d) did not differ between RIC and TEC, but again tended to differ between years (Table 2).

In TEC, 47 (1999) and 53% (2000) of all breeding attempts resulted in at least one fledgling; at RIC, these values were 47 and 56%, respectively. These proportions did not differ statistically (1999: χ^2 with Yates' correction = 0.02, $df = 1$, NS; 2000: χ^2 with Yates' correction = 0.007, $df = 1$, NS). Causes of brood failures were mostly predation at RIC (≥ 7 out of 14 failures), while burning and mowing of drainage canal banks and ditches were the most important factor in 1999 at TEC (14 out of 27 failures).
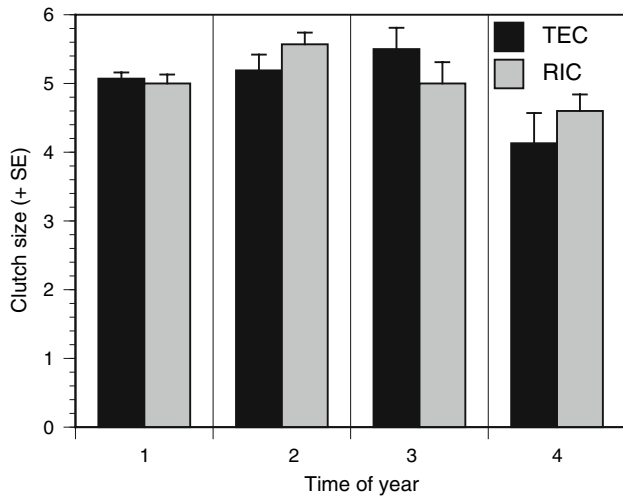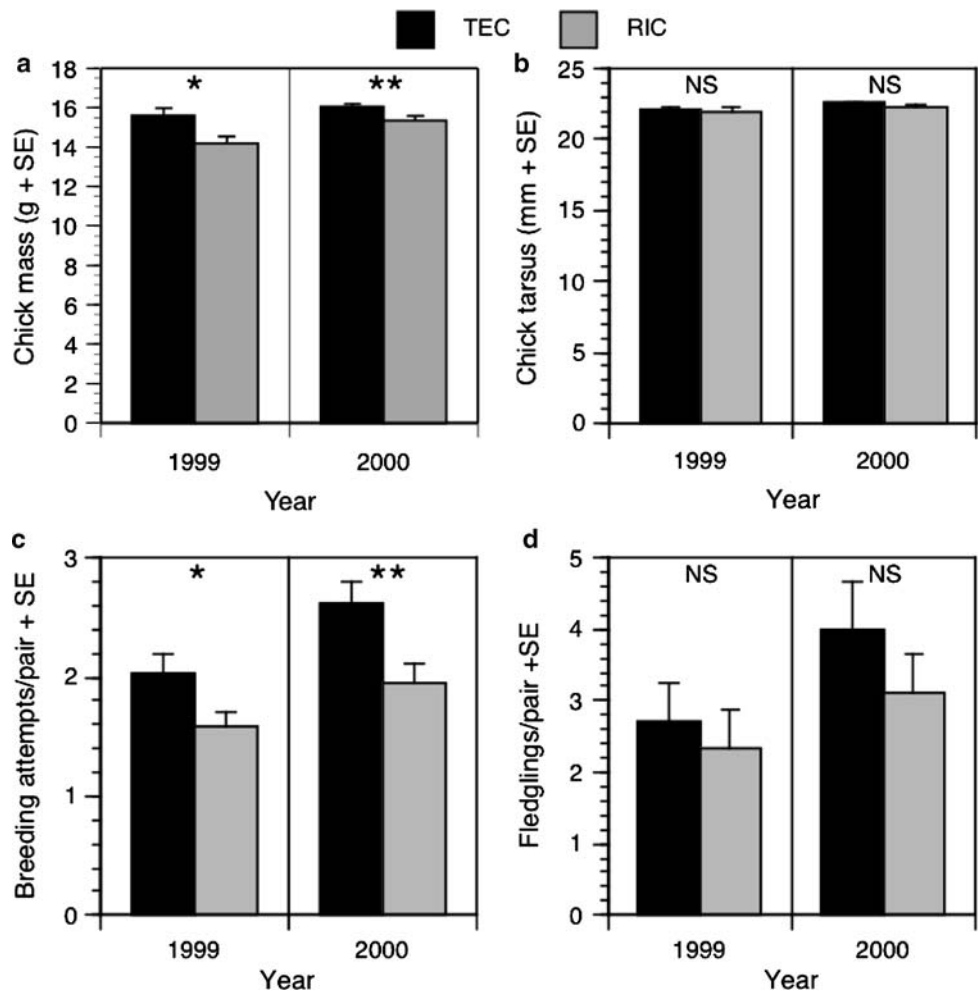
Fig. 4 Variation in average (±SE) clutch size according to farming regime (RIC vs. TEC) and season. *1* 18 March–20 April, *2* 21 April–20 May, *3* 21 May–20 June; *4* 21 June–20 July

Fig. 5 Variation in breeding parameters (mean ± SE) with respect to year and farming regime: **a** chick body mass (g), **b** chick tarsus length (mm), **c** number of breeding attempts per territory, **d** number of fledglings per territory. Results of *t* tests are indicated: *$*P < 0.05$; *$**P < 0.01$; *NS* non-significant. For further details see Appendix 2 and Table 2

Discussion

The results of our study show that prey availability, prey selection and reproductive performance of the Stonechat did not differ substantially between a revitalized, intensively cultivated (RIC) and a historical, traditionally cultivated (TEC) agroecosystem. The ideal study design would have consisted of a geographic replication of study plots. However, Central Valais is the very last lowland region in Switzerland where historical agricultural landscape structure and practices still persist. We were therefore limited by the availability of only one suitable traditionally cultivated farmland in the lowlands. Moreover, appropriately restored farmland landscape matrices with breeding Stonechat populations are rare in Switzerland: Geneva is one of the two best examples available countrywide. This situation also limited the choice of the second kind of agroecosystem, especially as the two study areas had to be relatively close due to field logistic constraints. It must be acknowledged here that the kind of comparison we carried out will become more and more difficult in the future because traditionally cultivated

landscapes will continue to shrink everywhere in Europe. In this context, this investigation can be viewed as a "last chance" opportunity. Although this lack of replication is a drawback that limits generalization, the two habitat matrices were characterized by climatic and biological (arthropod communities, this study) conditions, which, in our opinion, legitimize our comparison. The present results suggest that the installation of set-asides and wildflower areas in intensively cultivated farmland may support populations of Stonechats that apparently operate like populations in historical, extensive agricultural matrices.

Trophic ecology

Former studies of Stonechat diet (faecal analyses) have described the species as a generalist predator of invertebrates (Cummins and O'Halloran 2002; Flinks and Pfeifer 1987, 1988; Greig-Smith and Quicke 1983), which is chiefly confirmed here. This large prey spectrum may stem from the variety of foraging techniques used by Stonechats, who can either fly-catch insects in the air or collect them from bare ground or grass stalks (Greig-Smith 1983; Moreno 1984). From a taxonomic viewpoint, Coleoptera and Lepidoptera (mostly caterpillars) are well represented in all dietary investigations on Stonechat diet to date, including ours (e.g. Cummins and O'Halloran 2002). However, there are some geographic discrepancies. Orthoptera appear to be one of the most frequently eaten prey in Switzerland, whereas they lack in most other dietary studies. This is probably due to regional variation in habitat selection patterns: we have been working in xeric, central European agroecosystems while most previous works have been carried out in humid heatherland (Greig-Smith and Quicke 1983) or pastureland (Cummins and O'Halloran 2002; Flinks and Pfeifer 1987, 1988). Overall diet composition (orders) did not differ between our two study areas, which further supports our view that climatic and biotic conditions at our two study plots are very alike.

In the two agroecosystems studied here, diet composition and abundance of grass-dwelling prey showed a significant positive relationship, whereas a correlation with abundance of ground-dwelling prey was absent. Greig-Smith and Quicke (1983), who estimated food abundance using a vacuum, also failed to find a correlation between diet and ground-dwelling prey. Thus, it can be concluded Stonechat depend principally on grass-dwelling arthropod prey, despite their large prey spectrum and flexible feeding habits (e.g. Cummins and O'Halloran 2002). Central European Stonechats avoid monotonous, intensive cropland; they prefer meadowland, pastureland (Valais, TEC) and the first succession stages of wasteland, such as set-asides or wildflower zones within agro-ecosystems (e.g.

Geneva in the present study, RIC). The fact that the correlation between the trophic niche and grass–prey abundance was stronger at the RIC than at TEC presents a further argument supporting this view. Nest sites were surrounded by grassland at TEC, while the surrounding habitat at RIC encompassed more crops, which may be viewed as suboptimal habitats. As we sampled arthropod abundance along the linear landscape elements where nests were placed (drainage canals and ditches in Valais TEC, set-asides and wildflower strips at Geneva RIC), our estimation of prey abundance encompassed a larger part of the actual foraging ground at the RIC than at TEC since the habitat mosaic was more diverse at the latter study site. This is also reflected by a trend for smaller home ranges at TEC, probably due to a slightly more suitable habitat matrix there. One could argue that our trophic comparisons were performed by considering upper taxonomic units only (prey orders), suggesting therefore that relationships would become weaker at a finer taxonomic resolution. We believe, however, that the present approach is appropriate because the sensory perception—i.e. the "searching prey image"—of Stonechats is not likely to achieve a very fine-grained level of prey discrimination.

Stonechats appeared to preferentially select large prey items. Despite their small body size (12 cm, 14–17 g for adults), on several occasions we observed them catching prey as large as great green bushcrickets (Tettigoniidae) or field crickets (Gryllidae) (note here that large prey items were decapitated by parents prior to feeding chicks). The only noticeable exception for the preference of large prey in this study were small snails; as suggested by Flinks and Pfeifer (1987), snails might represent an important source of calcium for chicks' growth. We also noticed a temporal specialization on other relatively small prey, which may at times occur in large numbers (Cercopidae, Homoptera; RIC), suggesting some flexible foraging strategy.

Reproductive characteristics as a surrogate of ecosystem performance

The overall reproductive performance of Stonechats appeared to be quite similar in the two agroecosystems, with most breeding parameters converging. There were, however, some slight differences. First, the yearly number of breeding attempts in a given territory was significantly larger at TEC than at RIC. Stonechats nest on the ground and are therefore very vulnerable to predation and other sources of disturbance, such as floods and fires, which cause the failure of up to about half of the broods. In 1999, for example, 27.5% of the initiated broods at TEC were destroyed by human-ignited fires and the mowing of the drainage canals. As for every species with exposed

terrestrial nests (Brickle et al. 2000; Siriwardena et al. 2000; Wilson et al. 1997), natural selection has prompted a multiple successive breeding strategy in the Stonechat. Given the high proportion of nest failures, a higher number of breeding attempts at TEC could simply be a compensatory adjustment. Second, the physiological condition (body mass) of chicks at fledging was also slightly higher in both years at TEC. This slight difference might be due to subtle environmental variations: at RIC, suitable Stonechat habitats consist predominantly of the set-aside strips and wildflower areas, themselves within an cropland matrix, whereas at TEC, the habitats surrounding the areas where nests were located are mostly devoted to grassland.

Notwithstanding these slight discrepancies, it is worth noting that most variation in reproductive performance relates to a between-year effect rather than a study-area effect (i.e. agroecosystem type) and lies well within the confidence intervals of the inter-annual variation of the measured parameters. The climatic and meteorological conditions prevailing in 1999 and 2000 differed markedly and are probably the proximate causes of these differences between years.

Our results reinforce the view that revitalizing intensively cultivated agroecosystems by integrating wildflower strips and spontaneous set-asides as ecological compensation areas within the cultivated matrix is a promising option to counterbalance overall farmland biodiversity erosion and promote its restoration. Moreover, set-asides and wildflower strips may also provide real benefits to taxa situated at higher trophic levels along the food chain: the Stonechat population in the newly engineered agroecosystem investigated here seemed to function well, although possible additional negative effects, such as increased predation rate induced by narrow linear elements, may represent a problem (Donald and Vickery 2000; Vickery et al. 2001). The new common agricultural policy of the European Union decided upon in June 2003 decouples subsidies to farmers from the agro-production system, which is a policy that is already in force in Switzerland since 1999. These policies will continue to promote the creation of set-asides. Further economical incentives for the creation of set-asides and wildflower fields may be a promising option not only for the conservation of plant and invertebrate diversity, but also for supporting sustainable populations of farmland insectivorous vertebrates, as exemplified here by the Stonechat (Ormerod et al. 2003).

Zusammenfassung

Vergleichende Nahrungsökologie und Brutbiologie von Schwarzkehlchen S. torquata in ökologisch aufgewerteten, intensiv bewirtschafteten und traditionell genutzten Agrarlandschaften

Das Anlegen von Brachen und Blumenwiesenstreifen in intensiv bewirtschafteten Agrarlandschaften ist eine effiziente Strategie zur Erhöhung der Biodiversität. Es ist aber weitgehend unbekannt, ob die ökologische Leistung von solchen Anlagen vergleichbar ist mit derjenigen einer traditionell, extensiv bewirtschafteten Agrarlandschaft. Um diese Frage zu klären, verglichen wir während zwei Jahren die Nahrungsökologie und die Brutbiologie von Schwarzkehlchen (S. torquata) in zwei unterschiedlichen Agrarlandschaften in der Schweiz. Die erste war intensiv bewirtschaftet, wies aber viele ökologische Ausgleichsflächen auf (INT), die zweite war traditionell, extensiv bewirtschaftet (EXT). Die Nestlingsnahrung, die zum grössten Teil aus Heuschrecken, Schmetterlingslarven und Käfer bestand (>80% Biomasse), wie auch das Nahrungsangebot unterschied sich nicht zwischen INT und EXT. Der Bruterfolg gemessen als Anzahl Flügglinge pro Territorium und Jahr unterschied sich auch nicht zwischen INT und EXT, obwohl Schwarzkehlchen in EXT mehr Bruten aufzogen. Die Variation der Brutparameter zwischen INT und EXT war ähnlich gross wie die Variation zwischen den Jahren. Dies deutet darauf hin, dass zufällige Umweltschwankungen einen ähnlich grossen Effekt auf den Bruterfolg hatten, wie der Typ der Agrarlandschaft. Diese Resultate zeigen, dass die Anlage von Brachen und Wiesenblumenstreifen in intensiv bewirtschafteten Agrarland nicht nur die Biodiversität erhöhen, sondern auch zu funktionsfähigen Populationen von Wirbeltieren auf höheren trophischen Stufen beitragen können.

Appendix 1

Table 3 Abundance of prey (mean item frequency and mean biomass of 40 invertebrate categories) in the home ranges of Stonechat pairs in TEC (Valais, $n = 4$) and RIC (Geneva, $n = 5$) as estimated by two sampling techniques (hand-netting for grass-dwelling prey; pitfall trapping for ground-dwelling prey)

Category	Grass-dwelling prey				Ground-dwelling prey			
	Frequency		Biomass (mg)		Frequency		Biomass (mg)	
	TEC	RIC	TEC	RIC	TEC	RIC	TEC	RIC
Gastropoda	43.3	15.2	3,886.0	387.4	20.7	81.2	1,090.0	1,261.9
Opiliones	0.0	0.0	0.0	0.0	0.7	3.0	0.9	16.8
Thomisidae	1.3	1.4	1.4	4.3	3.0	12.0	14.8	33.0
Araneae alia	5.0	3.6	8.0	6.6	33.3	152.8	106.8	435.3
Isopoda	0.0	0.0	0.0	0.0	126.0	277.8	709.7	1,391.8
Chilopoda	0.0	0.0	0.0	0.0	2.0	2.6	14.3	3.2
Diplopoda	0.0	0.0	0.0	0.0	7.7	38.8	225.6	957.4
Collembola	0.0	0.0	0.0	0.0	11.0	51.6	1.2	3.4
Tetrigidae	0.5	1.2	4.7	9.7	0.0	0.6	0.0	5.7
Acridoidea	58.5	32.4	967.5[a]	490.1[a]	1.7	2.8	28.9	19.4
Tettigoniidae	2.5	1.4	181.2	25.0	0.0	1.8	0.0	1.8
Gryllidae	0.0	1.4	0.0	5.3	6.7	0.2	4.2	0.0
Mantis eligiosa	0.5	0.0	4.4	0.0	0.0	0.0	0.0	0.0
Dermaptera	0.0	0.6	0.0	6.1	1.0	8.0	8.5	19.5
Heteroptera	32.0	25.4	70.7	84.8	33.0	67.8	77.7	161.5
Auchenorrhyncha	131.8[a]	294.4[a]	79.6	935.6[a]	7.0	19.4	7.6	25.7
Sternorrhyncha	0.0	0.6	0.0	0.2	4.3	1.2	1.8	0.2
Neuroptera	3.5	0.8	6.6	1.0	0.3	0.0	0.0	0.0
Noctuidae	0.3	0.2	4.8	10.2	0.0	0.2	0.0	14.4
Sesiidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lepidoptera (imagos) alia	1.5	5.2	3.9	6.9	0.0	0.0	0.0	0.0
Lepidoptera (larvae)	1.5	2.4	3.9	23.1	2.3	2.8	57.6	28.3
Asilidae	1.0	0.0	4.4	0.0	0.0	0.0	0.0	0.0
Diptera alia (>1 cm)	1.8	7.0	4.2	10.5	0.3	2.8	2.0	14.0
Diptera alia (<1 cm)	118.8[a]	42.2	60.8	24.3	27.7	19.0	35.2	31.4
Formicidae	38.0	27.6	24.2	11.8	193.3[a]	262.0[a]	134.1	116.6
Hymenoptera alia (>1 cm)	1.3	5.2	6.9	27.0	0.7	2.6	11.9	114.7
Hymenoptera alia (<1 cm)	6.5	20.0	3.2	13.8	4.3	1.2	3.5	1.7
Carabidae	0.0	7.0	0.0	61.3	128.0	431.0[a]	2,523.8[a]	5,347.6[a]
Silphidae	0.0	0.0	0.0	0.0	272.0[a]	0.2	6,867.3[a]	12.2
Staphylinidae	0.0	0.2	0.0	0.6	44.7	36.2	155.3	127.8
Scarabaeoidea	0.0	0.0	0.0	0.0	1.3	1.4	12.1	6.7
Histeridae	0.0	0.0	0.0	0.0	2.7	2.6	12.8	89.6
Elateridae	1.5	0.4	12.2	0.2	15.7	5.2	204.2	45.3
Cantharidae	2.0	0.8	10.6	2.9	0.0	0.2	0.0	5.5
Coccinellidae	8.0	5.8	12.1	9.2	1.0	3.6	1.2	4.1
Dermestidae	0.0	0.0	0.0	0.0	13.3	28.6	26.7	231.5
Oedemeridae	0.3	3.4	0.3	6.5	0.3	0.0	0.3	0.0
Curculionidae	7.8	7.0	13.1	15.9	19.3	2.0	63.5	15.5
Coleoptera alia	19.3	76.8	29.7	35.1	31.0	16.2	77.3	53.1
Total	488.0	589.6	5,404.0	2,215.2	1,016.3	1,539.4	12,480.8	10,596.6

Invertebrate items smaller than 3 mm body length were not considered. The mass of Gastropoda includes the mineral mass (shell)

[a] Dominant categories

Appendix 2

Table 4 Summary statistics for breeding parameters (mean, SD, sample size and range) with respect to study site and year

Variable	Year	TEC				RIC			
		Mean	SD	n	Min–Max	Mean	SD	n	Min–Max
Clutch size	1999	4.88	0.9	26	3–7	5.27	0.7	15	4–6
	2000	5.16	0.9	37	2–7	5.06	0.7	31	4–6
Chick mass (g)	1999	15.60	1.3	12	13.9–18.4	14.19	0.9	7	12.8–15.3
	2000	16.06	0.5	21	15.0–17.0	15.38	0.8	18	13.3–16.3
Chick tarsus (mm)	1999	22.06	0.7	13	20.9–23.1	21.95	1.0	8	20.0–22.9
	2000	22.57	0.6	22	21.0–23.6	22.34	0.5	17	21.5–23.2
Breeding attempts/territory	1999	2.04	0.8	25	1–4	1.59	0.5	17	1–2
	2000	2.62	0.8	21	1–4	1.96	0.7	23	1–3
Fledglings/territory	1999	2.72	2.7	25	0–7	2.35	2.2	17	0–6
	2000	4.00	3.1	21	0–12	3.13	2.5	23	0–7

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