BioOne COMPLETE

Feeding preferences of Chorthippus parallelus (Orthoptera: Acrididae)

Authors: Gardiner, Tim, and Hill, Julian

Source: Journal of Orthoptera Research, 13(2) : 197-203

Published By: Orthopterists' Society

URL: https://doi.org/10.1665/1082-6467(2004)013[0197:FPOCPO]2.0.CO;2

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Feeding preferences of *Chorthippus parallelus* (Orthoptera: Acrididae)

TIM GARDINER AND JULIAN HILL

(TG)Centre for Environment & Rural Affairs (CERA), Writtle College, Chelmsford, Essex, UK, CM1 3RR. Email: tg@writtle.ac.uk
(JH) Faculty of Applied Science and Technology, Writtle College, Chelmsford, Essex, UK, CM1 3RR

Abstract

The aim of this study was to establish whether feeding preferences exist in *Chorthippus parallelus* among 4 grass species: *Cynosurus cristatus, Dactylis glomerata, Festuca rubra* and *Lolium perenne*. Ten grass microswards, each composed of equal areas of the 4 grass species, were established in early 2003. These were placed in insect cages in early June and the number of feeding signs monitored over a 2-week period, for early instar nymphs (1-2), late instar nymphs (3-4), early adults and late adults. *Dactylis glomerata* and *Lolium perenne* were the preferred food choices of late instar nymphs, early adults and late adults, perhaps because of these foods' superior nutritive value and palatability. *Festuca rubra* was less favored by *C. parallelus* at all stages of insect maturity, perhaps due to leaf hardness making it difficult for the mandibles to penetrate. An aphid infestation of *C. cristatus* during early July caused the leaves to senesce and resulted in reduced feeding on this species by early and late adults.

Key words

Chorthippus parallelus, feeding preferences, *Cynosurus*, *Dactylis*, *Festuca*, *Lolium*, nutrition

Introduction

Grasshoppers are important herbivores of extensively managed grassland (Brown 1983, Marshall & Haes 1988). They are an important component of the overall energy budget of grassland ecosystems, consuming approximately 3.5% of annual primary production (Köhler *et al*. 1987). Species such as *Chorthippus parallelus* Zetterstedt have been shown to select grasses in preference to forbs (Bernays & Chapman 1970a, b), although there have been occasional reports of the species feeding on herbaceous plants (Clarke 1948). Much detailed work has already been conducted on the feeding preferences of *C. parallelus* by Bernays & Chapman (1970a, b). Although these authors concluded that this species does not depend on any single grass species for its food, marked selection among grass species occurred at some sites. For instance, *Agrostis* and *Festuca*, common in the habitats studied, were important food sources for *C. parallelus;* grasses such as *Cynosurus, Dactylis* and *Holcus* were less important, perhaps as they were less common in the habitats studied (Bernays & Chapman 1970b). Recent research demonstrates that *C. parallelus* is most numerous in grasslands dominated by fine-leaved grasses such as *Agrostis* and *Festuca*, as opposed to those where *Lolium* predominates (Gardiner *et al*. 2002). These authors suggest that the suitability of fine-leaved grassland swards for *C. parallelus* may be a result of preferential feeding on fine-leaved grasses, sward structure and microclimatic factors.

The study reported in this paper attempted to identify feeding preference by *C. parallelus* between 2 fine-leaved grass species, *Cynosurus cristatus* L. and *Festuca rubra* L., and 2 broad-leaved grass species, *Dactylis glomerata* L. and *Lolium perenne* L. The results may help explain whether the latter 2 grass species offer habitats unfavorable for grasshoppers such as *C. parallelus* (Clarke 1948, Gardiner *et al*. 2002) through lack of suitable feeding resources at the differing stages of grasshopper maturity.

Methods

Ten microswards each composed of the 4 main grass species were established in early February 2003. Plant pot bases (diameter 31 cm) were filled with compost and then divided into 4 equal sections, each 182 cm^2 in area. Seed of *Cynosurus cristatus* (*var*. Southland), *Dactylis glomerata* (*var*. Sparta), *Festuca rubra* (*var*. Wilma) and *Lolium perenne* (*var*. Condesa) were sown at 10 g per m^2 into different sections of each microsward (Fig. 1). Each microsward was allowed to establish in a glasshouse for 4 mo. Germination of the 4 grass species occurred within 2 w of sowing and subsequent grass growth was fairly rapid due to the very warm glasshouse conditions (22 to 25^{0}C).

In early June each microsward was placed on the ground in a cylindrical frameless insect cage (net: 28-gauge Terylene). Each cage had a basal diameter of 35 cm; the net had a drop of 1 m and was fitted with a 45-cm zip for easy access (Alana Ecology, Bishops Castle, Shropshire, UK). The 10 cages were hung from a metal frame at a height of approximately 1.5 m (Fig. 2) and located in an area of grassland and trees on the Writtle College Estate in Chelmsford, Essex, UK (OS grid reference TL677067). The design of the net allowed the environment conditions inside to match those outside as closely as possible, leading to the behavior of the insects being representative of natural field conditions over the course of a season. To investigate the micro-environment inside the cage, data loggers (Gemini Data Loggers, Chichester, West Sussex, UK) were placed at ground level inside and outside the cage. The data loggers recorded hourly temperature from 18 August to 26 September. To obtain the temperature readings, data loggers were downloaded using GLM software (available from Gemini Data Loggers) on a standard PC.

Monitoring of feeding preferences.—One early instar grasshopper nymph (1 or 2) was introduced onto the microsward in each cage on 2 June 2003 at 1100 hours. The 10 nymphs were collected from an area of rough grassland on the Writtle College Estate where only *C. parallelus* occurs. The swards were monitored every 2 d to record feeding damage, with the last examination being made on 16 June 2003. All nymphs

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use



Fig. 1. A microsward 4 mo after sowing: top left *Lolium perenne*, top right *Festuca rubra*, bottom left *Cynosurus cristatus*, bottom right *Dactylis glomerata*.



Fig. 2. The experimental layout showing the 10 insect cages; 1 microsward was placed on the ground in each cage.

were then removed from the cages and returned to their original site.

Before the microswards were removed from the cages for each sampling of feeding damage, the perch of each of the 10 nymphs was recorded as being on 1 of the 4 grass species or on the net. Each sward was removed at 0900 h and visually checked for feeding damage. Each grass species was observed for 3 min to provide even coverage of observation and the number of feeding signs per species recorded. A well-defined bite on the leaf edge of at least 1 mm in width was counted as 1 feeding sign. Occasionally, especially on the larger-leaved grass species, feeding signs could be over 15 mm in width and were obviously the result of sustained feeding over a long time period, especially long for early instar nymphs. Where sustained feeding was observed 1 feeding sign was recorded, but a note made of the particularly severe damage. No attempt was made to weigh nymphs or analyse faecal pellets as in previous studies of Richards & Waloff (1954) or Bernays & Chapman (1970b), as this would have interfered with the processes of feeding. After assessment of each feeding sign, the leaf on which it occurred was cut off to ensure that the same sign was not recorded on subsequent examinations.

The experiment was repeated with identical method for 10 late instar nymphs (3 or 4) commencing on 29 June 2003, early adults commencing on 1 August 2003 (5 ♂, 5 ♀) and late adults commencing on 31 August 2003 (5 ♂, 5 ♀). The same observer recorded the feeding signs on every occasion.

Analysis of herbage properties.—Herbage properties such as leaf area and angle may have an important influence on grasshopper feeding. For example, Bernays & Chapman (1970a) suggested that grasshoppers may rest on particular grass species because of the orientation (or angle) of the leaves. For 100 randomly selected leaves the angle from the horizontal was measured (Rhodes 1981) and a mean leaf angle produced for each grass species. Leaf area may also be important because grass species with larger leaves offer grasshoppers more abundant foliage on which to feed. The leaf area of 100 randomly selected leaves of each grass species was calculated by measuring leaf length and width in mm and then multiplying this by 0.95 (Robson & Sheehy 1981).

Leaf hardness has been suggested as an important factor controlling feeding preferences (Bernays & Chapman 1970a). A simple leaf penetrometer was used to test leaf hardness and the method was modified from Williams (1954) and Bernays & Chapman (1970a). The weight (grams) of sand that it took for a pin to penetrate a leaf of each grass was the measure of leaf hardness. Readings were taken from 10 randomly selected leaves of each grass species. Leaf height above the ground was measured by randomly passing a pin, with a 2-mm diameter and sharp point, vertically through the sward and recording the height at which it came into contact with leaves (Robson & Sheehy 1981). One hundred pins were recorded for each grass species.

A palatability index was devised (Table 1) based upon the % of leaf senesced (brown/yellow coloration). A leaf with an index of 1 was fresh, with very little browning and could be considered the most favorable for grasshopper feeding, whereas, a leaf with a score of 5 (totally senesced) was highly unsuitable. Scores were given to 100 randomly selected leaves of each grass species. Once the sward measures had been conducted, each grass species was cut to ground surface in each replicate and the fresh weight recorded. The samples were then oven-dried at 80°C for 2 d and the dry weight calculated (Frame 1981).

Statistical analysis.—A comparison of the temperature inside the cages with the temperature outside was conducted using Student's t-test. Differences in herbage properties (mean herbage DM [dry matter] per m^2, DM content, leaf area, angle, hardness and height) were described using one-way ANOVA. Tukey's test was then performed to identify differences between the 4 grass species.

The total number of observations of grasshoppers on each grass species was subjected to a chi-square (χ^2) analysis to ascertain whether individuals were randomly distributed among the 4 grass species, therefore having no particular preference for one plant species as substrate.

Analysis of feeding preferences.—To determine whether the median number of feeding signs per grasshopper varied between the 4 species of grass for early instar nymphs (1,2), late instar nymphs (3,4), early adults and late adults, a two-way Quade test was used (Quade 1979). This statistic was appropriate for the nonparametric count data and allowed feeding preferences to be ascertained for each stage of maturity.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

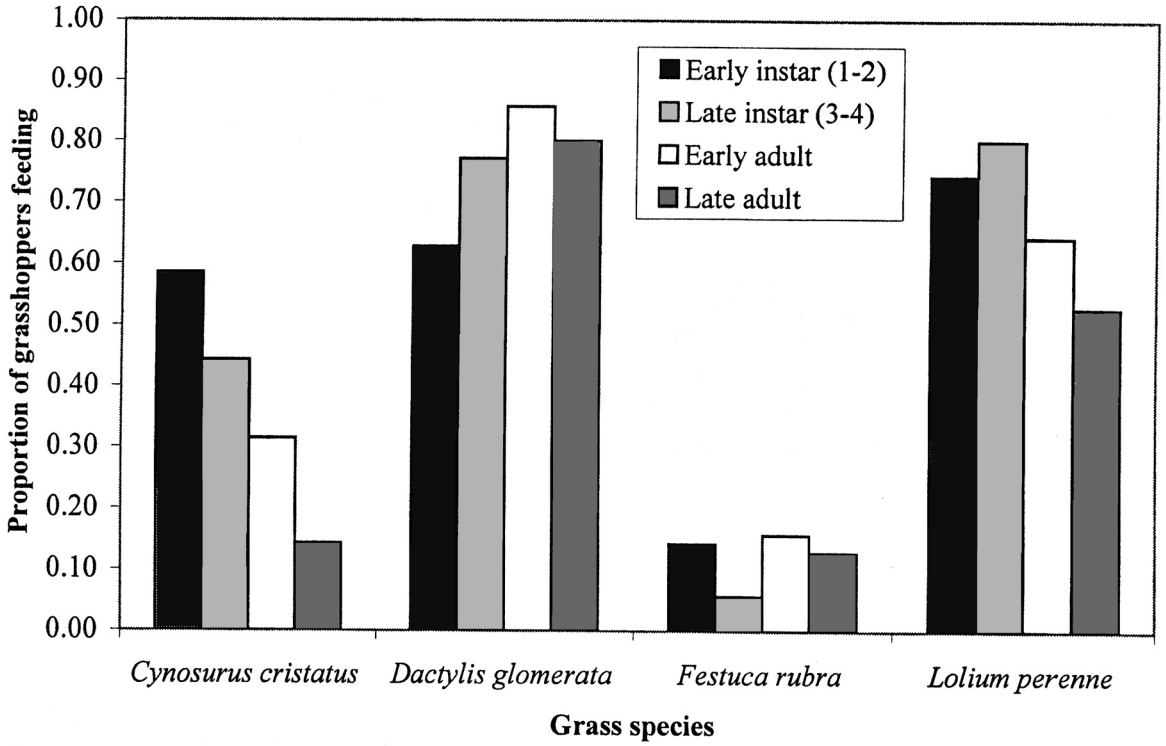


Fig. 3. Proportion of grasshoppers feeding on each grass species at differing stages of maturity.

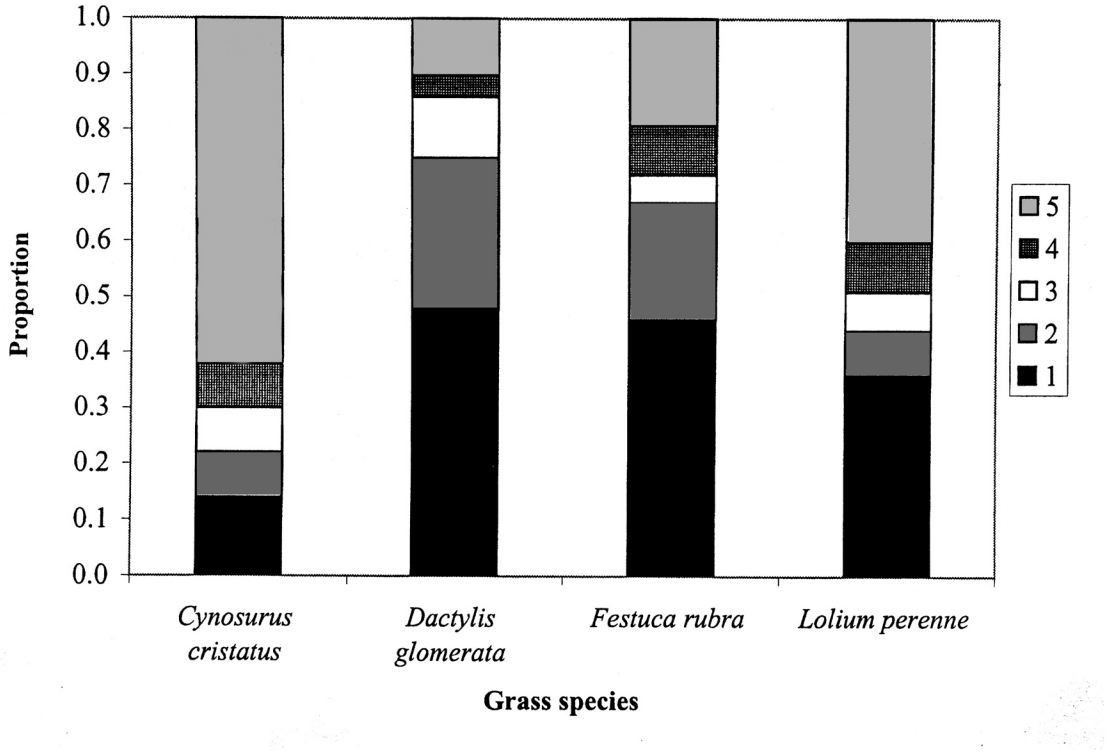


Fig. 4. Proportion of leaves with each palatability index score (see Table 1).

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Mixtures of different grass species may be important for grasshoppers (Bernays & Bright 2001). To determine if grasshoppers at each life stage were predominantly feeding on a very few of the grass species (1 to 2 species) or taking each as part of their diet (3 to 4 species), the total number of grasshoppers feeding on 1 to 2 species and 3 to 4 species were compared using chi-square (χ^2) analysis for early instar nymphs (1,2), late instar nymphs (3,4), early adults and late adults.

The Quade test was performed using Unistat Version 4.53 (Unistat 1998) according to the methods of Quade (1979). All other statistical analyses were performed using SPSS Version 10 (SPSS, 1999) according to the methods of Mead *et al.* (1993).

Results

Micro-climate of the nets.—A small (+0.3^{0}C) but significant increase in mean temperature inside the cage compared with outside the cage (17.9^{0}C ± 0.32 *vs* 17.6^{0}C ± 0.34; Student t statistic: 5.52, d.f. 941, p<0.01) was observed, indicating that the thermal environment inside the cages was dissimilar to the prevailing ambient environment.

Habitat preferences within the micro-swards.—Early and late instar nymphs were often observed on the *L. perenne* sward, although most nymphs were sighted on the net (Table 2). Early and late adults spent most of their time on the net (50 and 54 observations respectively). Overall, the highest total number of observations was on the net (183 or 63% of observed individuals); however grasshoppers were not randomly distributed on the 4 grass species (χ^2 = 7.78, d.f. 3, p<0.05).

Feeding preferences.— Grasshoppers frequently fed on *D. glomerata* and *L. perenne* at all stages of maturity, with *F. rubra* mainly avoided at all life stages (Fig. 3). As the grasshoppers matured, the proportion feeding on *C. cristatus* and *L. perenne* decreased (Table 3, Fig. 3) with a concurrent increase in feeding on the large-leaved *D. glomerata*.

Analysis of the median number of feeding signs per grasshopper confirmed that feeding preferences existed for early instar nymphs (Quade two-way ANOVA F = 7.92, d.f. 39, p<0.01), late instar nymphs (Quade two-way ANOVA F = 9.68, d.f. 39, p<0.01), early adults (Quade two-way ANOVA F = 4.00, d.f. 39, p<0.05) and late adults (Quade two-way ANOVA F = 14.04, d.f. 39, p<0.01). Small differences in the median number of feeding signs per grasshopper for *C. cristatus* and *D. glomerata* for early instar nymphs were observed with *L. perenne*, the preferred food choice at this stage of maturity (Table 3). The number of feeding signs was lowest on *F. rubra*, indicating an avoidance of this species. In late instar nymphs, the number of feeding signs per grasshopper was much higher on *D. glomerata* and *L. perenne* than on *F. rubra* or *C. cristatus*. A similar pattern was observed with early and late adults that preferred the former grass species to *F. rubra* and *C. cristatus* (Table 3).

The combinations of grass species could also be important for the nutritional requirements of *C. parallelus*. The number of grasshoppers feeding on 1 or 2 grass species was substantially higher than the number feeding on 3 to 4 species in late instar nymphs, early adults and late adults (Table 4). For early instar nymphs there was no difference between the number of grasshoppers feeding on 1 or 2 species and 3 or 4 species. Occurrences of no feeding signs in a two-day period were rare in all life stages.

These results suggest grasshoppers of greater maturity preferred to eat only 1 or 2 species of grass (Table 4) and the combinations of grass species were examined. Feeding was most frequently observed on a combination of the 2 large-leaved grass species, *D. glomerata* and *L. perenne* at all life stages (Table 5), whilst the lowest number of occurrences was observed for a combination of feeding on the 2 fine-leaved grass species, *C. cristatus* and *F. rubra*.

Table 1. Leaf palatability index.

Score	% browning	Description of leaf appearance
1	0-10	Fresh, green leaf, no leaf curl
2	11-25	Leaf starting to show signs of browning
3	26-50	Large areas of leaf brown in color
4	51-75	Leaf very brown, edges starting to curl
5	76-100	Dead, brown leaf, curled up edges

Herbage properties.—Biomass (DM yield per m^2) and leaf angle (^{0}) did not differ between the 4 grass species (Table 6). However, dry matter content was lower for *D. glomerata* compared with any of the other grass species. Leaves of *D. glomerata* were generally fresh and green (palatability index score 1), with a very low proportion of dead, brown leaves (palatability index score 5, Fig. 4). However, in contrast there was a high proportion of low palatability, senesced, brown leaves on *C. cristatus*, with very few fresh, green palatable leaves available to grasshoppers.

D. glomerata had much larger leaves than the other 3 species. Leaf hardness varied little between the grasses, apart from *F. rubra* which had harder leaves than any of the other species. Leaf height was similar for *C. cristatus*, *D. glomerata* and *F. rubra*. However, the leaves of *L. perenne* were situated significantly higher above the ground surface than those of the other 3 species.

Discussion

The study demonstrated that feeding preferences exist for *C. parallelus* at all stages of maturity (Table 3). Bernays & Chapman (1970b) concluded that *C. parallelus* readily feeds on 2 fine-leaved grass species, *Agrostis* and *Festuca*, both of which were common in the habitats in their study. They describe *Cynosurus* and *Dactylis* to be of lesser importance as a food resource as they were not so common in the areas of observation. However, their observations do not necessarily mean that these species of grass are not preferred food plants.

In our study, with equal amounts of 4 grass species in a micro-sward, the preferred grass species at most stages of maturity were the two large-leaved grasses, *D. glomerata* and *L. perenne* (Table 3, Fig. 3). This observation would suggest that *C. parallelus* foraged according to energy maximization models. The fine-leaved *F. rubra* was infrequently sampled or eaten by all life stages, particularly by late instar nymphs. This pattern of avoidance of *F. rubra* may have been due to aversion during foraging, reflecting the hardness (increased energy cost of chewing) of the leaves (Table 6), although Bernays & Chapman (1970a) suggest leaf thickness (potentially the interaction between biomechanical factors and anatomical constraints of the mandible) as the reason for the avoidance of this plant species by early instar nymphs.

D. glomerata in particular, may have been frequently eaten in this study as it had relatively high leaf moisture content throughout the summer (Table 6) and a high proportion of palatable leaves (Fig. 4). In contrast, *C. cristatus* started to wilt as the experiment progressed, perhaps due to very high temperatures and drought conditions in August (maximum air temperature at Writtle 35.7^{o}C,

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 2. Frequency with which *C. parallelus* individuals were observed on each grass species and the net (proportion in brackets).

	Life stage				
Grass species/net	Early instar (1-2)	Late instar (3-4)	Early adult	Late adult	Total no. observations
Cynosurus cristatus	7 (0.10)	8 (0.11)	2 (0.03)	2 (0.03)	19 (0.07)
Dactylis glomerata	6 (0.09)	5 (0.07)	3 (0.04)	8 (0.11)	22 (0.08)
Festuca rubra	5 (0.07)	3 (0.04)	8 (0.11)	4 (0.06)	20 (0.07)
Lolium perenne	14 (0.20)	13 (0.19)	7 (0.10)	2 (0.03)	36 (0.13)
Net	38 (0.54)	41 (0.59)	50 (0.71)	54 (0.77)	183 (0.65)

Heywood *pers. comm.*). Several areas of this plant species in the microswards were infested by aphids in July and August, insects which Spedding & Diekmahns (1972) note are common on this grass species in warm summers, when they destroy large quantities of foliage. The aforementioned factors may have led to a decline in the leaf palatability of *C. cristatus* and therefore a concomitant decrease in the frequency of grasshopper feeding on this species (Table 3, Fig. 3). The preference of grasshoppers for feeding on fresh, young green leaves over old yellow foliage has been suggested by Pfadt (1994).

Both *D. glomerata* and *L. perenne* are grass species that are commonly sown for agricultural purposes due to their high nutritive value to grazing livestock (Hubbard 1984, Spedding & Diekmahns 1972), although the former species is currently sown less than in the early 1900s (Hubbard 1984). It is suggested that these grasses were also preferred by *C. parallelus* as a result of their superior nutritive value and palatability. However, the less favored feeding resources of *C. cristatus* and *F. rubra* are much less frequently sown in pastures, reflecting their comparatively lower nutritive value and palatability to livestock (Spedding & Diekmahns 1972).

This study raises some interesting questions about the utilisation of grassland habitats by *C. parallelus*. *C. parallelus* is one of the most numerous species in grasslands dominated by fine-leaved grass species such as *F. rubra*, while swards with a predominance of *D. glomerata* (Clarke 1948) and *L. perenne* are less favored habitats (Gardiner *et al*. 2002). Initially it was thought that the unsuitability of swards dominated by the latter 2 grass species reflected the inaccessibility of the food resource (high energetic cost of feeding on species such as *Dactylis* reflecting the adverse biomechanical properties of the herbage). This study demonstrates that *D. glomerata* and *L. perenne* were the preferred food resources for *C. parallelus* and therefore other factors such as sward structure and microclimate may be more important in sward suitability for grasshopper populations.

Heathland swards dominated by *Agrostis capillaris* L. and *F. rubra* provide a short and sparse sward with a potentially favorable microclimate (Gardiner *et al*. 2002). Grasshoppers in these situations may possibly feed in patches of more coarse and large-leaved grasses, before returning to the areas of fine-leaved grasses for basking and reproduction.

Early instar nymphs were observed to feed frequently on 3 or 4 of the grass species (Table 4), suggesting perhaps that they require a wider range of grass species, as grasshoppers have been observed to grow faster on mixtures of grasses than on individual species (Bernays & Bright 2001). Grasshoppers often feed on various combinations of 2 grass species with the 2 large-leaved grasses, *D. glomerata* and *L. perenne* eaten most frequently at all stages of maturity (Table 5). There is also evidence that grasshoppers 'switched' from *L. perenne* to *D. glomerata* (Table 3, Fig. 3) as they matured, perhaps preferring the high leaf moisture content of the latter species (Table 6) as the leaves of the former species senesced in the high temperatures (Fig. 4).

It is quite possible that grasshoppers of all life stages could have learnt over the course of each 2-w experimental period, cues which showed the grass species providing the optimal balance of protein and carbohydrate to maximise growth (Dukas & Bernays 2000). Dukas & Bernays (2000) suggest that by learning, grasshoppers could orient towards their preferred food source, therefore reducing the amount of time taken travelling between suboptimal foods. Indeed in our experiment nymphs preferred to spend the majority of their time on *L. perenne* (Table 2) which was a preferred food source for early instar nymphs. Therefore, nymphs may have resided for most of their feeding time on this grass species once they had learnt that other species such as *F. rubra* were suboptimal feeding resources.

The results of this study should be viewed with some caution as the grasshoppers were captive and therefore could only eat the 4 grass species they were offered. In the field, grasshoppers potentially have a much wider choice of grasses and behavior may differ accordingly. Grasshoppers also spent a large proportion of their time on the net and consequently not on vegetation: so much time spent off vegetation is a situation that would rarely occur in the field.

Table 3. Median number of feeding signs per grasshopper on the 4 grass species at differing stages of maturity (standard deviation in brackets).

	Life stage			
Grass species	Early instar (1,2)	Late instar (3,4)	Early adult	Late adult
Cynosurus cristatus	12 (6)	6 (2)	3 (3)	1 (1)
Dactylis glomerata	13 (5)	25 (5)	37 (14)	31 (7)
Festuca rubra	1 (1)	0 (0)	1 (1)	1 (1)
Lolium perenne	33 (8)	19 (6)	40 (11)	10 (6)

Table 4. Number of grasshoppers feeding on 1/2 grass species and 3/4 grass species (proportion of grasshoppers feeding in brackets).

	Life stage			
Feeding status	Early instar (1,2)	Late instar (3,4)	Early adult	Late adult
1 or 2 grass species	42 (0.60)	41 (0.59)	46 (0.66)	53 (0.76)
3 or 4 grass species	27 (0.39)	25 (0.36)	24 (0.34)	10 (0.14)
χ^2 value	3.26	3.88*	6.91**	29.35**

* significant at $p<0.05$
** significant at $p<0.01$

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Table 5. Number of occurrences of different combinations of feeding (proportion of grasshoppers feeding in brackets).

	Life stage				
Combination	Early instar (1,2)	Late instar (3,4)	Early adult	Late adult	Total
Dactylis + *Lolium*	39 (0.56)	50 (0.71)	51 (0.73)	38 (0.54)	178 (0.64)
Cynosurus + *Dactylis*	34 (0.49)	32 (0.46)	29 (0.41)	17 (0.24)	112 (0.40)
Cynosurus + *Lolium*	32 (0.46)	35 (0.50)	27 (0.39)	13 (0.19)	107 (0.38)
Festuca + *Lolium*	9 (0.13)	10 (0.14)	16 (0.23)	14 (0.20)	49 (0.18)
Dactylis + *Festuca*	7 (0.10)	9 (0.13)	18 (0.26)	14 (0.20)	48 (0.17)
Cynosurus + *Festuca*	7 (0.10)	9 (0.13)	14 (0.20)	10 (0.14)	40 (0.14)

Table 6. Characteristics of the 4 grass species ($\pm s_{\bar{x}}$).

	Grass species					
Sward characteristic	*Cynosurus cristatus*	*Dactylis glomerata*	*Festuca rubra*	*Lolium perenne*	F value	d.f.
Mean DM yield (g) per m^2	42 ± 4^a	35 ± 3^a	46 ± 4^a	47 ± 5^a	1.51	39
Mean % DM content	51 ± 3^a	28 ± 1^b	42 ± 5^a	42 ± 2^a	9.93	39
Mean leaf area (mm)	36 ± 3^a	471 ± 21^b	39 ± 3^a	69 ± 4^a	390.45	399
Mean leaf angle (°)	64 ± 2^a	66 ± 2^a	68 ± 2^a	69 ± 2^a	1.56	399
Mean leaf hardness (g)	166 ± 9^a	153 ± 6^a	192 ± 4^b	165 ± 6^a	6.51	39
Mean leaf height (mm)	42 ± 2^a	40 ± 3^a	47 ± 2^a	62 ± 3^b	17.49	390

Mean values in each row followed by different superscript letters are significantly different at $p<0.05$ (one-way ANOVA).

The authors assume that high numbers of feeding signs on a particular grass species indicate that it is preferred as a food resource. However, it was not possible in this experiment to ascertain whether the number of feeding signs on a grass species correlated with the biomass and area of leaf eaten or length of time spent feeding. Generally many large feeding signs were observed on the preferred food choices such as *D. glomerata* (>15 mm), which were obviously the result of sustained feeding over a long time period. On other less favored grass species such as *F. rubra*, only small feeding signs were observed, which may indicate tasting and rejection of this species. Further studies should concentrate on determining the severity of feeding on the 4 grass species, and the growth and development of *C. parallelus* nymphs and adults because, as far as the authors are aware, there is no published evidence showing increases in growth, weight and shorter development times on *D. glomerata* or *L. perenne*. However, grasshoppers tend to prefer host plants which are beneficial for growth and survival (Capinera & Sechrist 1999).

Temperatures within the cage were higher than those recorded outside the cage, which may affect feeding behavior (Corcket *et al*. 2003). However, inspection of the daily temperatures inside and outside the cage showed that fluctuations in temperature inside the cage followed those of the air temperature outside. Therefore captive grasshoppers may have displayed relatively normal feeding patterns inside the cages in relation to the prevailing weather conditions.

The final important consideration is that the experiments were conducted on young grass growth (Fig. 1): as species such as *D. glomerata* mature they may become too coarse for grasshopper feeding and preferences may consequently change. Due to the aforementioned limitations of our feeding experiment, the results obtained are only preliminary and more research is needed into the feeding preferences of *C. parallelus* on more mature grasses under field conditions.

Conclusion

This study has established that in a situation of equal availability of grass, feeding preferences between fine-leaved grasses such as *F. rubra* and large-leaved species such as *D. glomerata*, do exist. Possible reasons for this preference may relate to the higher leaf moisture content of the latter species making it more favorable for feeding, or to the hardness of *F. rubra* leaves, which might be difficult for grasshopper mandibles to penetrate. *C. parallelus* has been found to favor grasslands dominated by fine-leaved grass species such as *F. rubra*, despite the apparent unsuitability of this species as a food resource.

Acknowledgements

The authors wish to thank Writtle College for funding this project. Thanks are also extended to 2 anonymous referees and Dr. Glenn Morris whose comments were extremely constructive and helpful in revising this paper.

References

Bernays E.A., Chapman R.F. 1970a. Experiments to determine the basis of food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. Journal of Animal Ecology 39: 761-776.

Bernays E.A., Chapman R.F. 1970b. Food selection by *Chorthippus parallelus* (Zetterstedt) (Orthoptera: Acrididae) in the field. Journal of Animal Ecology 39: 383-394.

Bernays E.A., Bright K.L. 2001. Food choice causes interrupted feeding in the generalist grasshopper *Schistocerca americana*: further evidence for inefficient decision–making. Journal of Insect Physiology 47: 63-71.

Brown V.K. 1983. Grasshoppers. Cambridge University Press, Cambridge.

Capinera J.L., Sechrist T.S. 1999. Grasshoppers (Acrididae) of Colorado identification, biology, and management (electronic publication). http://www.sdvc.uwyo.edu/grasshopper/ghcobio.htm.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Clarke E.J. 1948. Studies in the ecology of British grasshoppers. Transactions of the Royal Entomological Society of London 99: 173-222.

Corcket E., Callaway R.M., Michalet R. 2003. Insect herbivory and grass competition in a calcareous grassland: results from a plant removal experiment. Acta Oecologica 24: 139-146.

Dukas R., Bernays E.A. (2000) Learning improves growth rate in grasshoppers. Proceedings of the National Academy of Sciences of the United States of America 97: 2637-2640.

Frame J. 1981. Herbage mass, pp. 39-69. In: Hodgson J., Baker R.D., Davies A., Laidlaw A.S., Leaver J.D. (Eds) Sward Measurement Handbook. British Grassland Society, Hurley.

Gardiner T., Pye M., Field R., Hill J. 2002. The influence of sward height and vegetation composition in determining the habitat preferences of three *Chorthippu*s species (Orthoptera: Acrididae) in Chelmsford, Essex, UK. Journal of Orthoptera Research 11: 207-213.

Hubbard C.E. 1984. Grasses (3rd edition). Penguin Books, London.

Köhler G., Brodhun H.-P., Schäller G. 1987. Ecological energetics of Central European grasshoppers (Orthoptera: Acrididae). Oecologia 74: 112-121.

Marshall J.A., Haes E.C.M. 1988. Grasshoppers and Allied Insects of Great Britain and Ireland. Harley Books, Colchester.

Mead R., Curnow R.N., Hasted A.M. 1993. Statistical Methods in Agriculture and Experimental Biology (2nd edition). Chapman & Hall, London.

Pfadt R.E. (1994) Field guide to common western grasshoppers (electronic publication). http://www.sdvc.uwyo.edu/grasshopper/fieldgde.htm#Behavior.

Quade D. 1979. Using weighted rankings in the analysis of complete blocks with additive block effects. Journal of the American Statistical Association 74: 680-683.

Rhodes I.1981. Canopy structure, pp. 141-158. In: Hodgson J., Baker R.D., Davies A., Laidlaw A.S., Leaver J.D. (Eds.) Sward Measurement Handbook. British Grassland Society, Hurley.

Richards O.W., Waloff N. 1954. Studies on the biology and population dynamics of British grasshoppers. Anti-Locust Bulletin 17: 1-182.

Robson M.J., Sheehy J.E. 1981. Leaf area and light interception. pp. 115-139. In: Hodgson J., Baker R.D., Davies A., Laidlaw A.S., Leaver J.D. (Eds) Sward Measurement Handbook. British Grassland Society, Hurley.

Spedding C.R.W., Diekmahns E.C.(Eds) 1972. Grasses and Legumes in British Agriculture. Commonwealth Agricultural Bureaux, Slough.

SPSS. 1999. SPSS version 10. SPSS Inc, Chicago.

Unistat (1998) Unistat Version 4.53. Unistat Ltd, London.

Williams L.H. 1954. The feeding habits and food preferences of Acrididae and the factors which determine them. Transactions Royal Entomological Society London 105: 423-454.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Orthoptera-Research on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use