
Grazing Intensity and the Diversity of Grasshoppers, Butterflies, and Trap-Nesting Bees and Wasps

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Abstract: *The maintenance of grasslands as distinct habitats depends on regular management, usually through grazing or mowing, but their species diversity is known to decline with increasing management intensity. The reduction of management intensity can be a useful tool for the long-term conservation of the biological diversity of grasslands. We analyzed floral and faunal diversity on intensively and extensively (unintensively) grazed pastures and on 5- to 10-year-old ungrazed grasslands in northern Germany. Each of the three grassland habitats differing in grazing intensity was replicated six times. We related diverse taxa such as grasshoppers, butterfly adults and lepidopteran larvae, and trap-nesting solitary bees and wasps to vegetation structure. There was an increase of species richness and abundance from pastures to ungrazed grasslands. The percentage of parasitism of the most abundant trap-nesting species, the digger-wasp (*Trypoxylon figulus*), was also higher on ungrazed grasslands. Decreased grazing on pastures enhanced species richness for adult butterflies only, whereas the abundance of adult butterflies, solitary bees and wasps, and their natural enemies increased. Although the differences in insect diversity between pastures and ungrazed grassland could be attributed to a greater vegetation height and heterogeneity (bottom-up effects) on ungrazed areas, the differences between intensively and extensively grazed pastures could not be explained by changes in vegetation characteristics. Hence, intensive grazing appeared to affect the insect communities through the disruption of plant-insect interactions. A mosaic of extensively grazed grassland and grassland left ungrazed for a few years may be a good means by which to maintain biodiversity and the strength of trophic interactions.*

Intensidad de Pastoreo y la Diversidad de Chapulines, Mariposas y Abejas y Avispas

Resumen: *El mantenimiento de pastizales como hábitats distintos depende del manejo regular, generalmente, por medio de pastoreo o segado, pero se sabe que la diversidad de especies declina con el incremento de intensidad de manejo. La reducción de la intensidad de manejo puede ser una herramienta útil para la conservación a largo plazo de la biodiversidad de pastizales. Analizamos la diversidad florística y faunística en pastizales pastoreados intensiva y extensivamente (no intensivos) y en pastizales de 5 a 10 años no pastoreados en el norte de Alemania. Cada uno de los tres hábitats de pastizal diferentes en el grado de pastoreo fue replicado seis veces. Relacionamos diversos taxones como chapulines, mariposas adultas, larvas de lepidópteros y abejas y avispas solitarias con la estructura de la vegetación. Hubo un incremento en la riqueza y abundancia de especies de pastizales pastoreados a no pastoreados. El porcentaje de parasitismo de la especie de avispa más abundante (*Trypoxylon figulus*) también fue mayor en pastizales no pastoreados. La reducción del pastoreo incrementó la riqueza de especies de mariposas adultas solamente, mientras que incrementó la abundancia de mariposas adultas, abejas y avispas solitarias y sus enemigos naturales. Aunque las diferencias en la diversidad de insectos entre pastizales pastoreados y no pastoreados pudiera atribuirse a la mayor altura de la vegetación y a la heterogeneidad (efectos abajo-arriba) en áreas no pastoreadas, las diferencias entre pastizales pastoreados intensiva y extensivamente no podría explicarse por cambios en las características de la vegetación. Por consiguiente, el pastoreo intensivo aparentemente afectó a las comunidades de insectos por la disrupción de las interacciones planta-animal. Un mosaico de pastizales pastoreados extensivamente y pastizales sin pastoreo por varios años puede ser una buena estrategia para mantener la biodiversidad y la vigencia de las interacciones tróficas.*

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Introduction

Livestock grazing on rangelands and pastures greatly contributes to changes in vegetation and the associated insect community through alteration of plant growth, plant architecture, and vegetation diversity (e.g., Strong et al. 1984; Huntly 1991). According to Noss (1994), "many conservationists claim that livestock has done more damage on native biodiversity of western North America than all the chainsaws and bulldozers combined." Intensive grazing can dramatically simplify vegetation diversity by reducing plant species richness, plant vegetation architecture, and standing crop. Because plant diversity is considered a major determinant of diversity at a higher trophic level (Hutchinson 1959; Root 1973; Hunter & Price 1992), the diversity of phytophagous insects and their natural enemies is likely to decline with simplification of vegetation (Morris 1967; Lawton & Schröder 1977; Gibson et al. 1992; Rushton & Eyre 1992; McFerran et al. 1994; Tschamtkke & Greiler 1995).

Both short- and long-term effects of grazing on invertebrate diversity can be distinguished. Short-term effects are linked to (1) the simplification of plant architecture (e.g., the destruction of feeding niches) (Andrzejewska 1965; Morris 1967, 1981; Hutchinson & King 1980; Purvis & Curry 1981) and to (2) the grazed plants' regrowth so that young and nutrient-rich plant tissue becomes available (Moore & Clements 1984). Long-term effects include shifts in the composition of plant communities and thus in vegetation structure (Day & Detling 1990; Huntly 1991).

Reduction of grazing pressure increases the species richness and abundance of phytophagous insects and their parasitoids (Andrzejewska & Gyllenberg 1980; Morris 1981; Watts et al. 1982; Morris & Plant 1983). Therefore, traditional types of management such as low-intensity grazing or mowing once per annum are often associated with high biological diversity in grassland habitats (Tschamtkke & Greiler 1995; Wettstein & Schmid 1999; Di Giulio et al. 2001; Swengel & Swengel 2001). Thus, in aiming to preserve biodiversity on grasslands, nature conservation agencies have created various programs to maintain species-rich pastures with reduced grazing intensity.

We sought to examine the effects of reduced grazing intensity on plant and insect diversity and their interactions in grassland habitats. We used three different types of grassland, representing a gradient of grazing intensity: intensively grazed pastures, extensively grazed pastures, and ungrazed grasslands.

In our quantitative and experimental approach we used insect taxons differing in ecological characteristics, as advocated by Wettstein and Schmid (1999), to test for more general and applicable patterns of diversity within these three types of grassland. We studied three taxonomic groups of insects: (1) grasshoppers (Saltatoria), (2) butterflies and moths (Lepidoptera), and (3) solitary

bees and wasps and their natural enemies (Hymenoptera). Grasshoppers are leaf chewers throughout their life cycles, whereas Lepidoptera are leaf chewers as larvae but depend on flowers as resources as adults. Bee and wasp adults also use flowers for food (nectar and pollen), whereas the solitary wasps (Eumenidae, Pompilidae, Sphecidae) depend on spiders and insects for their entomophagous offspring. We combined field samples and surveys of grasshoppers, butterflies, and lepidopteran larvae with a field experiment in which we used standardized trap nests for bees and wasps (Gathmann et al. 1994; Tschamtkke et al. 1998).

We tested two hypotheses about the effects of reduced grazing intensity on insect species diversity. The diversity of insects is enhanced by (1) increased diversity (species richness and heterogeneity) and height (related to biomass) in vegetation (Strong et al. 1984; Siemann 1998) and (2) reduced disturbance and similar vegetation structure, resulting in a reduced disruption of trophic interactions and less separation of consumers from their resource (Tschamtkke 1997).

Methods

Study Area

The field sites were located in Schleswig-Holstein, northern Germany, in a heterogeneous landscape dominated by grasslands and forests. We studied three types of grassland habitat: intensively grazed pastures, extensively grazed pastures, and ungrazed grassland (ungrazed for 5–10 years). Each of the three habitat types was replicated six times, resulting in 18 study sites.

The management of the extensively grazed pastures was financially supported by the Schleswig-Holstein Department of Nature Conservation as part of an extensification program for pastures (a program to reduce grazing intensity with the aim to increase biodiversity). Thus, grazing intensity was limited to 1.5 cattle/ha and grazing was permitted only between 1 May and 15 November on extensively grazed pastures. The intensively grazed pastures were grazed between 1 April and 30 October. Consequently, grazing intensity differed significantly, between 5.5 ± 1.4 cattle/ha on intensively grazed pastures and 1.4 ± 0.1 cattle/ha on extensively grazed pastures ($F_{1,10} = 8.1$, $p = 0.02$, $n = 12$). Thus, the three habitat types represented a gradient from intensively grazed to ungrazed grasslands.

To standardize the site conditions, we selected sites to be similar in (1) former management, (2) area, and (3) localization within the investigation area. We selected sites with similar previous management because there is a long tradition of cattle grazing on the grassland areas in the "Bilsbek-Niederung." The selected pastures had continuity in management intensity for at least 4 years. Because of turnover of leaseholders, it was not possible to

determine the precise period without grazing for the ungrazed grasslands, but we selected only sites that were known to be ungrazed for at least 5 years. To avoid bias caused by local effects, we selected only those pastures included in the extensification program that were adjacent to intensively grazed pastures or long-term ungrazed grasslands. Thus, the final design consisted of six randomized blocks, each comprising one site of each of the three habitat types. The mean area of the sites did not differ significantly between the habitat types (intensive, 2.9 ± 0.4 ha; extensive, 3.6 ± 1.1 ha; ungrazed, 1.6 ± 0.4 ha; $F_{2,15} = 2.46$, $p = 0.120$, $n = 18$).

Characterization of the Vegetation

From May to August 1996, we recorded the species composition of vascular plant species on all sites on a monthly visit of 30 minutes per site, and also added the data from the measures described below. In addition, for each site we made a map of the vegetation mosaic by recording the distribution and abundance of all vegetation patches, distinguishable by obvious differences in the dominance of a particular plant species (e.g., grass patches with *Holcus lanatus*, patches dominated by *Trifolium repens*, thistle patches) or in species composition. For each vegetation patch with a total area of more than 50 m^2 , we recorded plant species composition, mean vegetation height (estimated vegetation height containing 75% of the aboveground vegetation), percent cover of each plant species, and total vegetation cover within an area of 25 m^2 at the end of May. The estimates of vegetation height and total vegetation cover were repeated in June and July. Vegetation heterogeneity per site was defined as the number of different types of vegetation patches on each site.

Insect Records and Samples

Species richness of Saltatoria was recorded during 30-minute transect walks conducted once a fortnight between the end of May and the end of September on each of the 18 sites. Species abundance was not recorded. Species were identified by (1) the sound of their stridulations, based on reference "calls" from a tape (Bellmann 1985a) and (2) sweep-netting and visual examination identification of sampled individuals (Bellmann 1985b). Biological data on species biology were provided by Detzel (1998).

We used two methods to study the species richness and abundance of Lepidoptera. Adult butterflies and burnet moths were sampled during five transect walks (monthly from May to September 1996) through each of the 18 sites. Along the transects, all individuals were recorded inside a transect width of 5 m during a 45-minute walk of the transect, provided weather conditions allowed butterfly monitoring (Pollard & Yates 1993). Because of

changes in weather conditions during transect walks on three sites, we conducted additional transect walks in the following week. Thus, the species richness and abundance of butterflies and burnets were adjusted to the number of transect walks (ranging from five to six). To evaluate the reproduction success of Lepidoptera, we counted and collected all lepidopteran larvae five times (monthly from May to September) along a transect. Each survey lasted 45 minutes in the pastures and 60 minutes in the ungrazed grasslands to compensate for detection of larvae being much more difficult as a result of the higher and more dense vegetation. For each species, we counted the number of occupied sites (number of sites where a species was observed) within each of the three habitat types. The identification of adult butterflies and burnets was based on the work of Higgins and Riley (1971) and Weidemann (1995). Nomenclature followed that of Ebert (1991, 1994, 1997).

We used trap nests to analyze the species richness and abundance of solitary bees and wasps and their parasitoids. Four trap nests were set in the center of each site. Each trap nest consisted of 150–180 internodes 15–20 cm long made of common reed (*Phragmites australis*) bundled into a plastic tube 13 cm in diameter (Gathmann et al. 1994; Tschamntke et al. 1998). Trap nests were set from the beginning of May to end of September. The trap nests on one of the six extensively grazed pastures were vandalized in August. Collected nests were stored at 5°C until further investigation was conducted. The internodes were dissected in the laboratory. Adults of bees, wasps, and parasitoids were reared from larvae and pupae in glass tubes sealed with cotton wool. Emerging adults were counted and identified. Brood cells with no emergence were dissected for a final identification. We used the identification keys provided by Gathmann and Tschamntke (1999).

Data Analysis

Insect and vegetation data for each of the 18 sites were pooled for further analyses. The data consisted of six replicates per habitat type for all but the trap-nest data on the extensively grazed pastures with five replicates. Grasshopper data included the overall sum of species by site recorded during the season. For butterflies and lepidopteran larvae, we analyzed the mean number of species or individuals per transect walk because the number of observations differed by site. The data set on bees and wasps consisted of the total number of species and individuals reared from four trap nests per site. Data sets were lognormal-transformed before analysis if they did not fit a normal distribution (Sokal & Rohlf 1995). We used one-way analyses of variance to test for the effects of grazing intensity (intensively grazed, extensively grazed, ungrazed) on vegetation and insect diversity. Tukey's honest significant difference test (HSD) was used for post hoc

comparisons. We performed stepwise multiple-regression analyses to identify the most important habitat and vegetation variables influencing insect diversity in the studied sites. Values given in the text and the graphs are arithmetic means; error values or bars represent ± 1 SE of the mean.

Results

Vegetation

The data presented are estimates from May to July within each site. Mean number of vascular plant species per 25 m² did not differ significantly among the three habitat types, with 11.7 ± 3.3 species on intensively grazed pastures, 13 ± 1.8 species on extensively grazed pastures, and 12.8 ± 0.6 species on ungrazed grasslands ($F_{2,15} = 0.11, p = 0.89, n = 18$). Vegetation heterogeneity was 4.8 ± 0.6 patches on intensively grazed pastures, 5.0 ± 0.7 patches on extensively grazed pastures, and 6.7 ± 0.8 patches on ungrazed grassland ($F_{2,15} = 1.92,$

$p = 0.18, n = 18$). We found a significant increase in mean vegetation height from pastures to ungrazed grasslands. Vegetation height was 29.0 ± 2.8 cm on intensively grazed and 32.0 ± 1.6 cm on extensively grazed pastures but was significantly higher (60.0 ± 4.8 cm) on ungrazed grasslands ($F_{2,15} = 26.6, p < 0.01, n = 18$). Other vegetation characteristics, such as percent cover of the vegetation ($F_{2,15} = 1.19, p = 0.33, n = 18$) and the herb/grass ratio ($F_{2,15} = 0.76, p = 0.48, n = 18$), showed no significant differences among the three grazing treatments.

Insect Species Richness and Abundance

SALTATORIA

Fifteen Saltatoria species were recorded across all 18 sites. Eight of these species, *Conocephalus dorsalis* Thunberg, *Tettigonia cantans* (Fuessly), *Stethophyma grossum* (L.), *Tetrix subulata* (L.), *T. undulata* (Sow-erby), *Chorthippus albomarginatus* (De Geer), *Ch. dor-*

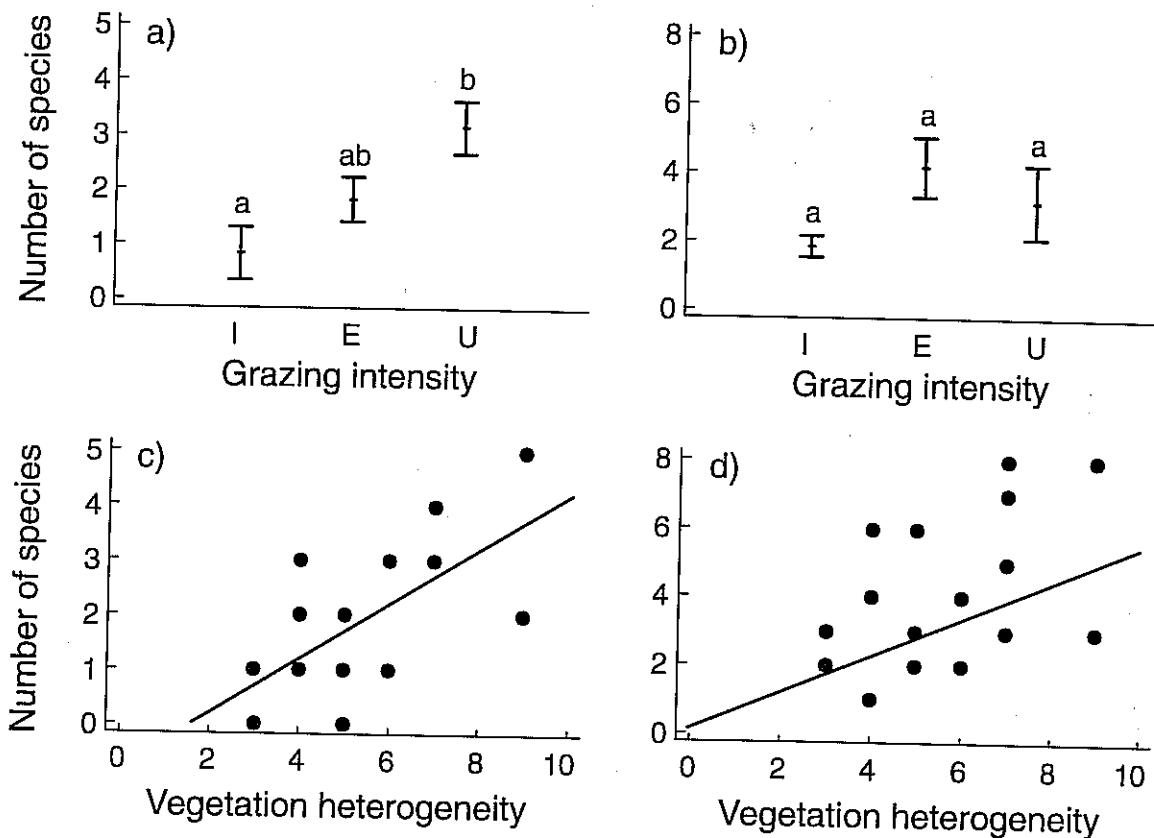


Figure 1. Effects of grazing intensity (I, intensively grazed pastures; E, extensively grazed pastures; U, ungrazed grassland) on the grasshopper (Saltatoria): (a) mean (± 1 SE) number of *Ensifera* species ($F_{2,15} = 6.7, p = 0.009, n = 18$) and (b) mean (± 1 SE) number of *Caelifera* species ($F_{2,15} = 2.0, p = 0.16, n = 18$). Different letters above bars indicate significant differences (Tukey's honest significant difference). Correlation between vegetation heterogeneity (number of different vegetation patches) and grasshoppers: (c) number of *Ensifera* species ($Y = -0.83 + 0.50X, F_{1,16} = 12.57, r^2 = 0.44, p = 0.003, n = 18$) and (d) number of *Caelifera* species ($Y = 0.10 + 0.54X, F_{1,16} = 4.7, r^2 = 0.23, p = 0.046, n = 18$).

satus (Zetterstedt), and *Ch. montanus* (Charpentier) are characteristic of mesophilic grassland (Detzel 1998). Total species richness of Saltatoria increased from intensively grazed pastures (2.7 ± 0.67) to extensively grazed pastures (6.0 ± 1.2) and ungrazed grasslands (6.3 ± 1.4), but these differences were statistically only marginally significant ($F_{2,15} = 3.23$, $p = 0.07$, $n = 18$). However, the species richness of the habitat specialists, the mesophilic grassland species, was significantly higher ($F_{2,15} = 4.4$, $p = 0.03$, $n = 18$) on extensively grazed pastures (4.0 ± 0.7) and ungrazed grasslands (3.5 ± 0.9) than on intensively grazed pastures (1.7 ± 0.2). The species richness of Ensifera species was significantly higher on ungrazed grasslands than on intensively grazed pastures, and the species richness on extensively grazed pastures was at an intermediate level (Fig. 1a). For Caelifera species this trend was not found (Fig. 1b). Stepwise multiple-regression analyses showed that the species richness of both Ensifera and Caelifera was significantly correlated with vegetation heterogeneity (Fig. 1c, 1d). The total species richness of Saltatoria was positively correlated with vegetation heterogeneity (X_1) and negatively

correlated with total percent vegetation cover of vascular plants (X_2) ($Y = 18.2 + 1.1 X_1 - 0.2 X_2$, $F_{2,15} = 14.7$, $r^2 = 0.66$, $p < 0.001$, $n = 18$).

BUTTERFLY ADULTS AND LEPIDOPTERAN LARVAE

Eighteen adult butterfly species (1437 individuals) were recorded on the 18 sites. The total number of butterfly species increased with declining grazing intensity, from 10 species on intensively grazed pastures to 14 species on extensively grazed pastures and 17 species on ungrazed grasslands. The mean number of occupied sites per species also increased with decreasing grazing intensity, from 1.9 sites on intensively grazed pastures to 3.2 sites on extensively grazed pastures and 3.8 sites on ungrazed grasslands. The most abundant species on the pastures (12 sites) were *Maniola jurtina* L. (26.3% of all individuals), *Aglais urticae* (L.) (25.7%), and *Pieris napi* L. (20.4%). On ungrazed grasslands, *Thymelicus lineolus* Ochsensh. (25.8%), *T. sylvestris* Poda (11.5%), and *M. jurtina* (17.4%) were the dominant species. None of

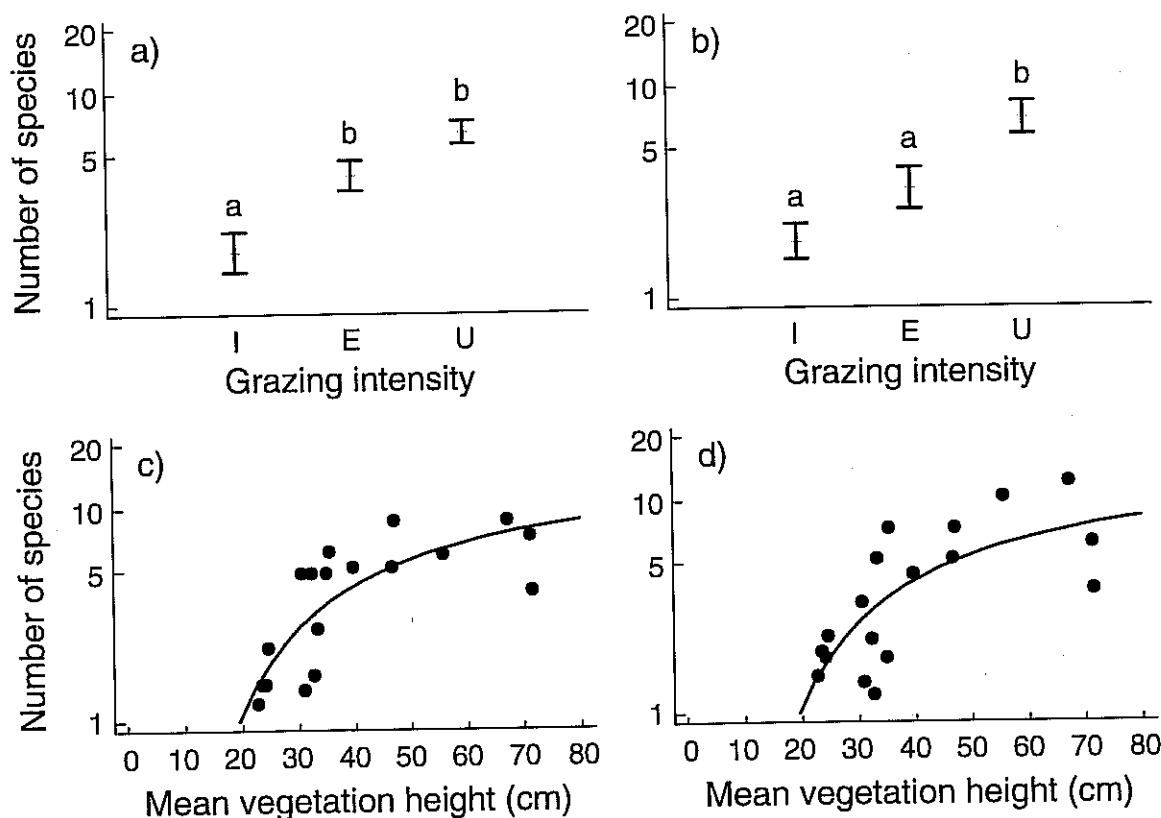


Figure 2. Effects of grazing intensity (I, intensively grazed pastures; E, extensively grazed pastures; U, ungrazed grassland) on butterfly adults and lepidopteran caterpillars: (a) mean (± 1 SE) number of adult species ($F_{2,15} = 13.9$, $p < 0.001$, $n = 18$) and (b) mean (± 1 SE) number of caterpillar species ($F_{2,15} = 11.35$, $p = 0.001$, $n = 18$). Different letters above bars indicate significant differences (Tukey's honest significant difference). Correlation between mean vegetation height and (c) number of adult butterfly species ($Y = 2.9 - 55.5/X$, $F_{1,16} = 28.6$, $r^2 = 0.64$, $p < 0.001$, $n = 18$) and (d) number of caterpillar species ($Y = 2.8 - 54.6/X$, $F_{1,16} = 19.47$, $r^2 = 0.55$, $p < 0.001$, $n = 18$).

these abundant species could be characterized as a habitat specialist.

Mean species richness and mean abundance of adult butterflies were significantly higher on ungrazed grasslands and extensively grazed pastures than on intensively grazed pastures (Figs. 2a & 3a). Multiple-regression analysis showed that both species richness and abundance were significantly positively correlated with vegetation height (Figs. 2c & 3c).

Across all 18 sites, we recorded 1272 larval individuals comprising 31 species or morphospecies. The most abundant species on all three habitat types were the butterflies *A. urticae* (34.7%) and *Inachis io* L. (20.9%). Species distributions by management type showed that the moth *Eurrhynx hortula* (L.) was especially abundant on intensively grazed pastures (5.2%) and ungrazed grassland (13.6%), whereas the butterfly *Araschnia levana* L. was abundant on extensively grazed pastures (42.1%).

The number of species increased significantly from intensively grazed pastures to ungrazed grasslands, but did not differ significantly between intensively and extensively grazed pastures (Fig. 2b). The abundance of lepidopteran larvae showed a similar pattern: abundance was highest on ungrazed grasslands and significantly lower on intensively grazed pastures (Fig. 3b). Abundance of Lepidoptera on extensively grazed pastures was at an intermediate level.

Results from multiple-regression analyses showed that mean vegetation height was the best predictor of both species richness and abundance of butterfly adults and lepidopteran larvae (Figs. 2c, 2d, 3c, & 3d).

SOLITARY BEES AND WASPS AND THEIR NATURAL ENEMIES

A total of 431 occupied internodes were dissected, containing 1741 brood cells (including 283 empty cells). After rearing, 1258 individuals emerged, comprising 23

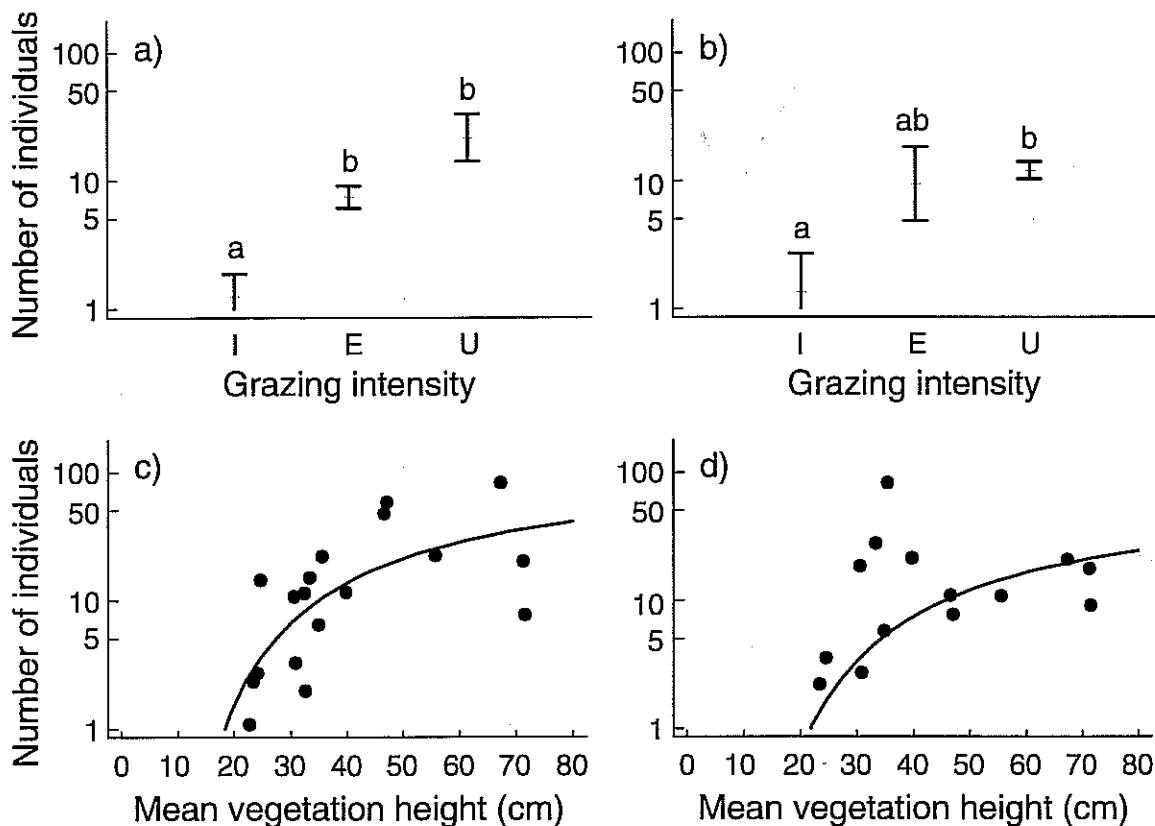


Figure 3. Effects of grazing intensity (I, intensively grazed pastures; E, extensively grazed pastures; U, ungrazed grassland) on the abundance of butterfly adults and lepidopteran caterpillars: (a) mean (± 1 SE) number of individual butterfly adults ($F_{2,15} = 16.8$, $p < 0.001$, $n = 18$) and (b) mean (± 1 SE) number of individual caterpillars ($F_{2,15} = 4.52$, $p = 0.03$, $n = 18$). Different letters above bars indicate significant differences (Tukey's honest significant difference). Correlation between mean vegetation height and (c) number of individual butterfly adults ($Y = 4.7 - 104.2/X$, $F_{1,16} = 15.9$, $r^2 = 0.50$, $p = 0.001$, $n = 18$) and (d) number of individual caterpillars ($Y = 4.36 - 95.26/X$, $F_{1,16} = 7.83$, $r^2 = 0.33$, $p = 0.013$, $n = 18$).

species. This insect community of bees and wasps consisted of five species of solitary bees (Megachilidae: *Chelostoma florissomme* [L.], *Megachile versicolor* Sm., *Osmia rufa* L., *O. uncinata* Gerst., Colletidae: *Hylaeus communis* NyL.), six species of digger wasps (Sphecidae: *Passaloeus corniger* Shuck., *P. gracilis* [Curt.], *P. insignis* [v.d. Lind.], *Psenulus pallipes* [Pz.], *Trypoxylon clavicerum* Lep. and Serv., *T. figulus* [L.]), five species of eumenid wasps (*Ancistrocerus gazella* [Pz.], *A. parietinus* [L.], *A. trifasciatus* [Müll.], *Symmorphus bifasciatus* [L.], *S. gracilis* [Brullé]), and one spider-hunting wasp (Pompilidae: *Dipogon nitidum* Hpt.). We found six species of natural enemies: two species of ruby-tailed cuckoo wasps (Chrysididae: *Chrysis cyanea* L., *C. ignita* L.), two species of ichneumon wasps (Ichneumonidae: *Ephialtes manifestator* L., *Hybomischos septemcinctorius* Thbg.), one species of chalcid wasp (Eulophidae: *Melittobia* sp.), and one drosophilid fly species (Drosophilidae: *Cacoxenus* sp.). The most numerous species were the digger wasp *T. figulus* (43% of all individuals),

the solitary bee *Osmia rufa* (11%), and one species parasitizing *T. figulus*, the ruby-tailed cuckoo wasp (*C. cyanea*) (9%).

The total species richness of bees, wasps, and their parasitoids was significantly higher on ungrazed grassland (11.5 ± 0.8) than on intensively (4.7 ± 0.9) or extensively (6.2 ± 1.0) grazed pastures ($F_{2,14} = 16.8$, $p < 0.001$, $n = 17$). The total number of emerged individuals of bees and wasps was highest on ungrazed areas (85.3 ± 13.7) but was also higher ($F_{2,14} = 14.8$, $p < 0.001$, $n = 17$) on extensively (46.8 ± 2.9) than on intensively grazed pastures (26.8 ± 5.9).

The species richness of bees and wasps was significantly higher on ungrazed grassland than on pastures (Fig. 4a). Parasitoid species richness was also highest on ungrazed grassland and lowest on intensively grazed pastures (Fig. 4b). Results for species abundance differed from that of species richness because there was also a significant increase in the abundance of bees and wasps (Fig. 5a) and their parasitoids (Fig. 5b) from intensively to extensively grazed pastures. As

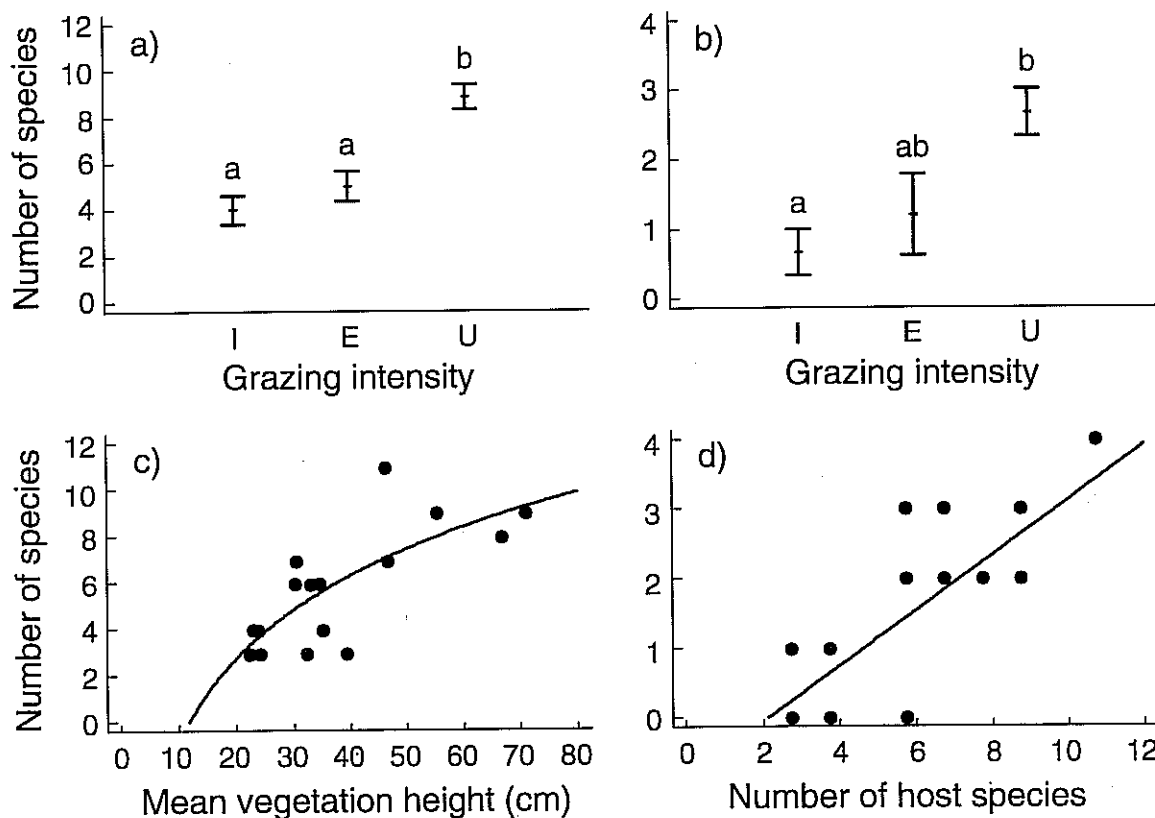


Figure 4. Effects of grazing intensity (I, intensively grazed pastures; E, extensively grazed pastures; U, ungrazed grassland) on species richness of trap-nesting bees and wasps and their natural parasitoids (Hymenoptera): (a) mean (± 1 SE) species richness of bees and wasps ($F_{2,14} = 18.7$, $p < 0.001$, $n = 17$) and (b) mean (± 1 SE) species richness of parasitoids ($F_{2,14} = 6.6$, $p = 0.009$, $n = 17$). Different letters above bars indicate significant differences (Tukey's honest significant difference). Correlation between (c) species richness of trap-nesting bees and wasps and mean vegetation height ($Y = -12.7 + 5.1 \ln(X)$, $F_{1,15} = 22.0$, $r^2 = 0.59$, $p < 0.001$, $n = 17$) and (d) species richness of parasitoids and species richness of hosts ($Y = -0.85 + 0.4X$, $F_{1,15} = 26.0$, $r^2 = 0.63$, $p < 0.001$, $n = 17$).

for the Lepidoptera, mean vegetation height was the best predictor of species richness and abundance of solitary non-parasitic bees and wasps (Figs. 4a & 5a). For the parasitoids in the trap nests, species richness correlated best with species richness of nonparasitic species (Fig. 4d), and parasitoid abundance correlated best with the abundance of non-parasitic species (Fig. 5d).

Percent parasitism of *Trypoxylon figulus* was caused by *Cbrysis cyanea* and ranged from 5% to 35%. Percent parasitism was lowest on pastures and significantly higher on ungrazed grasslands (Fig. 6a), and we found that percent parasitism was significantly positively correlated with both mean vegetation height and host abundance (Fig. 6b). Another cuckoo wasp, *Cbrysis ignita*, parasitized the five species of eumenid wasps. Pooled parasitism of these five species by the cuckoo wasp ranged from 23% to 67% and was positively correlated with eumenid abundance ($F_{2,14} = 4.8$, $r^2 = 0.49$, $p = 0.04$, $n = 17$), but there were no significant differences the three types of habitat.

Discussion

Our results indicate that reducing grazing intensity can be a useful measure to preserve and support insect diversity on grasslands. Generally, we found a significant difference in both insect species richness and abundance between intensively grazed pastures and ungrazed grasslands. The higher insect diversity in habitats with reduced or no grazing could be attributed to an increase in vegetation height with respect to butterflies and trap-nesting bees and wasps, whereas grasshopper species richness was more strongly related with vegetation heterogeneity. We found a stronger effect on insect abundance than on insect species richness for butterfly adults and trap-nesting bees and wasps but not for lepidopteran larvae. Grazing reduction on pastures, from intensive to extensive, was correlated with increased insect diversity of only a few taxa, but absence of grazing had a strong effect because the diversity of all insect taxa increased under this condition.

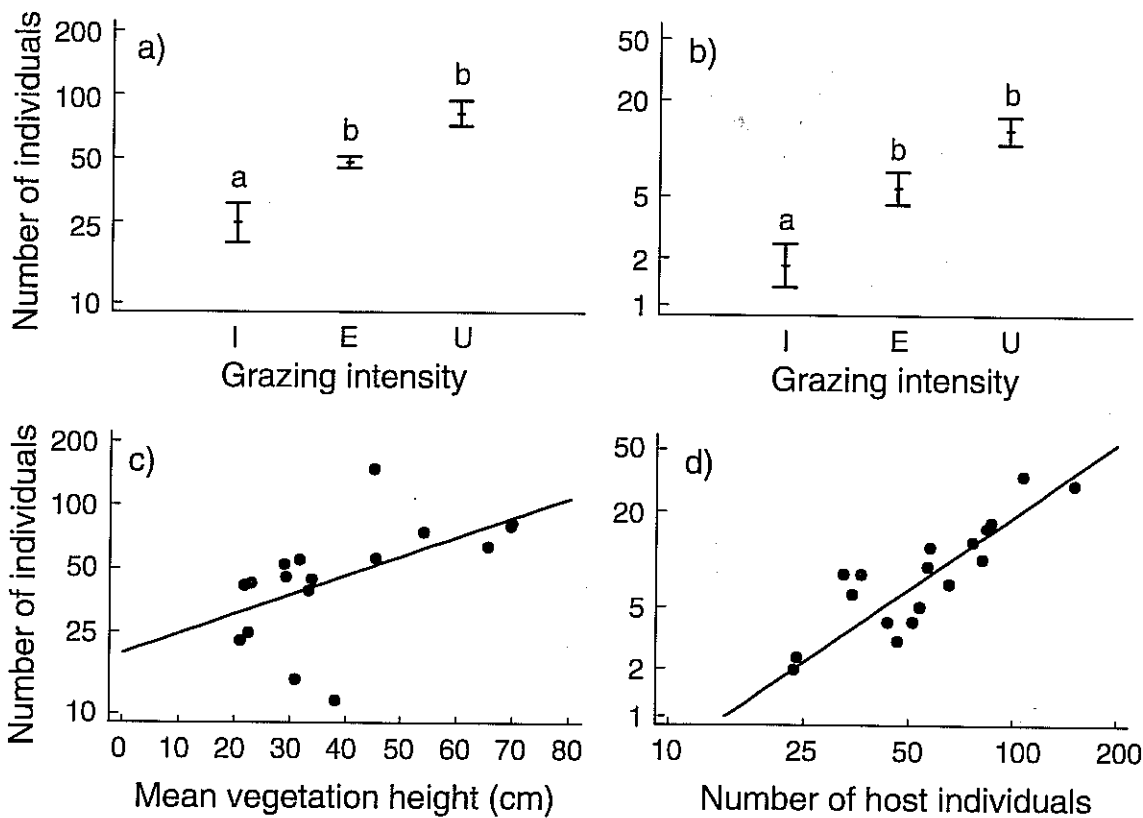


Figure 5. Effects of grazing intensity (I, intensively grazed pastures; E, extensively grazed pastures; U, ungrazed grassland) on abundance of trap-nesting bees and wasps and their parasitoids (Hymenoptera): (a) mean (± 1 SE) abundance of bees and wasps ($F_{2,14} = 14.8$, $p < 0.001$, $n = 17$) and (b) mean (± 1 SE) abundance of parasitoids ($F_{2,14} = 16.5$, $p = 0.001$, $n = 17$). Different letters above bars indicate significant differences (Tukey's honest significant difference). Correlations between (c) the abundance of trap-nesting bees and wasps and mean vegetation height ($Y = 2.9 + 0.02X$, $F_{1,15} = 6.7$, $r^2 = 0.31$, $p = 0.02$, $n = 17$) and (d) the abundance of parasitoids and their trap-nesting hosts (bees and wasps) ($Y = -5.1 + 1.7X$, $F_{1,15} = 73.8$, $r^2 = 0.88$, $p < 0.001$, $n = 17$).

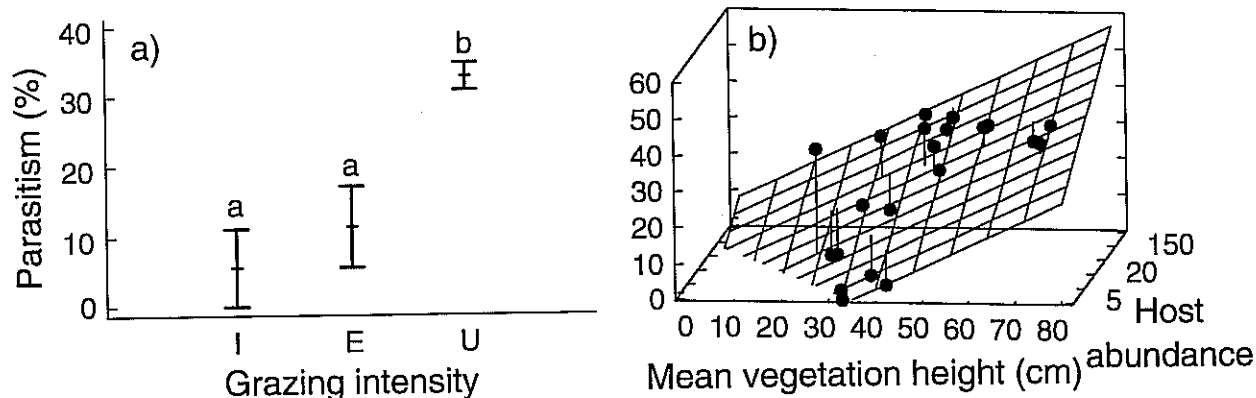


Figure 6. Parasitism of the digger wasp *T. figulus* in trap nests: (a) effect of grazing intensity (I, intensively grazed pastures; E, extensively grazed pastures; U, ungrazed grassland) on mean (± 1 SE) parasitism rate ($F_{2,14} = 10.1$, $p = 0.002$, $n = 17$) (different letters above bars indicate significant differences [Tukey's honest significant difference]); (b) correlation of percent parasitism with both mean vegetation height (X_1) and host abundance (X_2) ($Y = -19.9 + 0.6X_1 + 5.4X_2$, $F_{2,13} = 16.9$, $r^2 = 0.60$, $p < 0.001$, $n = 17$).

This increase of species diversity from intensively to extensively grazed pastures could not be linked to bottom-up effects, as predicted by the resource-heterogeneity and the resource-productivity hypotheses (Strong et al. 1984; Siemann 1998; Waide et al. 1999), because vegetation characteristics did not differ between the two pasture types. Thus, our results on the grazing intensity of the pastures differed from those of former studies in which insect diversity followed changes in plant architecture (Andrzejewska 1965; Brown et al. 1992; Lawton & Schröder 1977; Haysom & Coulson 1998), plant productivity or diversity (Walsingham 1978; Southwood et al. 1979; Lawton 1983; Hunter & Price 1992; Rosenzweig & Abramsky 1993; Siemann 1998), or destruction of feeding niche (Andrzejewska 1965). Our results correspond to the those of Di Giulio et al. (2001), who found that changes in grassland management are reflected in the insect communities of Heteroptera but not in the vegetation. However, our results on the grazing intensity of pastures are in agreement with a trophic-level hypothesis, which claims that trophic interactions such as between plants and herbivorous insects may become disrupted by disturbances such as intensive grazing (Southwood 1988; Tschamtkke 1997; Holt et al. 1999).

In contrast, the significant difference in insect diversity between pastures and ungrazed grasslands could be attributed to changes in vegetation characteristics (i.e., to bottom-up effects). The strong correlation of the species diversity of Lepidoptera and trap-nesting bees and wasps with vegetation characteristics showed that the latter were good predictors of insect diversity. Because vegetation height may indicate enhanced biomass and architectural complexity of plants, our results support the resource-heterogeneity and resource-productivity hypotheses (Strong et al. 1984; Siemann 1998). The positive correlation between the species richness of grass-

hoppers and vegetation heterogeneity reflects the requirement of grasshopper species for habitats that provide a vegetation mosaic of bare ground for oviposition and vegetation for food (Dempster 1963; Curry 1994). This agrees with the results of Wettstein and Schmid (1999), who found higher grasshopper diversity on grazed than on mown sites with a more homogenous vegetation. Moreover, the increase in vegetation height on the ungrazed grasslands was linked to a total lack of disturbance by grazing.

Intense grazing reduces both the volume and complexity of the habitat available to aboveground invertebrates (Curry 1994). The number of caterpillars (i.e., the reproduction success of Lepidoptera species) was not significantly increased by a reduction in grazing, but a ban on grazing resulted in significant changes in vegetation height, which was related to species richness and abundance. These findings support those of Balmer and Erhardt (2000), who found a more diverse butterfly fauna and more threatened species on old fallow land than on pastures and early fallow land. Wettstein and Schmid (1999) found higher butterfly densities on mown than on grazed grassland and attributed this to a higher abundance of nectar plants.

The hymenopteran species colonizing the trap nests also benefited from a reduction in grazing. Insect abundance but not species richness was higher on extensively grazed pasture than on intensively grazed pasture for bees, wasps, and their natural enemies. The percent parasitism of *T. figulus* by *C. cyanea* did not differ significantly between the two pasture types. On ungrazed grasslands, however, percent parasitism increased three-fold, supporting the hypothesis that disturbance affects the relative importance of higher trophic levels.

Grazing reduction on grasslands appears to be an important management practice by which to maintain and

increase insect diversity. Thus, financially supported extensification programs to maintain or restore traditional land-use practices may play an important role in the conservation of biological diversity on grasslands. Grassland ungrazed for some (5–10) years will further promote overall insect diversity (Kruess & Tscharnatke 2000) and will greatly contribute to the stabilization of trophic interactions such as parasitism. A mosaic of extensively grazed and ungrazed grasslands, with a resumption of grazing after a few years to prevent succession into woody habitats, may be the best strategy with which to maximize biological diversity and the strength of trophic interactions, which appear to be disrupted by disturbance through regular grazing.

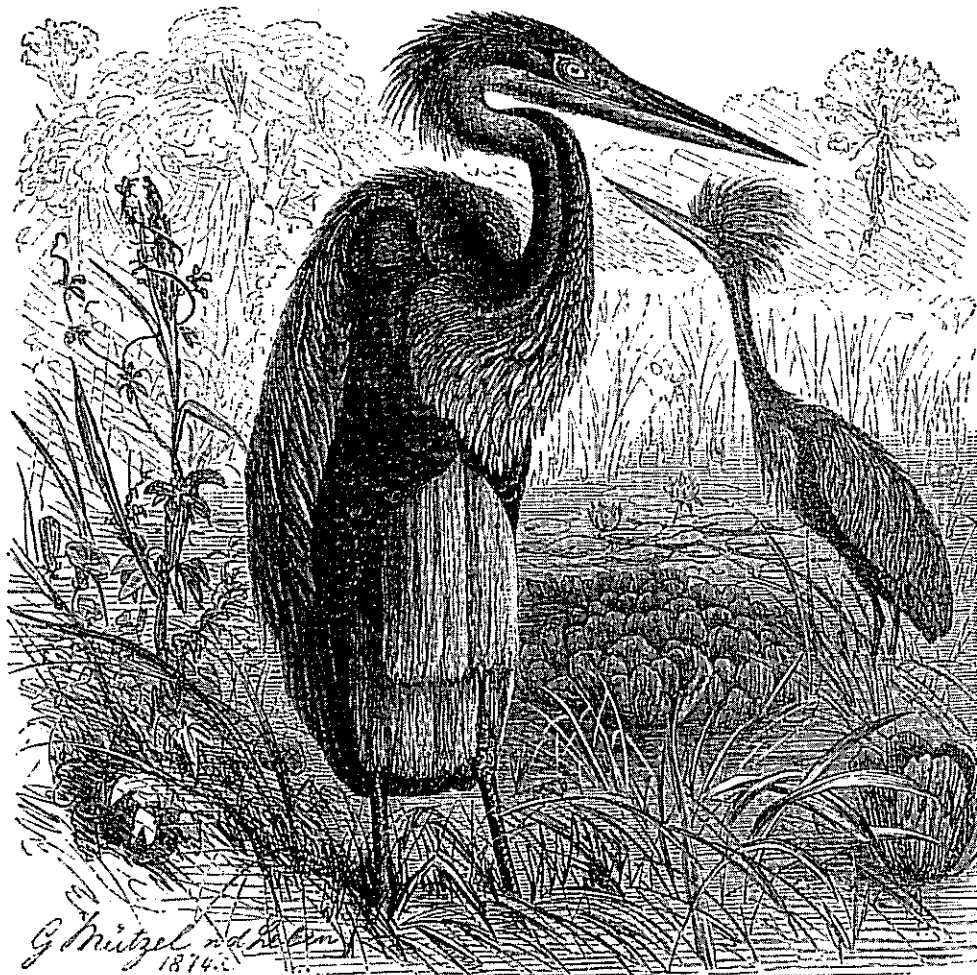
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Interspecific Effects of Artificially Propagated Fish: an Additional Conservation Risk for Salmon

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Abstract: For more than 120 years, hatcheries have released enormous numbers of Pacific salmon to compensate for numerous human insults to their populations, yet the ecological effects of this massive effort are poorly understood. We tested the hypothesis that hatchery-reared steelhead salmon (*Oncorhynchus mykiss*) released into the Snake River Basin negatively affect the survival of wild Snake River steelhead and chinook (*O. tshawytscha*) salmon. Because climatic conditions can influence salmon survival, we included an index of the El Niño–Southern Oscillation (ENSO) as a covariate in our analyses. Based on time series of hatchery releases and rates of smolt-to-adult survival, we demonstrate that the survival of wild chinook salmon is negatively associated with hatchery releases of steelhead. The state of the (ENSO) did not affect the strength of this relationship. We observed no relationship between survival of wild steelhead and steelhead hatchery releases. Our results suggest that industrial-scale production of hatchery fish may hinder the recovery of some threatened salmonids and that the potential interspecific impact of hatcheries must be considered as agencies begin the process of hatchery reform.

Efectos Interspecíficos de Peces Propagados Artificialmente: un Riesgo Adicional para la Conservación del Salmón

Resumen: Por más de 120 años, las granjas han liberado números enormes de salmones del Pacífico para compensar las numerosas agresiones humanas a sus poblaciones, sin embargo, los impactos ecológicos de este esfuerzo masivo son poco entendidos. Evaluamos la hipótesis de que la trucha cabeza de acero (*Oncorhynchus mykiss*) criada en granjas y liberada en la cuenca del Río Snake afecta negativamente la supervivencia de truchas cabeza de acero y salmones chinook (*O. tshawytscha*) silvestres. Puesto que las condiciones climáticas pueden influir sobre la supervivencia del salmón, incluimos un índice de la Oscilación del Niño del Sur como covariable del análisis. En base a series de tiempo de las liberaciones de las granjas y las tasas de supervivencia hasta adulto de peces migrantes al mar, demostramos que la supervivencia del salmón chinook silvestre está negativamente correlacionada con las liberaciones de truchas cabeza de acero de las granjas. El estado de la Oscilación del Niño del Sur no afectó el grado de correlación. No observamos relación alguna entre la supervivencia de las truchas silvestres y las liberaciones de las granjas. Nuestros resultados sugieren que la producción a escala industrial de peces de granja puede obstaculizar la recuperación de algunos salmónidos amenazados y que el impacto interespecífico potencial de las granjas debería ser considerado en cuanto las agencias inicien el proceso de reforma de las granjas.

Introduction

The decline of fisheries is a widely publicized example of resource mismanagement. A common solution to this

decline is to prop up fisheries with hatchery-reared fish or artificial propagation, sometimes on enormous scales. For example, each year hatcheries along the west coast of the United States release nearly 1.2 billion juvenile salmon (Mahnken et al. 1998), with 200 million salmon released into the Columbia River alone (Flagg et al. 2000). The merits of hatchery production have been challenged on two grounds. First, in many cases hatcher-

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