# Abundance of Invertebrates and Foraging Success ofBlack-Tailed Godwit Limosa limosa Chicks in Relation to Agricultural Grassland Management

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# Abundance of invertebrates and foraging success of Black-tailed Godwit *Limosa limosa* chicks in relation to agricultural grassland management

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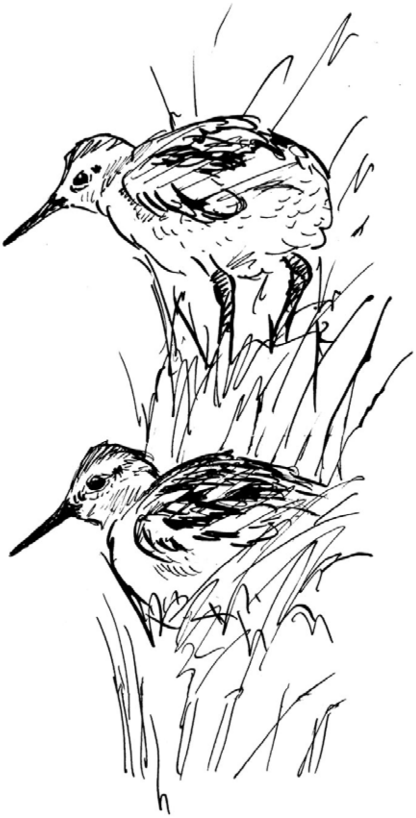
Effects of agricultural intensification on availability of grassland invertebrates as food for chicks of the declining Black-tailed Godwit *Limosa limosa* were studied in The Netherlands. Invertebrates were sampled with photo-eclectors in wet grasslands used for intensive dairy farming (high fertiliser input, 2–3 cuts starting early to mid-May) and in a meadowbird reserve (moderate fertiliser input, one cut in mid-June). Invertebrates were slightly more abundant in reserve than in agricultural fields before the first cut of the latter. In the 4–6 weeks between the first cut of agricultural fields and that of reserve fields, invertebrates were much more abundant on reserve fields. This is the main period of godwit chicks' presence. Mean size of arthropods was similar under the two management regimes, but large Coleoptera were more abundant in agricultural fields early in the season. In a foraging experiment, captive-raised godwit chicks ingested 31% fewer prey per unit time when foraging in cut agricultural grasslands than in uncut reserve fields, a difference large enough to compromise chick growth and survival. Wild broods strongly selected to stay in reserve fields, especially after agricultural fields had been cut, and travelled towards reserve fields over distances up to more than 0.5 km. Preference for reserve grasslands declined from early June onwards. We conclude that postponing mowing dates, in reserves or on farmland by means of agri-environment initiatives, improves feeding and survival conditions for godwit chicks and other insectivores feeding in the grassland sward, in addition to its beneficial effect on hatching success.

Key words: meadow birds, agricultural intensification, dairy farming, arthropods, fertiliser, mowing date, foraging success, chick survival



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## INTRODUCTION

Many bird species breeding in lowland wet grasslands in Europe have suffered considerable population declines over the past few decades (Donald *et al.* 2001, Birdlife International 2004, Thorup 2006). Loss of grassland habitat and negative effects on the birds' reproductive output of increasing intensity of agricultural use, affecting fertilizer input, water tables, mowing dates, grazing densities, and habitat heterogeneity, are thought to be the main causes of these declines (Beintema 1986, Witt 1986, Beintema *et al.* 1997, Chamberlain & Fuller 2000, Vickery *et al.* 2001, Newton 2004). The precise mechanisms involved differ between species and agricultural systems (Green 1988, Baines 1990, Berg 1992, Green *et al.* 1997, Wilson *et al.* 1997, Bradbury & Bradter 2004, Newton 2004), and are not in all cases well understood. Clearly, specific knowledge is important for defining appropriate conservation measures.

The Netherlands holds internationally important populations of grassland-breeding shorebirds (Charadrii), including 47% of the European population of Black-tailed Godwit *Limosa limosa limosa* (Thorup 2006). This species has been in decline since the 1960s, and national population estimates have fallen from at least 125 000 breeding pairs around 1975 to c. 68 000 in 2004 (SOVON 2002, Teunissen & Soldaat 2006). The main driver of this decline, especially in agricultural grasslands where 60–75% of the population occurs, is insufficient breeding productivity resulting from both reduced hatching success and low chick survival (Kruk *et al.* 1997, Schekkerman & Müskens 2000, Schekkerman *et al.* 2005).

Traditionally, research and policy concerned with conservation of Dutch grassland shorebirds focused on the survival of clutches, attempting to reduce mowing and trampling losses (Klomp 1951, Beintema & Müskens 1987, Guldemond *et al.* 1993, Kruk *et al.* 1996, Musters *et al.* 2001). The survival of chicks received attention only later (Beintema *et al.* 1991, Beintema 1995, Kruk *et al.* 1997, Schekkerman & Müskens 2000, Schekkerman *et al.* 2005). Postponing mowing and grazing until most clutches have hatched is a major aspect of meadowbird conservation practice in The Netherlands, both in reserves and in agri-environment schemes (Beintema *et al.* 1997, Kleijn *et al.* 2001, Verhulst *et al.* 2007). A second approach has been to involve volunteers in finding and marking clutches so that farmers can avoid losses due to farming operations and trampling (Guldemond *et al.* 1993, Kruk *et al.* 1996). Stimulated by the government, the number of protected shorebird nests fluctuated around 127 000 in recent years, including 22 000 nests of Black-tailed Godwit (van Paassen 2006).

Though nest protection allows more clutches to hatch, general farming practice, including fertiliser use, drainage, mowing dates and stocking densities, remains unchanged, and birds may still suffer detrimental effects of agricultural intensification. Godwit chicks, like those of most other shorebirds, are precocial and nidifugous, and feed themselves on a wide range of invertebrates living in the grassland vegetation (Beintema *et al.* 1991). In addition to direct mortality due to mowing and increased predation risk after loss of cover (Schekkerman *et al.* 2005), foraging conditions for chicks may be affected through changes in food availability.

A primary ingredient of intensification of agricultural grassland use is an increase of fertiliser inputs (Beintema *et al.* 1985, Vickery *et al.* 2001), which increases plant productivity and plant nutrient content, and reduces plant species diversity by a shift towards a few dominant species (Bakelaar & Odum 1978, Inouye & Tilman 1995). The total amount of nutrients available for invertebrate consumers generally increases and invertebrate abundance often responds positively to (nitrogen) fertilisation (Hurd & Wolf 1974, Haddad *et al.* 2000, Perner *et al.* 2005). However, in agricultural grasslands increased fertilizer inputs usually come with a suite of associated changes, like drainage, reseeding with grass monocultures, and intensive grazing or cutting, that may affect invertebrates in different ways (Schäfer & Haas 1979, Morris 1981a,b, van Wingerden *et al.* 1992). Under intense cutting or grazing, especially larger invertebrates may have difficulties completing their life cycles. The average size of grassland arthropods may decline with increasing fertilizer input (Kajak 1978, Siepel 1990, Blake *et al.* 1994), reducing the profitability (energy gained per unit handling time) of arthropod prey for foraging chicks, and this could reduce intake rate even if total biomass was unaffected (Beintema *et al.* 1991).

While these changes occur on a time scale of years, foraging success of chicks may also be sensitive to direct, short-term effects of farming practice. Nowadays, the first spring cut of agricultural grasslands overlaps extensively with the fledging period of chicks of Black-tailed Godwit and other grassland insectivores. If cut swards contain fewer invertebrates than uncut vegetation, this will reduce food availability for chicks and may affect their growth and survival.

In this study, we compare food availability for and feeding success of Black-tailed Godwit chicks between grasslands managed as a meadowbird reserve and for intensive dairy farming. These situations span the range in farming intensities found in areas with substantial meadowbird populations in The Netherlands. The abundance of grassland invertebrates is examined in relation to fertilizer input and mowing regime, water table level, and season. We also experimentally compared the foraging success of godwit chicks in cut and uncut grasslands, and described habitat selection of wild godwit broods. The implications for conservation of Black-tailed Godwits and other insectivorous birds in agricultural grasslands are discussed.

## MATERIALS AND METHODS

### Study area and management treatments

The study was conducted in an open grassland area on clay-on-peat soils near Baarn, The Netherlands (52°12'N, 15°19'E), in 1993–1996. Part of the 90 ha study site was managed as a meadowbird reserve (21 ha); the remainder was used by dairy farmers for silage production (first cut: 58 ha) and grazing (11 ha, increasing to 20–25 ha after the first cut). *Reserve management* had been in place for five years and consisted of moderate fertiliser input in the form of farmyard manure, to a total of c. 150 kg Nitrogen ha$^{-1}$ yr$^{-1}$, including c. 50 kg N ha$^{-1}$ yr$^{-1}$ by atmospheric deposition. There was one grass cut shortly after 15 June, followed by manure application and low-intensity grazing in the summer. Ditch water levels were maintained close to field level in winter, at 0.2–0.3 m below field level in spring, and lowered somewhat further in June to facilitate mowing. Two isolated reserve fields had water tables similar to agricultural fields. Under *agricultural management*, fertiliser input reached 300–350 kg N ha$^{-1}$ yr$^{-1}$, applied as cattle sludge and inorganic fertiliser. There were two or three silage cuts per year, the first in early or mid- to late May depending on the weather (Fig. 1), and the second in June. Ditch water levels in the agricultural part were 0.4–0.8 m below field level in spring and summer and 0.6–1.0 m below field level in winter. At a few fields adjacent to the reserve area, reserve water tables were maintained.

The vegetation of agricultural fields was dominated by the grasses *Lolium perenne* and *Poa trivialis*, with a variable amount of forbs (e.g. *Taraxacum officinale, Stellaria media, Ranunculus repens, Trifolium album* and *Rumex acetosa*). On reserve fields, other grasses (e.g. *Holcus lanatus, Alopecurus pratensis* and *Anthoxanthum odoratum*), and herbs (e.g. *Ranunculus acris, Plantago lanceolata, Cardamine pratensis, Bellis perennis* and *Lychnis flos-cuculi*) were more abundant. In the study period, on average 25 ± 1 (SE) godwit breeding territories (density 120 km$^{-2}$) were present in the reserve, and 21 ± 3 (30 km$^{-2}$) in the agricultural fields.

### Field characteristics and arthropod abundance

Abundance of grassland invertebrates, sward height, and abiotic field characteristics were measured in 1993–1995 between late April and early July, the period that godwit chicks are present in Dutch grasslands. A total of four or eight fields were sampled, one or two per combination of management (reserve or agricultural) and ditch water level (high or low). Two replications were

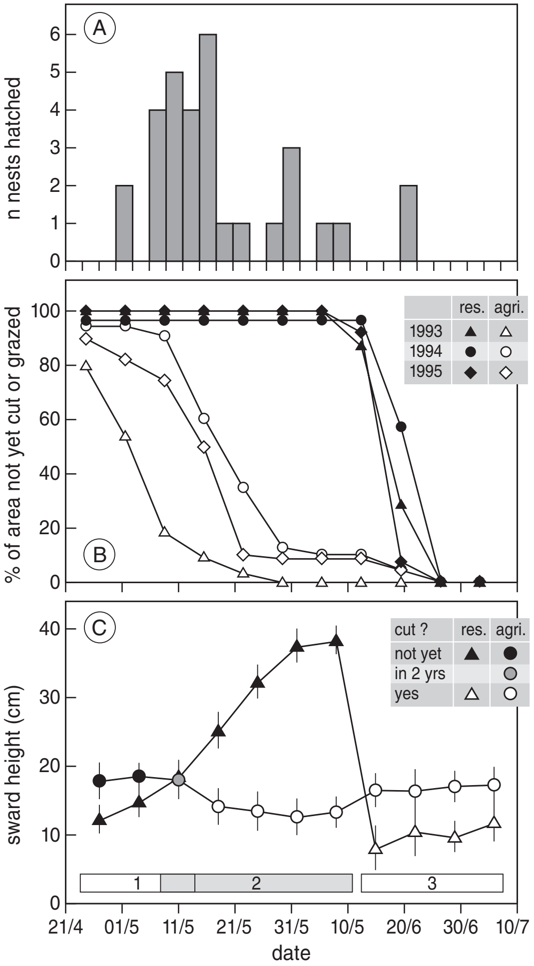

**Figure 1.** Seasonal patterns in 1993–1995 in (A) hatching dates of Black-tailed Godwit nests in the study area (grouped in 3-day periods), (B) percentage of the total area of reserve and agricultural fields in the study area that had not yet been cut or grazed and (C ) average sward height (± SE) on sampling fields (with indication of three periods used in analyses, see text). Shading of symbols denotes whether fields had been cut.

made in periods 1 and 2 in 1994 and period 1 of 1995, one in the remaining periods (see below for definition of periods).

Sward heights were measured weekly by taking 20 readings diagonally across the plot of the height at which a polystyrene disc (∅ 50 cm) rested on the vegetation. Groundwater tables were read weekly from piezometers placed in the centre of each field. Abundance of aboveground invertebrates was sampled with photo-eclectors or 'pyramid traps' (Funke 1971), pyramidal frames with 0.25 $m^2$ base area, covered by black cloth with a transparent trapping jar on top containing 4% formaline solution to kill and preserve invertebrates. Five traps were placed diagonally across each field, and emptied weekly and then reset a few m away. Sampling was discontinued during some weeks to allow mowing and manure application.

In the laboratory, invertebrates were counted and identified to taxonomic levels ranging from suborder (Hymenoptera, Homoptera, Collembola) to family (other groups). Body length was measured to the nearest 0.5 mm in animals ≤ 5 mm and to 1 mm in larger ones. Lengths were converted to dry mass using (taxon-specific) equations, given in Rogers *et al.* (1976) and Rogers *et al.* (1977) or derived by drying and weighing own material (Schekkerman 1997). All groups except Acarina and non-sminthurid Collembola were included in the analysis.

Numbers and biomass (dry weight) of invertebrates were expressed per $m^2$ and log-transformed before analysis to normalise the data. Mean dry mass of individual invertebrates was calculated by dividing the total dry weight by the number of individuals in each sample. Data were analysed with Linear Mixed Models (LMM; REML directive in Genstat version 8), with field, year and week as random variables to take into account that the same fields were sampled repeatedly over time. Differences between management categories were tested by including management type and water level (and their interaction) as fixed variables. Based on mowing schedules under the two management treatments, the season was divided into three periods. The first period comprised two weeks before any of the fields had been cut. The second period covered 2–4 weeks in which all agricultural fields had been cut once (on 8–23 May) but reserve fields not yet. The third period of 2–3 weeks ran from the first cut of the reserve fields (on 15–20 June, coinciding with the second cut of agricultural fields in two of the three years) until early July. The length of the periods differed between years, but periods included the same sampling weeks for each field within a year.

### Foraging experiment

In the main period of chicks' presence (period 2 of the invertebrate survey), foraging success of chicks was compared experimentally between (uncut) reserve and (cut) agricultural fields. In May 1995, five godwit eggs were collected from three clutches in the study area and hatched in an incubator. At age 1–2 days, the chicks were placed in grassland in an outdoor aviary of 5 x 10 m, with a small indoors section heated by an infrared lamp. Water and food (chicken pellets, supplemented with a small amount of live insects) were available *ad libitum*. Nevertheless, chicks spent most of the day searching for invertebrates in the grass of the aviary. Foraging experiments started when the chicks had become homeothermic at outdoor temperatures. After fledging, chicks were released into the field.

There were nine experimental days between 23 May and 5 June, with chicks aged 10–23 days (fledging occurs at 24–26 days). Each day consisted of two sessions. Each of two pairs of chicks was placed in a 50 $m^2$ circular wire-netting enclosure, either in a reserve field or in an agricultural field (both $n = 9$). In the next two hours, an observer seated beside the enclosure at a height of 2 m made 20 one-minute recordings of foraging rate and 10 recordings of walking speed on each chick. After a break of 1–1.5 h, the chick pairs were exchanged between fields and a second foraging session was held. Pairs were used because chicks often stopped feeding after a while if released into the enclosures alone. The composition of pairs was rotated between experimental days. All observations were made between 10:00 and 17:00 h, as feeding rate is relatively constant over this period of the day (Schekkerman 1997).

Foraging rate was defined as the number of prey items ingested per minute. Most prey were too small to be identified to type or size, but the swallowing movements were usually clearly visible. For each prey the height at which it was captured was recorded as 'high' (from vegetation at head height or upwards), 'low' (from vegetation below head level), or 'ground' (taken from the ground). Between sessions, observers moved together with the chicks, so that observer differences are aliased with differences between chick pairs and not with management type. Observer effects were explicitly accounted for in the statistical analysis.

Foraging rate and walking speed (steps $min^{-1}$) were analysed with a Linear Mixed Model (LMM) containing field type (reserve or agricultural) and session (morning and afternoon) as fixed variables and chick identity, observer and experimental day (with interactions) as random variables. Data were log-transformed before analysis.

To obtain an indication of the abundance and size distribution of grassland arthropods at the time and site of the experiments, four yellow 'sticky boards' (10 x 25 cm, adhesive on both sides) were placed vertically in the vegetation just outside the experimental enclosures at the start of the first session of each experimental day. After the second session, boards were collected and trapped arthropods were counted and their body length estimated. Sward height was measured in all experimental enclosures. Arthropod numbers (log-transformed) and sward height were compared between management types using analysis of variance, with experimental day as a blocking factor.

### Habitat use by broods

During weekly censuses of the study area between mid-April and late June 1993–1996, all Black-tailed Godwit pairs seen with chicks or giving alarm calls that reveal the presence of chicks were plotted on maps. The distribution of five grassland types was recorded simultaneously. Fields were classified as 'reserve' or 'agricultural' type, with either low (≤ 15 cm) or high (>15 cm) vegetation, or as 'grazed' by livestock (starting on the date that animals were introduced). Vegetation height on grazed fields depended on the time that animals had been present. Densities of godwit broods in different grassland types were analysed with Generalised Linear Models (GLM) with Poisson distribution and a log link function. To describe temporal changes in habitat use, the spring was divided into three periods, analogous to the invertebrate survey (Fig. 1).

## RESULTS

### Sward height and water table

Groundwater depth differed between fields with high and low ditch water levels (means 43 ± 4 cm (SE) vs. 57 ± 2 cm below field level, n = 8 fields, ANOVA: $F_{1,6} = 6.75$, $P = 0.06$), but not between reserve and agricultural fields ($F_{1,6} = 0.06$, $P = 0.83$, interaction water level x management $F_{1,6} = 0.17$, $P = 0.70$). Early in the season sward height was slightly larger on agricultural fields than on reserve fields (Fig. 1), especially on the dry ones (period 1, LMM, Wald test, effect of management type $\chi^2_1 = 20.7$, $P < 0.001$, water level $\chi^2_1 = 20.6$, $P < 0.001$, interaction $\chi^2_1 = 0.27$, $P = 0.60$). After cutting of the agricultural fields, the sward was much taller on (especially the dry) reserve fields ($\chi^2_1 = 118.6$, $P < 0.001$), while the effect of water level was no longer significant ($\chi^2_1 = 3.31$, $P = 0.07$). Sward height within agricultural fields showed a repeated saw-tooth pattern with maxima of 18–25 cm before cutting, but this does not show in Fig. 1 as individual fields were cut on different dates. With the first cut in the reserve and the second cut on agricultural fields, differences in sward height disappeared ($\chi^2_1 = 1.67$, $P = 0.20$).

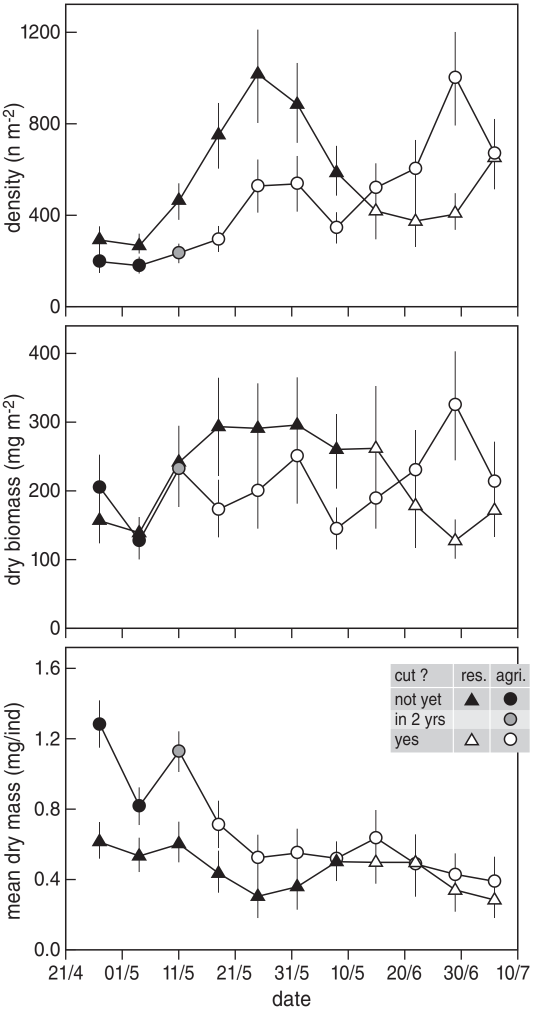

**Figure 2.** Average (± SE) total density, biomass, and mean individual size of arthropods caught in pyramid traps in reserve and agricultural fields, per week in 1993–1995. Shading of symbols denotes whether fields had been cut.

### Invertebrate abundance

Diptera (55%), Hemiptera (13%), and Araneae (12%) were the most numerous taxa in the invertebrate samples (total $n$ = 93 793 animals), while Coleoptera (5%, mainly Staphylinidae) were important in terms of biomass (31%). At the taxonomic levels considered, there was little difference in arthropod diversity between management types. Of 73 families/suborders identified, nine were exclusive to reserve fields, four of these occurring there regularly though in low numbers (Ephemeroptera, Trichoptera, Neuroptera and Lepidoptera-Nitidulidae). Four were found only in agricultural fields, with at most two specimens. There were a further nine groups of which the overall mean biomass was at least five times higher in reserve fields than in agricultural fields; there were no groups in which the reverse occurred.

The total abundance of grassland invertebrates showed strong seasonal variation, which differed between reserve and agricultural fields, and in which cutting dates marked transitions in the management type with the highest abundance (Fig. 2; LMM, Wald test: effect of period on density $\chi^2_2 = 47.8$, $P < 0.001$, on biomass $\chi^2_2 = 3.79$, $P = 0.023$, period x management interaction both $\chi^2_2 > 12.9$, $P < 0.001$). Therefore, effects of management type and water level were tested separately for each period. Before any fields were cut (period 1), total density of vegetation-dwelling arthropods was higher in reserve fields than agricultural fields (Table 1). This was reflected in the means for most major invertebrate groups, except for Coleoptera. Beetles tended to be more numerous in agricultural fields, and due to their large size reversed the difference in total invertebrate biomass. After the first cut of agricultural fields (period 2), total densities and biomass were 2–3 times as large on reserve fields as on agricultural fields. Though the difference in biomass was only close to significance, it was reflected in all major taxa. After reserve fields had been cut as well (period 3), there was a tendency towards higher abundance on the agricultural fields, but differences were not significant, possibly due to the small sample size. Similar results were obtained when only animals ≥ 1 mg dry mass – most profitable and most selected as food by godwit chicks (Beintema *et al.* 1991; Schekkerman 1997) – were included in the analysis (results not shown).

The above points to the importance of sward height in determining abundance of vegetation-dwelling grassland arthropods. Arthropod biomass increased with sward height, and neither cutting status nor management type had a significant additional effect once this was accounted for (Fig. 3). Nevertheless, sward height alone was a rather poor predictor of arthropod biomass, explaining 21% of the total variation in the data.

Differences in invertebrate abundance between ‘wet’ and ‘dry’ fields were not significant (all $P \geq 0.09$), with one exception: Diptera biomass was twice as high on dry as on wet fields in period 1 ($\chi^2_1 = 9.21$, $P = 0.002$). Interaction effects between management type and water level were not significant.

### Size distribution of invertebrates

The mean individual (dry) mass of grassland invertebrates was larger on agricultural fields than on reserve fields in the early part of the season (Fig. 2), but this difference disappeared in May as

**Table 1.** Abundance of invertebrates in reserve and agricultural fields in three periods of the spring. Means (±SE) of total density (n $m^{-2}$) and biomass (mg dry weight $m^{-2}$) are given, as well as mean biomass of the most important taxonomic groups. If difference between management types exceeds 30%, the higher value is printed bold.

| | | Period 1 (all fields uncut) | | | Period 2 (agricultural cut, reserve uncut) | | | Period 3 (all fields cut) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | *n* = 8 fields, 34 samples | | | *n* = 8 fields, 40 samples | | | *n* = 4 fields, 28 samples | | |
| | | Reserve | Farm | *P* | Reserve | Farm | *P* | Reserve | Farm | *P* |
| Total density | | **288 ±34** | 191 ±23 | 0.01 | **731 ±207** | 297 ±84 | 0.02 | 585 ±203 | 880 ±305 | 0.36 |
| Total biomass | | 147 ±28 | 182 ±36 | 0.43 | **307 ±108** | 118 ±42 | 0.06 | 218 ±78 | **319 ±114** | 0.44 |
| Biomass | Araneae | **16 ±6** | 9 ±4 | 0.30 | **12 ±8** | 1.7 ±1.0 | 0.02 | 64 ±39 | 51 ±30 | 0.77 |
| | Diptera | **59 ±9** | 41 ±6 | 0.07 | **110 ±44** | 29 ±12 | 0.01 | 71 ±35 | **113 ±56** | 0.49 |
| | Coleoptera | 41 ±14 | **99 ±35** | 0.07 | **126 ±46** | 67 ±25 | 0.22 | 8.2 ±7.0 | **20 ±16** | 0.40 |
| | Hymenoptera | **4.0 ±0.9** | 1.1 ±0.3 | <0.001 | **13 ±3** | 8.3 ±2.1 | 0.22 | 7.7 ±4.6 | 7.6 ±4.5 | 0.99 |
| | Aphidoidea[1] | 3.0 ±1.4 | 2.7 ±1.3 | 0.85 | **20 ±8** | 2.7 ±1.1 | <0.001 | 4.2 ±4.6 | **15 ±16** | 0.35 |

[1] Including Collembola of the family Sminthuridae.

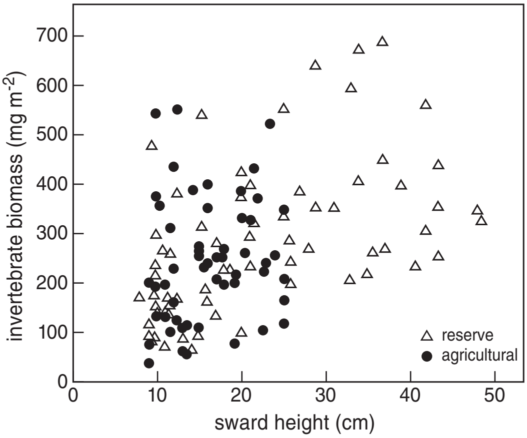

**Figure 3.** Relationship between arthropod biomass and sward height on reserve and agricultural fields sampled repeatedly over time. Arthropod biomass increased with sward height (fixed variable in LMM with field and year as random factors, $\chi^2_1 = 29.9$, $P < 0.001$; $\ln(y) = 4.90 + 0.027x$, $r^2 = 0.21$), and neither cutting status (cut or uncut, $\chi^2_1 = 1.42$, $P = 0.23$) nor management type (reserve or agricultural, $\chi^2_1 = 0.02$, $P = 0.89$) had a significant additional effect once sward height was accounted for.

the mean size of animals decreased (LMM, period $\chi^2_2 = 25.5$, $P < 0.001$, management $\chi^2_1 = 8.73$, $P = 0.003$, management x period interaction $\chi^2_2 = 8.06$, $P < 0.001$). Already in period 2 the effect of management type was no longer significant. It was caused mainly by differences between management types in relative abundance of taxa containing large (Coleoptera) and small animals (Hymenoptera, aphids), but the decline in average size over time was also caused by changes in size composition within major taxonomic groups (mean size of Diptera and spiders largest in period 1, of beetles largest in period 2 and smallest in period 3, all $P < 0.005$). During the main period of godwit chicks' presence in Dutch grasslands (early May to mid-June), the overall mean individual dry mass of arthropods was 0.44 ± 0.07 mg on reserve fields and 0.53 ± 0.07 mg on agricultural fields. Water table level had no significant effect on the mean size of grassland invertebrates ($\chi^2_1 = 1.65$, $P = 0.20$).

### Foraging success of chicks

The agricultural fields included in the foraging experiment had already been cut and the vegetation was in varying stages of regrowth. Average sward height was 53% higher on the still uncut reserve fields than on agricultural fields. The average total number of insects caught on sticky boards during the experiments did not differ between reserve and agricultural fields, but animals >4 mm body length, most important in the chicks' diet, were twice as abundant in reserve fields (Table 2).

The foraging behaviour of experimental chicks closely resembled that of chicks in natural families observed in reserve grasslands in enclosures measuring 0.2–0.6 ha (Schekkerman 1997). Of 9725 prey eaten by 'wild' chicks older than 9 days, 20.6% were taken high in the vegetation, 78.1% low in the vegetation and 1.3% from the ground. For experimental chicks in reserve fields, these proportions were similar (15.2, 81.5 and 3.3%, $n = 4565$). Foraging rate of experimental birds was on average slightly lower than shown by wild chicks at the same age and time of day (GLM, $F_{1,25} = 6.00$, $P = 0.022$), but within the same range of variation (range of daily means for experimental chicks: 4.7–8.0 prey min$^{-1}$, $n = 9$, for wild chicks 3.7–12.1, $n = 16$). Belting & Belting (1999) observed similar foraging rates of 5–9 prey min$^{-1}$ in wild godwit chicks.

On eight out of nine experimental days, the chicks' foraging rate was lower in the agricultural field than in the reserve field. Over the entire experiment, mean foraging rate was 31% lower in agricultural fields (Table 2). The difference was most pronounced for arthropods captured high in the vegetation (81% lower in agricultural fields), probably as a direct result of the shorter sward, but capture rate of prey from the lower vegetation level was reduced as well (by 26%). There was no significant difference in the rate at which prey were taken from (near) the ground. The reduction in feeding rate occurred despite a 17% higher walking speed in agricultural fields (Table 2). Hence, 41% fewer prey were ingested per distance searched in agricultural than in reserve fields.

**Table 2.** Summary of foraging experiments. Means (± SE) over nine experimental days for foraging rate and walking speed of chicks, and sward height and insect numbers caught on sticky boards in the experimental enclosures.

| | Reserve (uncut) | Agricultural (cut) | Test | *P* |
|---|---|---|---|---|
| Foraging rate (prey $\text{min}^{-1}$) | 6.06 ±0.72 | 4.19 ±0.50 | $\chi^2_1 = 156.9$ | < 0.001 |
| From high vegetation (prey $\text{min}^{-1}$) | 0.44 ±0.14 | 0.09 ±0.03 | $\chi^2_1 = 255.9$ | < 0.001 |
| From low vegetation (prey $\text{min}^{-1}$) | 4.08 ±1.18 | 3.02 ±0.88 | $\chi^2_1 = 55.0$ | < 0.001 |
| From ground level (prey $\text{min}^{-1}$) | 0.07 ±0.01 | 0.07 ±0.01 | $\chi^2_1 = 0.27$ | 0.60 |
| Walking speed (steps $\text{min}^{-1}$) | 68.4 ±4.0 | 79.9 ±4.6 | $\chi^2_1 = 44.5$ | < 0.001 |
| Sward height (cm) | 29.7 ±1.7 | 19.4 ±1.4 | $F_{1,8} = 19.8$ | 0.002 |
| Total arthropods (n $\text{board}^{-1}$) | 204 ±33 | 213 ±35 | $F_{1,8} = 0.03$ | 0.86 |
| Arthropods >4 mm (n $\text{board}^{-1}$) | 53 ±10 | 27 ±5 | $F_{1,8} = 6.67$ | 0.032 |

## Habitat use by broods

The average total number of godwit broods in the study area was much higher in period 2 (8.8 ± 1.5 broods) than in periods 1 (1.1 ± 0.7) and 3 (2.2 ± 1.3) (Fig. 4). GLMs revealed significant effects on brood density of both period ($F_{2,105} = 28.3$, $P < 0.001$) and grassland type ($F_{4,105} = 30.4$, $P < 0.001$). Densities were significantly higher in reserve grasslands with sward height >15 cm than in all other types (pairwise differences, $t \geq 2.50$, $P \leq 0.014$), and significantly higher in agricultural fields >15 cm than in grazed fields ($t = 2.07$, $P = 0.041$) and agricultural fields <15 cm ($t = 3.03$, $P = 0.003$). Hence, godwit broods selected the highest vegetations available, which until cut in mid-June were located on reserve fields. In period 3, uncut reserve fields were no longer available and the remaining broods were found in agricultural fields with a regrowing sward (≥ 15 cm) and grazed fields (Fig. 4).

In the period of maximum brood abundance (period 2), broods were more concentrated in the reserve part of the study area (67%, $n = 137$, years combined) than were the breeding territories (54%, $n = 185$; $G^2_1 = 6.13$, $P = 0.02$). The maximum number of 23 broods observed in the reserve area on a single day exceeded the number that had hatched there in that year (14–17, unpubl. data). Hence, broods actively moved towards the reserve when agricultural fields were mown. Such movements were repeatedly observed in the field, the birds sometimes arriving from distances of more than 500 m. However, the preference for reserve fields over agricultural grasslands declined somewhat in the last 10 days before cutting of the reserve fields in mid-June, and some late broods that hatched on reserve fields were seen to move to agricultural grasslands with a sward that had regrown to >15 cm.

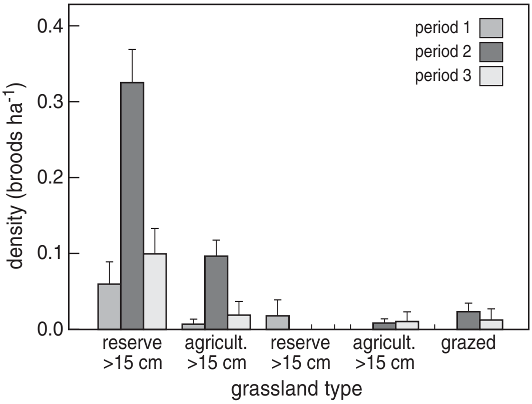

**Figure 4.** Mean density (± SE) of godwit broods in three periods during spring in five types of grassland: reserve and agricultural meadows with sward height lower and higher than 15 cm, and grazed pastures (sward height usually <15 cm). In 1993–1996, a total of 9, 13 and 4 censuses were made in the three periods, respectively, involving 10, 132 and 9 broods.

## DISCUSSION

### Arthropod abundance and size

Photo-eclectors provide useful estimates of food availability for godwit chicks, as they sample the density of a wide range of vegetation-dwelling arthropods, and their efficiency is less dependent on vegetation structure than that of suction samplers or sweep nets. Photo-eclectors did not capture many invertebrates that live on the grassland floor (e.g. Lycosid spiders, Carabid beetles, and slugs), but in this they resemble godwit chicks, that take more than 95% of their prey from the vegetation layer. Faecal analysis has shown that almost all major invertebrate taxa found in grasslands, from 1.5 mm aphids to beetles and craneflies ≥ 15 mm, occur in the diet (Beintema *et al.* 1991), so that the use of a broad-range sampling technique is justified. Nevertheless, chicks may actively select or avoid certain types of invertebrates while foraging.

In addition to grassland arthropods, godwit chicks sometimes feed on earthworms and soil-dwelling larvae of tipulid midges and other insects. However, remains of soil fauna are found in only a small fraction (2–13%) of godwit chick faeces (Beintema *et al.* 1991), and probing into the soil does not become an important feeding technique until after fledging (Schekkerman 1997). Chicks did occasionally take slugs (Limacidae and Arionidae, Gastropoda), and these reached ≥ 10 times higher densities in the reserve than in agricultural fields (unpubl. data from pitfall traps).

This study revealed large seasonal variation in the abundance of grassland invertebrates, and differences between management types that were associated with the mowing regime of the fields. The effect of management type was largest in period 2, when total densities and biomass were 2–3 times as large on the uncut reserve fields as on the agricultural fields that had been cut in early to mid May. Short-term effects of cutting thus were a major factor affecting invertebrate abundance. Similar results were obtained by Struwe-Juhl 1995 by sweepnet sampling. Removal of a large part of the vegetation results in the disappearance of much of the entomofauna, and some time is needed for populations to recover (Andrzejewska & Gyllenberg 1980). For Black-tailed Godwits, this short-term effect is highly relevant, as mowing dates in agricultural grasslands coincide with hatching of the chicks (Fig. 1).

Long-term effects of management on arthropod abundance are not always so straightforward (Schäfer & Haas 1979) and may depend on the species (e.g. Morris 1981a,b). In the current study, they should be most apparent before either type of fields were cut. In period 1, the total density of arthropods was higher on reserve fields, but this was not reflected in biomass because large Coleoptera (especially rove beetles Staphylinidae) were more numerous on agricultural fields. Their low presence in faeces (7%, Beintema *et al.* 1991) suggest that rove beetles are not frequently eaten by godwit chicks. Diptera, which dominate the chicks' diet numerically (Beintema *et al.* 1991), did reach a significantly higher biomass on reserve fields. There was a non-significant trend in the same direction in three of the four other major arthropod taxa. Hence we found indications for both a short-term and a long-tem negative effect of high-intensity agricultural grassland use on the abundance of invertebrates as food for chicks.

Although arthropods tended to be more abundant on dry than on wet fields, the differences did not reach significance at the replication level of this study. However, low water tables generally lead to early mowing as a result of earlier vegetation development and enhanced access for heavy machinery (e.g. Guldemond *et al.* 1995). Because of the large reduction of invertebrate abundance due to early mowing, the net impact of lowering water tables on food supply for chicks will usually be negative.

Siepel (1990) reported a strong decline in the mean weight of grassland arthropods over fertiliser levels of 0, 50 and 400 kg N $ha^{-1}$ $yr^{-1}$, mainly due to the disappearance of larger species. Similar effects were found by Kajak (1978) in spiders and by Blake *et al.* (1994) in ground beetles. In contrast, this study found a larger mean size of arthropods on heavily fertilised agricultural fields than on reserve fields in the early part of the chick period, but the difference between management types was relatively small and was caused mainly by large beetles that are not a frequent prey of chicks. The same photo-eclectors as in our study were employed by Siepel (1990), but this author sampled grasslands on sandy soils and over a longer season (April–September). Comparing the results despite these differences suggests that the relationship between invertebrate size distribution and fertiliser input may be nonlinear, with the largest change occurring at fertiliser levels below 100 kg N ha$^{-1}$ yr$^{-1}$ (Fig. 5). Further work is needed to confirm this pattern, but it would mean that scope for influencing prey size through management is limited in Dutch agricultural grasslands, as such low fertiliser inputs are nowadays found almost only in nature reserves.

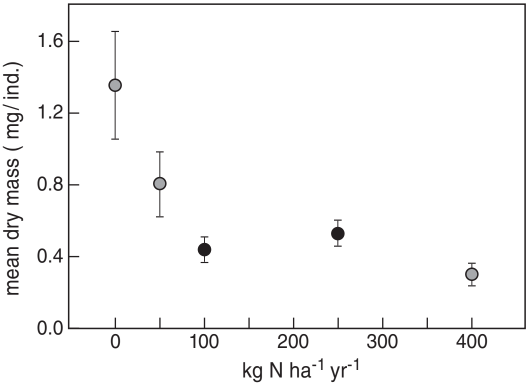

**Figure 5.** Relationship between fertiliser Nitrogen input and individual dry mass (mean ± SE) of grassland arthropods as sampled with photo-eclectors by Siepel (1990, grey dots) and in this study (black dots).

## Chick foraging success

Total invertebrate abundance may be a poor indicator of feeding conditions for chicks, if intake rates are constrained by other foraging factors such as handling time or the fraction of the total fauna that is available to chicks, or by conflicting interests such as vigilance for predators. The foraging experiment however confirmed that the lower abundance of grassland invertebrates in (cut) agricultural fields than in reserve fields in period 2 translated into a lower foraging rate of chicks. Prey ingestion rate of the experimental chicks was on average 31% lower in the agricultural fields. The difference was even larger (41%) when expressed relative to the area searched, due to the higher walking speed in agricultural fields. It is not clear whether this higher speed was an attempt to compensate for a lower prey density, or a result of mechanical constraints on walking in the taller vegetation of the reserve fields. Although the size of the enclosures affected the experimental chicks' foraging behaviour to some extent (they spent part of the time walking along the fence), their prey ingestion rate in uncut fields was within the range of that of wild chicks, suggesting that the foraging rate of the hand-raised chicks was a useful indicator of foraging conditions at least in a comparative sense.

We measured feeding rate of chicks as the number of prey ingested per unit time, but most items taken were too small to estimate their size. Theoretically, the experimental chicks could have compensated for the lower ingestion rate by taking larger prey in agricultural fields. Because no significant difference in the mean size of invertebrates was found between management types in the photo-eclectors in period 2, and the sticky board samples indicated that larger insects (>4mm) were more abundant in the reserve fields at the time of the experiments, any such differences in prey size would have to result from active selection by the chicks. This could improve foraging success only if chicks foraged suboptimally in reserve fields, depressing their intake rate by taking too many small prey. It seems therefore unlikely that compensation occurred and the prey ingestion rate of foraging chicks probably reflected energy intake.

## Field selection by broods

The better feeding conditions in (uncut) reserve grasslands were reflected in the habitat selection of godwit broods. The majority of broods were found in reserve fields, both before and especially after agricultural grasslands were cut, and active movements toward reserve fields occurred over distances of several 100s of meters. Grasslands with a sward height below 15 cm, including most grazed fields, were avoided as long as taller grass was available. In addition to offering the best feeding opportunities, tall vegetation provides shelter from wind (Klaassen 1994), and protective cover from predators (Whittingham & Evans 2004, Schekkerman *et al.* 2005). The small chicks are less visible in tall grass, while predator detection is probably less affected as this is mainly done by the larger parents. These benefits are all correlated with sward height, so that their relative importance cannot be easily judged.

The preference for uncut reserve grasslands became less strong from early June onwards. At this time the vegetation of the reserve fields had grown quite tall (Fig. 1), and started to flatten due to wind and rainfall. In addition, invertebrate abundance in the uncut reserve fields started to decline from the end of May onwards (Fig. 2), especially in the year with the earliest vegetation development. As herbs stop flowering and seed-set and lignification occur in the grasses, phytophagous invertebrates decline in reaction to the reduction of their food resources (Andrzejewska & Gyllenberg 1980). Foraging in reserve grasslands thus becomes less profitable for chicks later in the season, due to physical obstruction by the vegetation and a reduction in prey availability.

### Implications for chick growth and survival

Due to the mobility and strong habitat preference of godwit families, the effect of management on growth and survival of chicks could not be measured directly by comparing broods raised in different grassland types. No broods in the study area stayed in cut agricultural fields throughout the fledging period; all moved to uncut (reserve) fields permanently or intermittently. However, some insight into the potential consequences of intensive farming for godwit chicks can be gained from energetic considerations.

Schekkerman and Visser (2001) constructed energy budgets for godwit chicks on the basis of laboratory and field measurements and found that only 27% of the total energy metabolised up to fledging is allocated to growth (decreasing from 50% shortly after hatching to 15% at fledging). The remaining part of the budget, consisting of maintenance and activity, cannot be substantially economised upon in periods of food shortage, because food intake is inevitably tied to activity in the self-feeding chicks. Scope for compensating a reduced intake rate by foraging longer is also limited, as godwit chicks already spend c. 80% of the daylight period foraging even in reserve grasslands (Schekkerman & Visser 2001). This implies that reductions in foraging success may quickly result in insufficient energy being available for growth.

The 31% difference in feeding rate between reserve fields and agricultural fields observed in our experiment is of similar magnitude as the growth component in the chicks' energy budget. Effects on growth and survival are therefore to be expected, especially during inclement weather, when foraging success is already reduced (Schekkerman 1997) and feeding time for young chicks is constrained by an increased need for brooding (Beintema & Visser 1989). Godwit chicks carry only small fat reserves and starve within a few days without food (Schekkerman & Visser 2001). In addition, a poor body condition may increase the risk of predation (Swennen 1989, Schekkerman *et al.* 2005), or parasitic infection and disease (Gershwin *et al.* 1985, Lochmiller *et al.* 1993), while a reduced growth rate delays fledging and prolongs the period of vulnerability to (mammalian) predators and mowing machines.

### Management implications

This study has shown that modern intensive dairy farming, as found over much of the grassland area of The Netherlands, negatively affects feeding conditions for Black-tailed Godwit chicks. Fewer invertebrates occur in the vegetation of intensively used agricultural grasslands in comparison to reserve grasslands, especially after cutting. Current cutting dates in agricultural grassland approximately coincide with the peak of hatching of young godwits (Fig. 1). In addition, the timing of the first cut and the hatching dates of godwit chicks are correlated between years, as both vegetation development and godwit laying dates are sensitive to spring temperature (Kruk *et al.* 1996). A large proportion of chicks in agricultural areas are thus born into a situation in which many fields have already been cut and offer a reduced food supply. Foraging success is reduced to such an extent in these grasslands that the chicks' growth and survival are compromised.

The preference for tall vegetation puts godwit chicks at risk of being killed directly during mowing, though a significant proportion are able to escape the machines (Kruk *et al.* 1997). Surviving broods respond to the loss of shelter and feeding habitat by moving to uncut fields, but increased mechanisation and the shift from hay to silage production have led to increasingly large areas of grassland being cut within a short period. Any uncut refuges may become too small to accommodate all broods, and chicks in isolated pockets of tall vegetation may suffer increased predation risk. Recent studies confirmed that the survival of Black-tailed Godwit chicks is positively correlated with the proportion of late-cut grasslands in the breeding area (Schekkerman & Müskens 2000, Schekkerman *et al.* 2005).

These results indicate that conservation measures that increase hatching success, such as nest protection, may be ineffective for Black-tailed Godwits unless they are accompanied by measures promoting chick survival. Agri-environment schemes in which farmers postpone the first cut of grasslands should improve survival of godwit chicks outside reserves, in addition to their merit in reducing egg losses. By mid-June (or a week later in the North of the country; Beintema 1995) the majority of chicks have fledged, and the uncut swards have become less attractive to the remaining broods, so that further postponement of cutting does not yield benefits for godwits, although it may do so for other bird species. The magnitude of the short-term effects of cutting on invertebrate abundance found in this study shows that late mowing improves feeding conditions for insectivorous birds even when no changes in fertiliser use or water table occur, although the sampling results in period 1 suggest that benefits increase on a longer term when fertiliser input is reduced and a more diverse vegetation develops.

Other insectivorous grassland birds such as Eurasian Curlew *Numenius arquata*, Common Redshank *Tringa totanus*, Ruff *Philomachus pugnax* and certain passerines may be affected in the same way as Black-tailed Godwit chicks, although others like Northern Lapwing *Vanellus vanellus* and Common Starling *Sturnus vulgaris*, forage more profitably in short swards (Devereux *et al.* 2004). Adult godwits, which feed by probing for soil invertebrates, similarly show a preference to feed in shorter swards, and occasionally leave their brood in their mate's care to feed in nearby cut fields (unpubl. data). The proximity of differently managed fields within the same area may thus allow different bird species and age classes to each use their preferred grassland type (Benton *et al.* 2003). Godwit broods actively migrate towards the late-mown 'refuges' within heterogeneous landscapes, and this will also enhance the effectiveness of nest protection carried out in the surrounding fields. The desired spatial configuration of such 'management mosaics' depends on the maximum density at which broods can co-occur and the distances that they can safely bridge, and deserves further study.

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## SAMENVATTING

In dit artikel worden de effecten bestudeerd van landbouwintensivering op de voedselbeschikbaarheid voor kuikens van de Grutto *Limosa limosa*. De ongewervelde fauna werd bemonsterd in de vegetatie van graslanden gebruikt voor intensieve melkveehouderij (hoge mestgift, 2–3 maaibeurten vanaf het begin of het midden van mei) en in een weidevogelreservaat (matige mestgift, één maaibeurt in het midden van juni). Voorafgaande aan de eerste snede op agrarische percelen waren ongewervelden iets talrijker op de reservaatpercelen. In de 4–6 weken tussen de eerste snede op agrarische percelen en die in het reservaat was het verschil veel groter en waren insecten en spinnen veel algemener in de ongemaaide vegetaties van het reservaat. Juist in deze periode zijn veel gruttokuikens aanwezig in Nederlandse graslanden. De gemiddelde grootte van individuele ongewervelden was vergelijkbaar in beide typen grasland, maar vooral vroeg in het seizoen waren de relatief grote kevers talrijker in agrarische percelen. In een experiment werd het foerageersucces van in gevangenschap grootgebrachte gruttokuikens vergeleken tussen gemaaide agrarische percelen en nog niet gemaaid reservaatgrasland. In het reservaat bemachtigden de kuikens 31% meer prooien per tijdseenheid foerageren, een verschil dat groot genoeg is om te leiden tot effecten op hun groei en overleving. Vrij levende gruttofamilies vertoonden een sterke voorkeur om te verblijven in ongemaaide reservaatpercelen, vooral nadat het meeste agrarische grasland was gemaaid. Ze trokken actief naar zulke percelen toe, soms over afstanden van 500 m of meer. Deze voorkeur voor ongemaaid grasland nam vanaf begin juni af, vermoedelijk doordat de vegetatie hier te hoog en dicht werd en insecten er in aantal afnamen. Wij concluderen dat het uitstellen van de eerste snede, in reservaten of door beheersovereenkomsten in agrarisch grasland, niet alleen de uitkomstkansen van weidevogellegsels vergroot, maar ook gunstig uitwerkt op de foerageeromstandigheden en de overleving van gruttokuikens, en mogelijk van andere insectenetende vogelsoorten die foerageren in de graslandvegetatie.

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