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Summaries of diploma and PhD theses (1999)

Diploma theses (12)

Effects of management on seed predation in wildflower strips

Einfluss der Bewirtschaftungsform auf den Samenfrass in Buntbrachen; 56 pp.

SERAINA BASSIN

1 In summer 1999, seed predation on *Prunus avium* and three arable weeds (*Agrostemma githago*, *Centaurea cyanus*, *Camelina sativa*) was investigated in wildflower strips within arable land in the Klettgau area (northern Switzerland). The five strips had been sown with a standard wildflower mixture six years ago. The focus of the study was on three common management methods (fallow, mowing, harrowing) that might have affected vegetation and fauna of the study sites. Seeds were presented in selectively accessible dishes to determine which animal guild (molluscs, insects, rodents, birds) was responsible for the differential losses in the test species, and how these losses were affected by management.

2 Each site was divided in nine plots which had a length of 19 m; the plots were randomly assigned to the different treatments in late winter 1998/99, with three replicates per site. In the plots either feeding dishes (to determine predation rates) or Longworth life traps (to determine rodent abundance) were placed in fixed positions. The seeds of the test species were presented in individual dishes; seed losses were recorded for seven days in four experiments from June to August.

3 Management had only a moderate effect on the structure of the vegetation. In summer only two vegetation types could be distinguished: a more or less closed canopy in the fallow and mown plots, and a rather sparse plant cover in the harrowed plots. A total of 101 plant species were identified in the wild-

flower strips; in most plots the vegetation was dominated by *Tanacetum vulgare* and *Agropyron repens*. In the harrowed plots annual weeds had established, among others *Centaurea cyanus*, *Matricaria chamomilla* and *Papaver rhoeas*.

4 Rodents and slugs were the main seed predators. Seed predation by insects and passerine birds was negligible. Rodents strongly preferred *Centaurea cyanus*, whereas more than 80% of the seeds of *Camelina sativa* were destroyed by slugs.

5 After seven days seed losses amounted to 43–51% in *Camelina sativa* and 23–25% in *Centaurea cyanus*, whereas seeds of *Agrostemma githago* were least preferred (10–12%). This rank order of seed preference was similar for the three management types and both study periods. The losses of seeds of *Centaurea cyanus* and *Prunus avium*, which are mainly taken by rodents, were independent of management. Predation of *Camelina sativa* was significantly reduced in harrowed plots.

6 In August rodent abundance was about four times higher than in June. In general, more individuals of *Microtus arvalis* were recorded than of *Apodemus flavicollis* or *A. sylvaticus*. *Microtus arvalis* was stronger affected by management and avoided the harrowed plots, whereas *Apodemus* spp. were more evenly distributed. The results of the life trapping suggested that *Apodemus flavicollis* and *A. sylvaticus* were the main species which caused seed losses in *Prunus avium* and *Centaurea cyanus*.

Seed predation at forest edges – spatial patterns and potential explanations

Ursachen für das räumliche Muster des Samenfrasses an Waldrändern; 65 pp.

MARCO BUSCHOR

1 This study focuses on the effects of forest edges on the intensity of postdispersal seed predation. The three main objectives are to investigate (1) whether there is an edge effect or not, (2) to what extent this effect is influenced by the structure of the forest edge, and (3) which are the reasons for the observed edge effect. The study also determines the identity and distribution of the animal species responsible for seed predation.

2 The research was conducted in twelve forest sites near Hemmental (northern Switzerland) from May to August 1999. Six of the forest edges had a luxuriant shrub vegetation, whereas in the other six the shrubs had been recently cut. In each of the study sites three parallel transects were laid out from the forest edge into the forest interior. For studying seed predation and vegetation structure, six plots were established along each transect, at 1, 3, 6, 12, 25 and 50 m from the edge line. The rates of predation were investigated in experimental feeding trays with seeds of the fleshy-fruited species *Prunus avium* and *Viburnum lantana*. The effect of distance to the forest edge was analysed with multiple logistic regressions. Experiments with selectively accessible seed dishes and life traps were used to identify the relevant seed predators. The data on changes in vegetation structure along the transects were

used to investigate the habitat preferences of the predators and to explain the observed edge effect.

3 For both study species (*Prunus avium*, *Viburnum lantana*) seed predation was significantly higher near the forest edge at the sites with an undisturbed shrub belt. At sites with reduced shrub cover no edge effect on seed predation was found. Clearly, the edge effect on seed predation was at least partly affected by the type of forest edge.

4 Changes in the cover of the shrub layer from the edge line into the forest were the main determinants for the intensity of seed removal from the experimental dishes. Predation was highest under dense shrub cover.

5 The main predators of seeds were *Apodemus flavicollis*, *A. sylvaticus* and *Clethrionomys glareolus*, whereas no predation by molluscs or insects was observed. Rodent abundance was highest under dense shrub canopy and this may explain the observed spatial patterns in seed predation.

6 The results of this study reveal the importance of the edge structure for the observed edge effect, and they contribute to a better understanding of the mechanistic reasons for the edge effect. As in related studies in temperate Europe the thesis shows that small rodents are the main predators for seeds of fleshy-fruited species.

Burglary at daylight: Nectar robbing in *Melittis melissophyllum* L.

Einbruch bei Tag: Nektarräuberei bei Melittis melissophyllum L.; 60 pp.

MARCEL GÄCHTER

1 *Melittis melissophyllum* produces the biggest flowers among the Lamiaceae in Switzerland.

Due to the long corolla tube, it is mainly pollinated by the long-tongued *Bombus hortorum*

and by moths. Short-tongued bumblebees, e.g. *Bombus terrestris* and *Bombus lucorum*, can only reach the nectar by biting a hole through the corolla near the nectarium to suck nectar. The diploma thesis investigates the influence of nectar robbery on seed set, variation in robbing intensity among populations, the possibility of selfing and the question whether floral traits are under selection or not.

2 Nectar robbery lessened seed set, the number of mature seeds, and in one population mean seed weight. However, ants could have an even worse effect on the plant than bumble bees. They not only seemed to deplete nectar but also nibbled at the developing seeds of many flowers.

3 The frequency of robbed flowers varied among populations. In the Aargauer Jura the nectar robbing intensity was significantly lower than at Uetliberg and Oensingen. It is

suggested that the food supply during the flowering period of *Melittis melissophyllum* was less diverse in the latter two sites.

4 Due to inappropriate weather conditions only a small test for selfing could be carried out. The results suggest that *Melittis melissophyllum* is self-incompatible, but further investigations are needed to check this hypothesis.

5 No correlation was found between seed set and the 12 measured floral traits. The examined floral characteristics seem therefore not to be under direct selection. Experiments over multiple years, however, would be necessary. Further investigations should show whether seed set in *Melittis melissophyllum* is limited by pollination or by resources. In the latter case, selection for traits which increase the acquisition of essential resources may be more important than selection for higher pollination success.

Population structure of the mistletoe (*Viscum album*): is there any gene flow among the subspecies?

Populationsstruktur der Mistel (Viscum album): Gibt es Genfluss zwischen den Unterarten? 96 pp.

HANNES GAMPER

1 *Viscum album* L. (Viscaceae) is a hemiparasite growing on woody gymno- and angiosperms. As a dioecous plant the mistletoe possesses a reproductive system of obligate allogamy. The white pseudoberries, which ripen in winter, are dispersed endo- and epizoochorously by different species of passerine birds. This study investigates the population structure of mistletoe, particularly with regard to potential gene flow among the three subspecies *V. album* ssp. *album*, *V. album* ssp. *abietis* and *V. album* ssp. *austriacum*. The determination of the subspecies is mainly based on the corresponding host tree species.

2 Leaves were sampled from 30 individuals of each subspecies along the eastern shore of

Lake Uri (Central Switzerland). For a molecular analysis of the three subspecies I chose biparentally inherited nuclear markers, i.e. RFLPs of the ITS region and microsatellites. A non-coding fragment from the Large Single Copy of the chloroplast genome, varying in length among the subspecies, and a microsatellite were used as maternally inherited chloroplast markers.

3 The results of the molecular genetic analysis provided clear evidence for gene flow between the subspecies *V. album* ssp. *album* and *V. album* ssp. *austriacum*. No direct indication of gene flow, based on a special genotype, was detected for *V. album* ssp. *abietis* and *V. album* ssp. *austriacum*. However, absolute genetic

isolation of these two subspecies was doubtful based on the fixation indices F_{ST} . Distribution of maternally and biparentally inherited markers indicated the existence of a set of hybrids within the subpopulation of mistletoes with deciduous tree hosts.

4 Nine out of 92 individuals were descendants of hybrids. Either they were individuals of an advanced filial generation or they originated from repeated backcrosses with one of the parents, as in none of these individuals the pure nuclear type of the ITS region fitted with the type of chloroplast. In two of the nine cases the ITS type did not match with the host species type. In all these cases the monomorphic ITS locus probably originated either from recombination or from

concerted evolution. Surprisingly, all investigated loci had lost the genetic material of the mother plant.

5 All individuals whose type of chloroplast did not "fit" the particular host tree on which they had become established must have been transported by birds since chloroplasts are inherited maternally, unless they are descendants of hybrids or the mother plant has previously switched the host. The difference in frequency between two different types of descendants of hybrids suggests a relatively frequent dispersal of the pseudoberries among the different host tree species. However, based on the present results host switching without previous hybridisation appears to be extremely rare, if it occurs at all.

The influence of proximity to forest on the diversity of heteroptera in extensively cultivated meadows

Einfluss der Distanz zum Wald auf die Diversität der Heteropterae in extensiv bewirtschafteten Wiesen; 73 pp.

MICHAEL JUDEX-RATHI

1 This thesis investigates how the distance of an extensively cultivated meadow from forest influences the diversity of heteroptera in meadows. The research was carried out near Ruswil-Buttisholz in the canton of Lucerne (Switzerland). During 1998, insects were collected from 31 meadows using the sweep net method. The same method was used again in 18 of the 31 meadows at the end of May and in July 1999.

2 A total of 70 species of heteroptera were found in the samples from the 31 sites in 1998 and from the 18 sites in 1999. The most common species were *Lygus rugulipennis* (Poppius 1911) and *Notostira erratica* (Linnaeus 1758). In 1998, 54 species were caught in the sub-set of 18 sites, of which 50% were single individuals. The samples from 1999 contained 136 in-

dividuals and 36 species. At all 18 sites the plant species composition indicated nutrient-rich conditions.

3 The results of univariate data analysis were not significant because the numbers of species and individuals were insufficient for an appropriate evaluation of all sites. Combining the samples from the two years improved the results only marginally. However, strong similarities between the sites were found, especially amongst those which were situated remotely from the forests. Many species had high turnover rates.

4 Correspondence analysis revealed significant differences between the years. Canonical correspondence analysis demonstrated a significant correlation between the number of heteroptera species and the abundance of co-

niferous trees in the adjacent forest stands. Additional environmental factors seemed to be important in 1999. The number of legume species in the meadows explained the largest fraction of the total variation in species richness, followed by the distance to the nearest forest. The average light indicator value of the vegetation and the distance to the nearest forest also correlated significantly with the species composition and abundance of heteroptera.

5 In the ordination for 1999, sites could be split into two distinct groups: those at the forest edge and more remote meadows. A further split of the second group into “sites with

forests” and “isolated sites” could also be recognised. The average humidity and nitrogen indicator values of the vegetation separated the three groups almost completely.

6 The position of most species in the ordination could be easily interpreted. A few species were apparently confined to meadows. Most other species appeared associated with woody plants or forest-edge habitats. A few species seemed to prefer meadows with rare plants. The effect of the number of leguminous species on the number of heteroptera species could not be explained with habitat preferences, but the effect of the distance of sites to forests could be understood in this way.

Spatial habitat modelling as exemplified by the yellowhammer *Emberiza citrinella*

Räumliche Habitatmodellierung am Beispiel der Goldammer Emberiza citrinella; 207 pp. + Appendix and maps

PHILIPP KÄSTLI & BJÖRN REINEKING

1 A quantitative description of the relationships between landscape characteristics and species presence is of substantial interest in both ecology and landscape planning. Taking the yellowhammer (*Emberiza citrinella*) as an illustrative example, this study investigates three crucial aspects for the successful application of habitat models in landscape management: (1) selection of landscape characteristics that are used to describe habitat preferences, (2) analysis of habitat associations at different spatial scales, and (3) impact of different social factors on the habitat of the focal species.

2 The advantages and disadvantages of data-driven and data-independent selection of habitat variables (i.e. data mining vs *a-priori* approaches) are described, and four data-mining methods are presented. These are PCA-based variable selection, stepwise variable selection, evolutionary selection algo-

rithm-based variable selection and “group-wise” variable selection. Data mining proves inadequate to assess the significance of specific variables. However, data mining is a useful instrument for generating hypotheses if there is a lack of well-established theories. The evolutionary selection algorithm used proves to be a promising method for efficient and effective data mining.

3 The habitat association of yellowhammers was investigated in five areas in northern Switzerland. The main investigation areas were a 33-km² area in the Grosses Moos (BE) and two areas in the Klettgau area (SH), i.e. Langfeld (2.35 km²) and Widen (5.3 km²). Yellowhammer densities varied between 2.5 pairs km⁻² (Grosses Moos) and 14 pairs km⁻² (Langfeld). Habitat preference at the home range scale (a 40-m radius from the estimated home range centre) was modelled using multiple logistic regression. The best out of four

models specified *a priori* – each with eight or nine landscape variables – used exclusively information that can be extracted from aerial photographs and maps. This model correctly predicted the presence/absence of yellowhammers in 82% of the cases; the sensitivity, i.e. the proportion of correctly classified yellowhammers, was 76% (Grosses Moos) and 79% (Klettgau). The most important variables at the home range scale were hedgerows and woodland, the distribution of field sizes, and crop diversity. Rowcrops correlated negatively with yellowhammer presence, while cereals and grassland had no significant influence at the home range scale. The spatial autocorrelation of yellowhammers was highly significant.

4 At the larger spatial scale the habitat association of yellowhammers was analysed by modelling yellowhammer presence in 11-, 16- and 25-ha plots using multiple Poisson regression. Again, land use diversity correlated positively with yellowhammer occurrence. The degree to which cropland was

weeded and the floristic diversity of grassland correlated significantly with yellowhammer occurrence at these larger spatial scales. At the 25-ha spatial scale no positive correlation of yellowhammers with hedgerows was found. The density of yellowhammers in Langfeld, changing from 9.8 to 14 pairs km⁻² over a period of three years, had no significant influence on the selectivity of habitat choice.

5 The laws on nature protection and landscape planning largely determine the yellowhammer habitat. Additional important influences are agricultural practice and landscape change following melioration. The execution of the law on nature protection and hunting is characterised not so much by its importance but rather by its ease of optimisation. The “*ökologische Ausgleich*” (ecological compensation) as practised under the “*Direktzahlungsverordnung*” (regulation on financial compensation for ecological measures in agriculture) appears to be of minor importance to the yellowhammer in the investigated areas.

Ecology and conservation biology of a large rainforest skink (*Egernia major*, Scincidae)

Ökologie und Artenschutz einer grossen Regenwaldeckse (Egernia major, Scincidae); 88 pp.

ANJA KLINGENBÖCK & KONRAD OSTERWALDER

1 The land mullet, *Egernia major*, is one of the largest of all Australian skinks and ranks amongst the largest 5% of lizard species in the world. It is distributed in rainforest areas along the central eastern coast of Australia. Although the restriction to rainforests might threaten its long-term survival (75% of the rainforest area has been lost in Australia), there has been no previous scientific study of this species in its natural habitat.

2 To study the land mullet's patterns of habitat use, movements and thermoregulation, we

surgically implanted miniature temperature-sensitive radio transmitters into 12 adults from a population living at Barrington Tops 250 km north of Sydney, NSW. The animals were monitored over a seven-week period in spring (October to December). Additionally, we observed free-ranging animals for a total of 14 hours, to obtain data on feeding behaviour and social interactions.

3 Highest densities of land mullets occurred in forests with intermediate canopy cover (vs. open eucalypt forest or dense-canopy rainfor-

est) since here ground cover and large hollow logs provided suitable refugia and sufficient sunlight penetrated to the ground to allow basking. Thus, the species primarily uses ecotonal areas at the fringe of rainforest clearings.

4 The activity of radio-tracked animals was centred on large hollow logs on the forest floor. The home range of each animal consisted of a clearly defined core ($2253 \pm 1909 \text{ m}^2$) containing one to several such logs plus an outer foraging area ($10,951 \pm 8149 \text{ m}^2$), less frequently visited. The lizards moved on average a daily straight-line distance of $51.2 \pm 19.0 \text{ m}$; the actual distance moved (including meandering) was approximately 100 m per day. Net displacement from one day to the next averaged $24.7 \pm 16.0 \text{ m}$. Mean home range areas and distances travelled were similar in the two sexes, but females were significantly more likely to make occasional long-distance moves away from their normal home range.

5 The land mullet is omnivorous with both plant and animal matter in its diet. Helio-

thermy enables it to maintain an average temperature of $32.8 \pm 6.3 \text{ }^\circ\text{C}$ throughout most of its activity time (12–15 h) even in relatively cool weather. Unlike virtually all other reptiles studied, land mullets live in social groups of several adult males and females plus juveniles of all age classes. Home ranges of different groups show little overlap, whereas home ranges of individuals within the same group overlap almost completely.

6 Because of its omnivory and utilisation of ecotonal habitat, the land mullet's conservation status appears to be relatively secure over much of its range. Human disturbance, such as timber harvesting, clearing and road construction, is deleterious in some respects, but also enhances opportunities for basking and dispersal. However, the species' dependence on large hollow logs is a point of potential vulnerability. Land-use practices that do not maintain an adequate recruitment of such logs might ultimately exclude the land mullet from otherwise suitable habitats.

Educational Unit "The Diversity of Life"

Unterrichtseinheit "Die Vielfalt des Lebens"; 60 pp.

NICK MAROLF

1 The objective of this diploma thesis was to develop an educational unit on biodiversity, geared to the 9th to 11th grade primarily of Swiss schools. The 60-page unit is divided up into background information, teaching aids and worksheets.

2 The educational unit sets an emphasis on Swiss biodiversity and tries to convey an optimistic view about environmental conservation. Finding the right balance between optimism on the one hand and the urgency of proactive action on the other hand has proven to be a difficult task. Attention has also been paid to the balance between scientific exact-

ness and an easily understandable language that reaches all pupils.

3 During the four months provided to work on the diploma thesis a final draft has been compiled and subsequently revised by several scientific and educational experts. The remaining steps to take before the unit can be published consist of as a series of test runs with school classes and layout work.

4 The draft was submitted and accepted by the Klett Verlag in February 1999, and at the same time financing was offered by the Swiss Agency for the Environment, Forests and Landscape (SAEFL/BUWAL). How-

ever, in the meantime negotiations between the parties involved have proceeded very

slowly and the unit has not yet been published.

Pollination and population biology of *Ophrys sphegodes* s.l.

Bestäubungs- und Populationsbiologie von Ophrys sphegodes s.l.; 48 pp.

CHARLOTTE SALZMANN

1 The status of many taxa within the genus *Ophrys* (Orchidaceae) is unclear, partly due to their pollination system. Therefore, this study investigated the two species *Ophrys araneola* and *Ophrys sphegodes* within the *O. sphegodes*-complex with pollination experiments in the field. Flowers of *O. araneola* were pollinated with pollen of the same individual (selfing), of a different individual of the same species (outcrossing), and of *O. sphegodes* (inter-specific pollination).

2 The seed set of *O. araneola* was pollen-limited. Hand-pollinated flowers produced more seeds than flowers that were open-pollinated.

3 The quality of the seeds differed significantly between the different pollination

treatments. Out-crossed and inter-specifically pollinated flowers produced more fertile embryos than open and self-pollinated flowers.

4 Neither seed set nor total seed mass per capsule were reliable measures of reproductive success. More important was seed fertility which correlated with the average seed mass.

5 The interspecific crosses with *O. sphegodes* revealed compatibility between the two species.

6 An analysis of the population structure did not show any correlation between genetic similarity and spatial distance in a population of *O. araneola*.

Vegetation survey 1999 on the islands Cousin and Cousine, Seychelles

Vegetationserhebung 1999 auf den Inseln Cousin und Cousine, Seychellen; 308 pp.

EVA SCHUMACHER & MATTHIAS WÜTHRICH

1 The islands Cousin and Cousine are part of the Seychelles archipelago, the only group of tropical granitic islands in the world. In the early 19th century the two islands were altered profoundly by planting coconuts (*Cocos nucifera*). In addition, tourism has become important on Cousine island. Currently, the main management objective for the islands is to preserve the threatened endemic land birds. This objective calls for scientific investigations of the ecological status of the vegetation.

2 To assess the vegetation comprehensively and efficiently, we applied the "trail-transect" survey method, investigated some sites more

intensively, and established permanent monitoring plots. The ecological potential and the state of invasion of alien species were assessed by their "prominence value" (combining frequency and abundance) and "importance value" (combining frequency, density and dominance). Changes in habitat potential were derived from the analysis of the stand structures and by extrapolating data from the "Oxford Leading-Tree System".

3 The most prominent tree species on the flat parts of Cousin island were *Pisonia grandis*, *Ochrosia oppositifolia* and *Morinda citrifolia* (in decreasing order). On the hills these were

Euphorbia pyrifolia, *Ficus lutea* and *Ficus reflexa*. The most prominent species for the whole island was the indigenous *Pisonia grandis*. *Pisonia* supported large colonies of seabirds and showed highly efficient regeneration. Due to its high growth rate and its successful regeneration, *Pisonia* seems to be able to invade open grassland areas and coconut plantations.

4 *Cocos nucifera* was not particularly prominent in the tree layer any more. Nevertheless, it was still the most prominent species among saplings, so that it could inhibit the natural regeneration of a native forest. This should be prevented by chopping down the saplings. The native creeper and climber *Canavalia cathartica* had advanced in many parts of the plateau and appeared to be invasive. *Canavalia* was found to climb up even tall trees and to cover them entirely, which should also be prevented by management. *Ochrosia oppositifolia* was the tree species expected to become co-dominant in the future; the plateau forests will probably develop to a *Pisonia-Ochrosia-Morinda* community.

5 The most prominent tree species on Cousine were *Pisonia grandis*, *Ficus reflexa*, *Euphorbia pyrifolia*, *Morinda citrifolia*, *Cocos nucifera* and *Pandanus balfourii* (in decreasing order). The status of *Pisonia* and *Cocos* was similar to Cousin island. The vegetation of the hills appeared to be relatively stable, whereas changes are expected to happen on the plateau. The re-establishment of native coastal woodland should be the principal management aim for this island.

6 As long as the management of Cousin island prevents introduction of alien species such as Cinnamon (*Cinnamomum verum*) or diseases such as the Takamaka-wilt and keeps to its management goals, it will maintain the integrity of the island as a place rich in biodiversity.

7 With the establishment of new tourist facilities on Cousine island management faces a new challenge regarding nature conservation. A native island ecosystem as a place rich in biodiversity might promote sustainable tourism and would have high conservation value at the same time.

Comparative population structure of a host (*Pinus sylvestris* L.) and its parasite (*Viscum album* L. ssp. *austriacum*)

Vergleichende Populationsstruktur eines Wirts (Pinus sylvestris L.) und seines Parasiten (Viscum album L. ssp. austriacum); 50 pp.

TANJA STUDER

1 The mistletoe, *Viscum album* L., is a dioecious hemiparasite and lives epiphytically on a wide range of host trees. *Viscum album* is insect-pollinated and its seeds are dispersed by birds. Based on host specificity, three subspecies are distinguished in Europe, i.e. *V. album* L. ssp. *album* (on deciduous trees), *V. album* L. ssp. *abietis* (Wiesb.) Abromeit (on fir), and *V. album* L. ssp. *austriacum* (Wiesb.) Vollmann (on pine). In this study, the popula-

tion structure of both the mistletoe on pine and its primary host, the Scots pine, *Pinus sylvestris* L. were investigated and compared with each other. *Pinus sylvestris* is wind-pollinated and the seeds are also dispersed by wind.

2 Four populations of both host and parasite from different parts of Switzerland were investigated. The genetic population structure of the host and parasite were analysed using microsatellites as molecular markers. Three

nuclear loci and one chloroplast locus were used for each species.

3 All loci were polymorphic, except the chloroplast locus of *V. album*. The genotypes of both host and parasite population showed deviation from Hardy-Weinberg equilibrium. This was caused by an excess of homozygous genotypes in both systems, leading to a relatively high inbreeding coefficient ($RHO_{IS} = 0.140$ for *V. album*, and $RHO_{IS} = 0.216$ for *P. sylvestris*). Possible reasons include the small sample number, inbreeding, a bottleneck, founder effects and the Wahlund's principle.

4 The host populations were genetically not differentiated ($RHO_{ST} = -0.005$), whereas the parasite populations were very much so ($RHO_{ST} = 0.456$). Only the mistletoe population pair Brig-Martigny was not differentiated ($RHO_{ST} = -0.009$). Using the private alleles method based on nuclear loci, 4.63 migrants

per generation were estimated for host populations and 0.04 migrants per generation for parasite populations. No isolation by geographical distance was found (Mantel test, $P = 0.63$ for *P. sylvestris*, and $P = 0.75$ for *V. album*). The differences in population structure between host and parasite could be attributed mainly to their different pollination and dispersal strategies. The effective population size or the postglacial history could also be responsible for these differences.

5 The data suggest that *P. sylvestris* has had an evolutionary advantage over the parasite *V. album*, and that *P. sylvestris* shows some resistance against sympatric parasite populations. On the other hand, one would expect that *V. album* shows the highest virulence against allopatric host populations and has therefore an evolutionary disadvantage over sympatric host populations.

“Oligotrophication of fen meadows” – effect of an additional mowing in June on the vegetation

“Oligotrophierung von Streuwiesen” – Auswirkungen einer zusätzlichen Juni-Mahd auf die Vegetation; 55 pp.

ALVARO ZORZI

1 Fen meadows in Switzerland are traditionally mown in September–November. In past years, most lowland fen meadows have become more productive due to nutrient inputs from farmland, atmospheric deposition or inadequate management. Eutrophic fen meadows are usually poorer in species diversity than oligotrophic ones, and thus, of lesser interest for nature conservation. Therefore, it has been often tried to return eutrophic fen meadows to an oligotrophic state by mowing more frequently.

2 This study investigates the effects of additional mowing in June during four to five years on species composition, above-ground

phytomass and its N and P contents in three moderately eutrophicated fen meadows near Zurich. Experimental plots of 100 m² each, all mown every year in September (traditional management), were attributed to one of three treatments in a randomized block design: additionally mown in June every year (six plots), additionally mown in late June every two years (five plots), and never mown in June (control, six plots). Treatments started in 1995/1996. Vegetation relevés were carried out in June 1999 in all plots, and phytomass samples were taken in late June and late August 1999.

3 Plots additionally mown in June generally had higher species richness and higher even-

ness than the control plots, but the effect was only significant for plots mown in June every two years. Several dominant tall grass or forb species appeared weakened by additional mowing in June, which might explain the higher species richness in the treated plots.

4 Above-ground biomass production was slightly reduced after four to five years of additional mowing in June, but the dry mass of 550–650 g m⁻² was still higher than values measured in oligotrophic fen meadows (350–400 g m⁻²). Thus, at least in the short term, additional mowing in June could not return the yield of the investigated fen meadows to the desired level.

5 The N and P contents in the above-ground plant parts of several dominant plant species (determined in June) differed only slightly and not consistently among treatments, even though some of these species had been weakened by the additional mowing. Nutrient contents were therefore unsuitable indicators for the effect of mowing on individual plant species.

6 Overall, the results indicate that additional mowing in June is suitable for enhancing botanical diversity in eutrophicated fen meadows, but substantial effects can only be expected after more than five years of management.

PhD theses (6)

The influence of red deer (*Cervus elaphus* L.) upon a subalpine grassland ecosystem in the Swiss National Park

Der Einfluss von Rotwild (Cervus elaphus L.) auf subalpinen Grünland im Schweizer Nationalpark; 93 pp.

GERALD ACHERMANN

1 This thesis focuses on three questions regarding the influence of free ranging red deer (*Cervus elaphus* L.) on a subalpine grassland ecosystem in the Swiss National Park (SNP): (1) What changes have occurred in tall-herb communities since the cessation of agricultural management and what has been the role of red deer in these changes? (2) What factors affect the spatial distribution of nocturnal grazing by red deer on subalpine grasslands? (3) Is there a nutrient transfer from the preferred grazing sites to the surrounding forest, and if so, what are potential consequences for the vegetation?

2 Long-term vegetation change in subalpine tall-herb communities in the SNP was analysed using a total of 93 relevés conducted on

nine permanent plots at regular intervals over a period of up to 80 years. After the abandonment of agriculture in the SNP around 1914, the standing crop of tall-herb vegetation increased rapidly, but no major changes in the species composition occurred until 1940. Since 1940 the vegetation has changed on five out of nine plots from a tall-herb community (dominated by *Aconitum compactum*, *Chenopodium bonus-henricus*, *Urtica dioeca* or *Rumex alpinus*) to a short-grass community dominated by *Festuca rubra*. Another three plots have changed from tall-herb stages to a tall-grass stage dominated by *Deschampsia caespitosa*, and only one plot persists in the tall-herb stage with *Aconitum compactum* as the most abundant species. The transition to grassland

dominated by *Festuca rubra* took place between 1940 and 1960, the same period when the summer population of red deer increased from 4 to 8 individuals per km² of productive area in the SNP. It is likely that the change in the vegetation reflects the increased grazing pressure of red deer.

3 The spatial distribution of nocturnal grazing by red deer was studied on the subalpine grassland "Alp Stabelchod" in the SNP. Direct observations of red deer were based on scan-samplings at every full hour of 54 nights during summer in 1998. The data were interpreted in terms of a range of environmental factors including structure and composition of vegetation, former agricultural management, phosphorus content of the soil and several variables related to the vigilance behaviour of red deer. The structural variable "short green" explained over 45% of the variation in the spatial distribution of grazing hinds. This variable was highly positively correlated with the phosphorus content of the soil and with the presence of *Aconitum*, *Deschampsia*, *Trisetum* and *Festuca*. Eighty years after the end of agricultural use, the pattern of nutrients in soil previously created by pasturing, mowing and irrigating still seemed to be the main factor determining the spatial pattern of grazing hinds. Variables related to vigilance and protective behaviour (e.g. disturbance and overview) were the second most important set of variables explaining the spatial pattern of habitat use by grazing hinds.

4 On the same subalpine grassland a grid of 268 plots (20 m x 20 m) was set up to investigate the spatial patterns of vegetation, soil nutrients, grazing red deer, and faeces. Total phosphorus in the soil was investigated because P is relatively immobile in the soil but can be translocated as a result of the feeding and excretion behaviour of herbivores. The estimated soil phosphorus pool (0–10 cm

depth) varied between 200 and 1100 kg P ha⁻¹. Grazing offtake by red deer was 48% of the estimated total annual harvestable yield. The highest export rate by grazing offtake was estimated to 2.5 kg P ha⁻¹ year⁻¹, the highest input rate by dung to 1.5 kg ha⁻¹ year⁻¹. For the whole grassland "Alp Stabelchod" (10.7 ha) an annual net grazing export for 1998 of 3.3 kg P was estimated. Plots with vegetation of earlier successional stages generally had higher phosphorus content in the soil and higher net export rates than those with vegetation of later successional stages. This temporal change in the soil phosphorus pool could be explained adequately in terms of leaching at a rate of 1 kg P ha⁻¹ year⁻¹ together with a net export of P by grazing deer. At a smaller scale, the phosphorus content of the soil was very variable and reflected in factors such as the distance to the next tussock of *Carex sempervirens* or germination conditions for *Pinus montana* seedlings. The considerable variation in phosphorus pools among plots within the same successional stage of vegetation (up to 600 kg ha⁻¹) may be mainly explained by the differences in the history, location and spatial processes of these plots.

5 Based on these findings I conclude that red deer may have a significant impact on vegetation dynamics on nutrient-rich soils. For example, they can change tall-herb communities to a short-grass community dominated by *Festuca rubra*. Under continued high grazing pressure this short-grass community may remain relatively constant for a long period of time, during which the phosphorus pool in soil is progressively depleted.

The ecological role of bamboo (*Chusquea* spp.) in the old-growth *Quercus* forests of the Cordillera de Talamanca, Costa Rica

Die ökologische Rolle von Bambus (Chusquea spp.) in Eichen-Wäldern der Cordillera de Talamanca, Costa Rica; 183 pp.

YVONNE EDWARDS-WIDMER

1 This thesis concerns aspects of the taxonomy and ecology of bamboos of the genus *Chusquea* in the *Quercus* forests of the Cordillera de Talamanca in Costa Rica. The study had five main objectives: (1) description of three new species of *Chusquea*, (2) characterisation of the environment and the vegetation in the *Quercus-Chusquea* forests, (3) comparison of the population dynamics of different *Chusquea* species, (4) survey of the distribution and flowering behaviour of various *Chusquea* species, and (5) description of the life history of *Chusquea* in relation to the forest environment.

2 In Chapter 1 three new species of *Chusquea* from the Upper Montane Forests of the Cordillera de Talamanca are described and illustrated. *Chusquea tomentosa* and *C. subtilis* belong to section *Longifoliae* and are closely related to *C. foliosa*. The third species, *C. talamancensis*, is a member of the section *Swallenochloa* and shows similarities to both *C. tonduzii* and *C. vulcanalis*. Revised keys to the species of section *Longifoliae* and section *Swallenochloa* in Costa Rica are provided.

3 Chapter 2 presents the results of a survey of the vegetation and soils of the oak forests on Cerros Cueric and Cerro Abarca. The plots studied were selected to include one of the *Chusquea* species present in the area (*C. talamancensis*, *C. tomentosa* or *C. foliosa*) and to represent one of three types of canopy closure (closed canopy, intermediate canopy, gap). Based on a PCoA of the floristic data eight plant communities were recognized which could be associated with differences in topography, soil characteristics and canopy

closure. The *Chusquea* species appeared to be indicators for particular topographic situations and soil types. The data on size distribution of trees showed the inhibitory effect upon tree growth of the dominance of bamboo in gaps.

4 Chapter 3 examines in more detail the soil conditions of sites where *C. talamancensis*, *C. tomentosa* or *C. foliosa* were abundant, and presents data on soil pH, organic content and concentrations of plant nutrients. The soils supporting the different species of *Chusquea* bamboos were mainly acidic (pH 3.3–6.0) and derived from volcanic ash. However, individual bamboo species appeared to have distinct requirements in terms of soil conditions. The soils carrying *C. talamancensis* were richer in organic matter, had a higher C:N ratio and were more acidic than those with *C. tomentosa* or *C. foliosa*. *Chusquea tomentosa* grew on more nutrient-rich soils than the other two species.

5 In Chapter 4 the effect of canopy closure on the growth and spatial pattern of the three understory *Chusquea* species is described. Clumps of all species tended to be few and large under open conditions, and numerous and small under more shady conditions. The smaller clump density in gaps implies that intraspecific competition and density-dependent mortality occur when bamboos become dominant under favourable light conditions. The species differed in their response to light conditions: *C. tomentosa* and *C. foliosa* had a higher degree of morphological plasticity than *C. talamancensis*, which in turn appeared to be more shade-tolerant.

6 Chapter 5 describes the mass flowering of *C. talamancensis*, *C. tomentosa* and *C. subtilis* between 1987 and 1990, followed by the death of all plants. The different phenological states were coupled with the seasonal pattern of rainfall. Flower and fruit formation and seed germination occurred in the rainy season, whereas pollination, fruit maturation and abscission occurred in the dry season. On population level different flowering phases of cohorts were recognized. There was no seed production when isolated plants flowered, indicating that reproductive success depends on cross-pollination.

7 Chapter 6 presents observations on the distribution and flowering of six *Chusquea* species in the northwestern Cordillera de Talamanca. The most abundant species of *Chusquea* bamboos (*C. foliosa*, *C. longifolia*, *C. patens*, *C. subtilis*, *C. talamancensis* and *C. tomentosa*) showed an altitudinal zonation

and distributional differences between the Atlantic and Pacific slopes. *Chusquea longifolia* was associated with Lower Montane Forest, *C. patens* and *C. foliosa* with Lower and Upper Montane Forests, and *C. subtilis*, *C. talamancensis* and *C. tomentosa* with Upper Montane Forest. In the study area, the six species exhibited mass flowering with interspecific overlap of the flowering periods within a ten-years period.

8 In the final discussion it is concluded that *Chusquea* species have a major influence on the dynamics of the *Quercus* forests. The flowering and death of the bamboo is probably the most important type of disturbance in these forests, and tree regeneration is coupled with these events. Regarding the evolution of the bamboo life cycle, it is hypothesized that the forest environment may have been the driving force for the selection of periodic flowering in bamboos.

On the development of site factors and vegetation on the landslide at Goldau

Zur Standorts- und Vegetationsentwicklung im Goldauer Bergsturz; 332 pp.

ANDRÉ GRUNDMANN

1 The landslide of Goldau on the southern side of the Rossberg in central Switzerland dates from 1806 and covers an area of 6.7 km²; the geological bedrock is block debris of marl and nagelfluh. Its area extends from the submontane (500 m a.s.l.) to the higher montane zone (1500 m), and it is covered mostly by forest vegetation.

2 The vegetation in the lower parts of the landslide (<800 m) was investigated on different types of rock surfaces and in more or less homogenous forest stands between the rocks. Additionally, vegetation complexes were delineated. The survey method was adapted to the often inhomogeneous and patchy distribution of the vegetation units, and to the

small-scale changes between different plant communities.

3 The forest communities on the landslide are related to the alliances Molinio-Pinion, Cephalanthero-Fagion and Eu-Fagion, partly Tilio-Acerion; some of the communities occur in acidic variants. Wet sites support communities of the alliance Alno-Fraxinion. Spruce (*Picea excelsa*) is naturally abundant, especially in early successional habitats in the lower parts of the study area.

4 Steep block flanks are dominated by various moss communities (Tortello-Ctenidietum mollusci, Neckero-Anomodontetum viticulosi, Thamnetum alopecuri), and communities of higher plants which root in small crev-

ices (Asplenio-Cystopteridetum). On flat rock surfaces, an acidic moss community (Dicrano-Hypnetum) is prominent.

5 Moderately tilted block surfaces display a mosaic of moss communities, ferns and phanerogamous plants. Dry stands resemble fragments of the alliance Molinio-Pinion. Stands rich in *Calamagrostis varia* and *Achnatherum calamagrostis* may belong to the alliance Stipion calamagrostis. Less dry block habitats support fragments of the alliances Cephalanthero-Fagion, Eu-Fagion and Eurhynchion. Fern-rich stands on moist soil or under humid microclimate are related to Tilio-Acerion and Alno-Fraxinion communities. On large block surfaces small stands of multilayered forest communities have often developed.

6 The vegetation complexes which were differentiated in this study span from dry or periodically dry types with low nutrient supply to mesophilous, moderately humid or wet types.

7 The soils in the study area belong to the types pararendzina, marl rendzina (with variable soil humidity), as well as brown earths and brown earths with topsoil acidification. In the upper region of the landslide skeleton-rich, early-successional soils occur on bare marl and nagelfluh. Along banks of little streams alluvial soils exist, and in places with constantly high water supply gleyic soils have developed. On the rock surfaces, only a shal-

low layer of organic humus was found (partly base-rich, partly neutral or acidic).

8 The climate at Goldau is humid and rather oceanic, as is typical for the Northern Alps, but it is also influenced by foehn events. In the block area the microclimate is strongly differentiated depending on exposition and relief form. Thus, within short distances cool humid sites with high nutrient supply alternate with sunny habitats that are rather dry and warm.

9 If no further disturbance of the vegetation occurs in the near future, the processes of succession and soil development will proceed, which will lead eventually to changes in the spatial patterns of the present vegetation types. Older landslides nearby at the Rossberg and mature forest stands in the region of Goldau suggest the direction towards which the forest succession on the landslide will proceed in the long term.

10 The mosaic of various habitats and plant communities on the landslide is certainly of high conservation value. In this area processes can take place at different spatio-temporal scales that are rarely observed in other parts of the Swiss Alps. The entire landslide area should be protected as a nature reserve. This would include areas with unrestricted natural dynamics and adjacent sites which need extensive management to preserve certain rare species and plant communities.

Genetic variation, spatial distribution, and reproductive biology of pseudoflower-forming rust fungi (*Uromyces pisi* and relatives) on *Euphorbia cyparissias*

Genetische Variabilität, räumliche Verteilung und Fortpflanzung von "Pseudoblüten"-bildenden Rostpilzen (Uromyces pisi und verwandte Arten) auf Euphorbia cyparissias; 98 pp.

MONIKA PFUNDER

1 Insects play a major role in many fungal life cycles, either as vectors to transmit the fungus to a new host, or as "pollinators" to transfer the gametes of fungi among mating types.

Some rust fungi of the genera *Puccinia* and *Uromyces* use flower-like traits to attract insect "pollinators". Plants infected by these fungi are generally inhibited from flowering.

Instead, they are induced to form pseudoflowers, rosettes of yellow leaves that are clustered on the top of the stem in a flower-like shape. Not only do fungal pseudoflowers visually resemble true flowers, but just like true flowers, they present a sweet-smelling nectar that is produced by the fungus on the surface of the host leaves. The nectar contains fungal gametes (spermatia) that are transferred by nectar-feeding insects.

2 Rusts of the species complex *Uromyces pisi* (Pers.) Wint. produce pseudoflowers on cypress spurge, *Euphorbia cyparissias* L. Although they were suspected to depend on insects for their reproduction, no study has been done so far to confirm this assumption. By conducting an insect-exclusion experiment, I was able to show that fungal sexual reproduction does rely on insect vectors.

3 In the course of the insect exclusion experiment, I observed a conspicuously high number of ants on the fungal pseudoflowers as well as on the non-infected flowering host plants. A study on the role of ants as "pollinators" of non-infected and infected *Euphorbia* plants showed that ants were able to pollinate the non-infected *E. cyparissias* plants, but did not fertilise the fungus.

4 Flying insects, especially flies and solitary bees, often visited and moved freely among non-infected host flowers and fungal pseudoflowers. Therefore, I hypothesised that pseudoflowers and true flowers might interact through these "pollinators" by either competing for insects or by facilitating each other's visits. An artificial array experiment showed that true flowers were strongly preferred over pseudoflowers. However, no mutual influence on visitation rates of the two species could be observed when pseudoflowers and true flowers co-occurred in mixtures. In a non-manipulative field study I then measured the reproductive suc-

cess of pseudoflowers and true flowers in combination with the density and frequency of neighbouring pseudoflowers and true flowers. This study, in contrast to the array experiment, showed that pseudoflowers were serious competitors for true flowers, whereas pseudoflowers were not seriously influenced by non-infected hosts.

5 Although it is known that the species complex *U. pisi* consists of 11 described species that all induce pseudoflowers on *E. cyparissias*, I was not able to distinguish among the different species in the experiments described above. The reason for this was that the fungal species are morphologically indistinguishable on *E. cyparissias*. Only after successful fertilisation through insects do they switch to another host. The taxonomy of the different species is based on the choice of this alternate host, as well as on the shape and surface of teliospores produced on this host. For further studies on the ecology of these rusts it will be indispensable to differentiate them while they produce pseudoflowers. I therefore used a molecular method, sequencing the internal transcribed spacer region (ITS) in the rDNA, to identify the different species. The ITS region has been found to be appropriate for phylogenetic analyses of other fungi, and also provided valuable markers for the study on *Uromyces*. I was able to isolate DNA from five different species in the *U. pisi* complex, as well as from two species in the closely related species complex *Uromyces scutellatus*. Phylogenetic analyses suggested that *Uromyces scutellatus*, a microcyclic fungus with a simple life cycle of only 2–3 spore stages, may have evolved from the macrocyclic ancestors in the *U. pisi* species complex. I further applied this molecular method to evaluate the species distribution of *U. pisi* within and among *E. cyparissias* populations in Switzerland. Although I found five different species of *U. pisi*

on Fabaceae, only two of them were also isolated from freshly collected *E. cyparissias* (*U. pisi* s.s. and *U. striatus*). One further species was identified on *E. cyparissias* from a her-

barium specimen. *U. pisi* s.s. and *U. striatus* co-occurred within the same host population and were both found at elevations from 500 to 2000 m a.s.l.

From m² to km²: scaling of the plant species diversity of an agricultural landscape

Von m² zu km²: räumliche Skalierung der Artenvielfalt der Vegetation in einer Agrarlandschaft; 75 pp.

HELENE WAGNER

1 This study aims at integrating measures of plant species diversity and its main aspects, richness and evenness, at different spatial scales so as to gain a better picture of the overall plant diversity of an agricultural landscape and its potential for biodiversity conservation.

2 The effects of habitat variability and habitat heterogeneity were quantified based on the partitioning of landscape species diversity into additive components. I derived components of within- and between-community diversity at four scale levels (plot, patch, habitat type, landscape) for three diversity measures (species number, Shannon index, Simpson diversity). The approach is illustrated with a case study from central Switzerland, where I recorded the occurrence of vascular plants in a stratified random sample based on the land-use pattern. The diversity components depended strongly on the habitat type and on the diversity measure. Landscape composition had a strong influence on landscape species richness, but not on evenness.

3 I simulated how the four non-parametric richness estimators *Jack1*, *Jack2*, *Chao2* and *ICE* are affected by the abundance distribution and by spatial heterogeneity. In contrast to other simulation studies, different models of species abundance were fitted to real data, and instead of assuming a global aggregation factor, I modelled for every species the effects

of spatial autocorrelation, of an environmental gradient and of a boundary zone (edge effect). Spatial structures and species abundance distribution influenced the performance of richness estimators *via* sample representativeness. The sampling design should be adapted to obtain random samples of ecological conditions instead of geographical space.

4 The thesis is also concerned with the concept of habitat specificity and quantifies the contribution of the various spatial elements to the total occurrence of individual species. The robustness of specificity estimates was investigated with vascular plant and mollusc data from a biodiversity-monitoring program in the Swiss Canton of Aargau. With field data of this thesis, I tested hypotheses on the effect of landscape structure on landscape species richness. Re-sampling results suggested that unbiased estimates of relative specificity can be obtained by an adequately stratified sampling design. Specificity can be combined with measures of other aspects of the rarity of a species to obtain an integral measure of the contribution of a landscape element to a hierarchical set of conservation goals as formulated in the national biodiversity strategy of Switzerland.

Effects of wildflower strips in an intensively used arable landscape on skylarks, *Alauda arvensis*

Auswirkungen von Buntbrachen in einer ackerbaulich intensiv genutzten Landschaft auf Feldlerchen (Alauda arvensis); 104 pp.

URS WEIBEL

1 Until recently the skylark, *Alauda arvensis*, was a common and widespread bird of farmland in Europe. However, in the last few decades their populations have decreased dramatically in all countries of central and western Europe. Many factors associated with the intensification of agriculture may have contributed to their decline, including the reparation of agricultural land, the loss of natural and semi-natural elements, a reduction in crop rotations, more frequent application of agro-chemicals, and earlier and more frequent mowing of grassland. Since 1993, Swiss farmers have been encouraged to use some of their arable land for "ecological compensation", as part of a policy aimed at enhancing biodiversity. Wildflower strips are one of the several officially recognised types of ecological compensation area and are of particular importance in arable regions. They consist in 3–10 m wide strips which are sown with a mixture of annual, biennial and perennial species from both arable land and grassland; they are not sprayed with herbicides.

2 The study described here was carried out from 1996 to 1998 in the Klettgau region of northern Switzerland. Most of the work was carried out at a site called Widen (5.3 km²); an additional site was used for an artificial nest experiment (Plomberg, 4.7 km²). In these intensively used arable areas, large numbers of wildflower strips have been established as part of a major scheme sponsored by the Swiss Ornithological Institute and the cantonal authorities.

3 The selection of nesting sites by skylarks, breeding success, nestling growth and nes-

ting diet were investigated. In addition, predation from nests was studied using artificial nests. A major aim of the work was to determine the effects of wildflower strips on the skylark populations. The relative use of different crop types as nesting sites and of different locations within fields was studied using compositional analyses. The Mayfield method was applied to estimate survival probabilities of both skylark nests and artificial nests. The diet of nestlings was investigated with the help of neck collars.

4 The suitability of different crop types as nesting sites changed during the breeding season, according to the state of vegetation development. Overall, wildflower strips, set-aside land and grassland had the highest use. In addition, more nests were found in locations close to the field boundary than in the centre of fields. The mean size of clutches was 3.6 ± 0.04 eggs ($n = 396$) whereas the mean number of chicks at nest leaving was 3.3 ± 0.07 ($n = 202$). For both stages the mean number increased from April to June and decreased in July. Clutches in territories with wildflower strips (3.7 ± 0.06 ; $n = 175$) were significantly larger than in those without (3.5 ± 0.05 ; $n = 221$).

5 Mean breeding success, defined as the probability that at least one nestling leaves the nest per nesting attempt, was $22.4 \pm 0.5\%$ averaged over the study period, though it varied between years; it was $17.8 \pm 0.5\%$ in the period 1995–1997 and $37.8 \pm 0.9\%$ in 1998. Breeding success ranged from $3.5 \pm 2.9\%$ on tracks to $34.1 \pm 0.7\%$ in cereal fields; it was relatively low in wildflower strips ($18.0 \pm$

0.2%). The failure rate of nests close to the field border was higher than in the middle of a field. Predation caused 72% of all nest failures ($n = 193$) and was more frequent during the nestling stage than during incubation.

6 Daily growth increments measured in terms of both weight and length of the third primary feather varied widely (weight -2.0 – 6.5 g d⁻¹; feather length 0 – 8.5 mm d⁻¹): The data for weight were especially variable, and 16% of the recorded daily growth increments were either zero or negative ($n = 642$). Growth in terms of both weight and feather length was significantly influenced by hatching date, brood size and temperature; the results for feather length were also positively affected by the area of wildflower strips in a territory. The growth performance index tended to be higher in territories which included wildflower strips, especially during periods when growth was poor.

7 Up to 75% of the diet of skylark nestlings consisted of spiders (Araneae), dipterans (Diptera) and beetles (Coleoptera); butterflies (Lepidoptera) and hymenopterans (Hymenoptera) made up another 15%. The proportions of beetles, dipterans and hymenopterans increased with increasing age of nestlings, while those of butterflies and spiders decreased. There was no convincing evidence that dietary composition was affected by the presence of wildflower strips in a territory.

8 The success probabilities of artificial nests were affected by crop type, ranging from $3.3 \pm 13.2\%$ to $28.8 \pm 3.6\%$. The daily survival probability was lower in the first week of exposure (0.83 ± 0.004) than in the second (0.94 ± 0.004) and the third (0.96 ± 0.004). Between the two study years, the failure rates decreased in one study area, but increased in the other. Success probability seemed unrelated to the distance of nests to the field boundary. Except in wildflower strips, the

survival probabilities of artificial nests were lower than those of skylark nests. Of the total of 1493 artificial nests which were predated, 14% of the losses could be attributed to corvids and 12% to small rodents. A further 14% were taken by larger mammals, which were probably also responsible for the 60% of eggs which were removed without trace.

9 Overall, this study shows convincingly that wildflower strips are beneficial for breeding skylarks. In particular, they offer suitable sites for nesting and hunting throughout the breeding season. However, these habitats are only of value to skylarks if the vegetation is sufficiently low and sparse.

