Hillside lagomorph grazing and its influence on Orthoptera

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Abstract

The effects of lagomorph grazing on the Orthoptera of a small hill in Mistley (southeast England) were studied during the summer of 2020. Transect counts of Orthoptera revealed low sward height with abundant bare earth due to high wild rabbit Oryctolagus cuniculus grazing on the high slopes. This intensive grazing led to only field grasshopper Chorthippus brunneus (Thunberg, 1815) adults being found in any number on the high slopes, perhaps utilizing the short swards and bare earth as basking and egg-laying habitat. Aspect was also important, with significantly more grasshopper nymphs and C. brunneus adults on the south-facing slope than on the northern slope. Soil slippage areas seem like valuable micro-habitats on the south-facing slope, with these 'sun traps' providing excellent basking habitat for nymphs and C. brunneus. This study confirms that lagomorph grazing alters hill summit habitats for Orthoptera, benefiting C. brunneus and, to a lesser extent, the meadow grasshopper Pseudochorthippus parallelus (Zetterstedt, 1821). However, overgrazing of higher hill slopes can exclude tall grass species, such as long-winged conehead Conocephalus fuscus (Fabricius, 1793), and reduce assemblage diversity.

Keywords

Acrididae, altitude, bush-crickets, ecology, elevation, hill, rabbit, Tettigoniidae

Introduction

Orthoptera form an important part of grassland ecosystems across Europe (Köhler et al. 1987, Ingrisch and Köhler 1998). Grazing (by both domesticated and wild animals) affects the properties of grasslands that are crucial for orthopteran life-history processes (Gardiner 2018). Intensity of grazing, type of grazer, and rotational or seasonal aspects of the regime have an impact on characteristics of grasslands such as vegetation height, biomass, and plant species (Marini et al. 2008, Fabriciusová et al. 2011, Kurtogullari et al. 2020). In turn, these factors influence the oviposition, dispersal, and feeding behaviors of grasshoppers, thereby affecting the dynamics within Orthoptera assemblages and communities (Gardiner 2018).

Fonderflick et al. (2014) found that the impact of sheep grazing exerted a species-specific influence on a grasshopper assemblage that varied greatly over the season in Mediterranean steppelike grasslands. They concluded that extensive grazing by sheep tended to homogenize the vegetation structure and led to a temporary reduction in Orthoptera abundance at a pasture scale. Species-specific responses to grazing were also noted in submontane pastures in the Hrubý Jeseník Mountains in the Czech Republic, where the abundance of rufous grasshopper Gomphocerippus rufus (Linnaeus, 1758) increased substantially with cattle grazing (Rada et al. 2014). The response of Orthoptera may change from scenarios with introduced domestic livestock to those with wild grazers such as lagomorphs and ungulates. In the Swiss Alps, Spalinger et al. (2012) found no direct effect of wild ungulate grazing (red deer and chamois), although they did observe small-scale alteration of habitats and plant nitrogen (N) content by ungulates that may have affected Orthoptera abundance and diversity.

On sea wall pollinator strips, wild rabbit *Oryctolagus cuniculus* grazing had a significant impact on sward height and adults and nymphs of Roesel's bush-cricket *Roeseliana roeselii* (Hagenbach, 1822) (Gardiner and Fargeaud 2020). The cutting of the pollinator strips allowed rabbits to graze the closed grassland, reducing grass growth and creating patches of exposed soil due to their burrowing activities, which may be favorable for basking nymphs (Gardiner et al. 2002). Grasshoppers of all species have been found in high densities (2.9 adults/m²) on rabbit-grazed sea walls in Essex when compared with mown flood defenses (0.7 adults/m²) due to the shorter swards created by lagomorphs (Fargeaud and Gardiner 2018).

Clarke (1948) suggested that excessive grazing by rabbits promoted sparser vegetation comprised of less vigorous grass species, such as sheep's fescue *Festuca ovina*, which was consequently more favorable to grasshoppers. In another study on a heavily rabbit-grazed grassland, the field grasshopper *Chorthippus brunneus* (Thunberg, 1815) was more abundant within an exclosure than on the surrounding grazed grassland (Grayson and Hassall 1985). The authors of that study suggested that the taller vegetation in the exclosure provided better cover from vertebrate predators and higher-quality food resources for grasshopper nymphs than the shorter grazed vegetation. Intensive grazing by wild rabbit populations in Epping Forest in the UK contributed to the extirpation of the locally scarce common green grasshopper *Omocestus viridulus* (Linnaeus, 1758) from hillside slopes, a species with a preference for tall grassland (Gardiner 2010). The grazing on the slopes created a very homogenously short grassland sward resembling a 'lawn' (Crofts 1999), which may not have provided the necessary shelter or 'cool' microclimate for *O. viridulus*.

Short swards established by lagomorph grazing will have excessively hot temperatures (> 40 °C) (Gardiner and Hassall 2009), unlikely to be favorable for grasshoppers in the absence of 'cool' tussocks. In short-grassland habitats, grasshoppers may therefore overheat and have a higher susceptibility to water loss and desiccation than in taller grassland where humidity may be higher and temperatures lower (Haskell 1958). The large body size (and therefore surface area) of grasshoppers such as meadow grasshopper Pseudochorthippus parallelus (Zetterstedt, 1821), in which adult females are 16-22 mm long (Marshall and Haes 1988), could make it difficult to cool down quickly in hot environments, meaning behavioral thermoregulation (dispersal to cooler tussocks) is the only option for survival (Gardiner and Hassall 2009). Across Europe, homogenously short swards established by overgrazing are the greatest threat to Orthoptera (affecting 262 species; Hochkirch et al. 2016).

To investigate the overgrazing associated with wild lagomorph grazing, transect counts of Orthoptera on a small hill at Lound Lakes (Suffolk, south-east England) revealed that low sward height due to wild rabbit grazing on the high slopes led to the general absence of tall grass species such as O. viridulus and R. roeselii. Only nymphs and C. brunneus adults were found in any number on the higher slopes, perhaps utilizing the short swards and bare earth as basking habitat (Gardiner 2021). The near exclusion of several orthopteran species from hill summits by rabbit grazing could be an important conservation issue for certain species such as O. viridulus, which are scarcer in south-east England (Gardiner 2010). However, the Lound Lakes study was limited due to its relatively small sample size (c. 1500 orthopterans) and lack of replication. A larger dataset with replication is required to further investigate the dynamics of hillside rabbit grazing and, together with the Lound Lakes study, ascertain how it affects Orthoptera abundance in low-altitude landscapes.

The aim of this short paper is to report a detailed study on the orthopteran assemblage of a rabbit-grazed hill in Essex, south-east England. Transect survey results are discussed in relation to grazing by lagomorphs and sward characteristics, and the conservation implications are considered.

Materials and methods

Study site.—The study site at Furze Hills Local Wildlife Site (LoWS) (51°56'9.9528"N, 1°4'41.9412"E) in Mistley, Essex, southeast England, was a small grassy hill composed of grasses such as sweet vernal *Anthoxanthum odoratum* and fescues *Festuca* spp. with a summit of 21 m (69 ft) and 10 m prominence (33 ft) over the surrounding countryside. The hill has free-draining, neutralacidic sand and gravel soil. Both the southern and northern faces have gentle slopes (maximum gradient 7% and 6%, respectively), while the eastern slope is an agricultural field and the west is rank grassland with ruderal plants and scrub (5% slope). The hillside grassland of the north and south slopes is grazed by lagomorphs: mainly rabbits, but the brown hare *Lepus europaeus* is known in the area. The slopes are composed of *Festuca* spp. and sheep's sorrel *Rumex acetosella* grassland on the upper slopes, along with harebell *Campanula rotundifolia* and the occasional pignut *Conopodium majus*, the latter indicating semi-improved grassland. Semi-improved grassland refers to grassland that has had some agricultural improvement, such as chemical input or reseeding, but still retains floristic interest (Magnificent Meadows 2019). Damp grassland with widespread *H. lanatus*, rush *Juncus* spp., and occasional ragged robin *Silene flos-cuculi* was recorded in wetter locations on the lower slopes and in the basal pastures.

Transect surveys.—Eight 1-m wide × 50-m long transects were established in the lagomorph grazed grassland of the hill (4 transects each for the north and south slopes, Fig. 1), closely following the methodology of Gardiner et al. (2005), Gardiner and Hill (2006), and Gardiner (2021). On both the north and south slopes, two 50-m long transects were located on the low slope (15–17 m AOD) and two on the high slope (18–20 m AOD). All transects were at least 10 m apart to reduce the chances of double-counting individuals during surveys and can be considered independent replicates, similar to bird point counts or line transects (Nur et al. 1999).

Each transect was walked once at a slow, strolling pace (2 km/ hr) on 17 occasions from 15 May to 26 August 2020. Nymphs flushed from a 1-m wide band in front of the observer were recorded along transects. As it is difficult (though not impossible, see Thommen 2021) to distinguish between species in the early

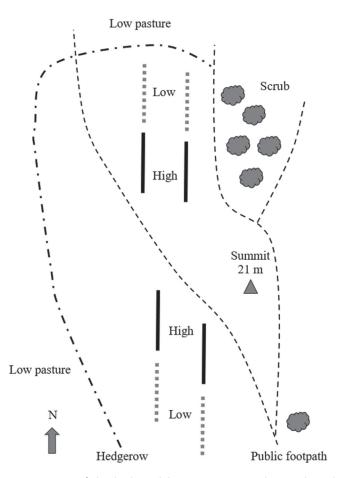


Fig. 1. Layout of the high and low transects on the north and south slopes of Furze Hill. Not to scale.

instars without capture, nymphs of all species were lumped together for recording purposes. With practice, it was relatively easy to ascertain the species of adults without capture (Gardiner and Hill 2006). Adult individuals of all species along transects were recorded to determine assemblage composition and species richness. The weather conditions on survey days were favorable for insect activity, being largely sunny and warm (>17°C).

Sward height, bare earth, and rabbit grazing evidence.—A total of 80 sward heights were recorded at random positions using a 1-m rule for each of the two transects for both north and south slopes, split evenly between high and low sections in June 2020 (a total of 160 sward heights each for north and south slopes and 160 heights each for high and low slopes). The presence of bare earth in a 1×1 m quadrat was also recorded at 10 random locations along each transect. In addition, during the sward height surveys, the number of wild lagomorph (hare and rabbit) droppings (dung balls) were counted for high and low transects) to ascertain the level of grazing pressure on each strip (Wood 1988, Gibb and Fitzgerald 1998, Millett and Edmondson 2013). To provide further evidence of wild rabbit grazing, the number of burrow excavations was also recorded on the transects.

Statistical analysis

To correct for non-normality, all data were square-root transformed before analysis (Heath 1995). To determine whether adults (for species where there was enough data for analysis) and nymphs were randomly distributed on the hill slopes, the data for nymphs and adults were pooled for high and low transect sections for the two transects for both the north and south slopes and subjected to a two-way ANOVA (Heath 1995). The independence of transects was assumed, and data for each transect was pooled in a similar way to allow for data analysis in other monitoring studies (Nur et al. 1999). Species richness was also compared for the two transects for both the north and south slopes and subjected to a two-way ANOVA. The frequency of burrow excavations, lagomorph droppings, and sward height were also compared between high and low transect sections on both north and south slopes using a 2-way ANOVA. Significance was accepted as evidence on the following scale in accordance with Muff et al. (in press): p-value >0.1 little or no evidence, 0.05-0.1 weak evidence, and <0.05 moderate evidence. There were no instances of strong (p < 0.01) or very strong (p < 0.001) evidence in this study.

Results

Seven species of Orthoptera were recorded on the south slope of the hill: 6 species on the low transects and 3 species on the high transects (Table 1). In contrast, only 5 species were recorded on the north slope low transects, compared to 3 on the high transects. Species richness was significantly lower on the high transects, although it was unaffected by aspect (Table 2). The most commonly recorded species was *Pseudochorthippus parallelus* (788 adults, 66% of total adults), followed by *Chorthippus brunneus* (385 adults, 32%). Less common species included longwinged conehead *Conocephalus fuscus*, lesser marsh grasshopper *Chorthippus albomarginatus* (De Geer, 1773), and *Roeseliana roeselii*. Dark bush-cricket *Pholidoptera griseoaptera* (De Geer, 1773) and slender groundhopper *Tetrix subulata* (Linnaeus, 1758) were rare species on the south slope, with just one sighting each. Aspect influenced nymphs, with the south-facing slope having a significantly higher abundance than the northern one, although no elevation effect was noted (Table 2). Numbers of *C. brunneus* adults were significantly influenced by aspect and elevation, with greater abundance on the high transects and the south slope (Table 2). Interestingly, the percentage of nymphs of the total Orthoptera recorded was similar on the low slopes and the north high slope at c. 70% (Table 1). However, on the south high slope, nymphs formed 81% of total Orthoptera.

Lagomorph droppings were significantly more numerous on the high transects compared to the low transects and on the south slope, a pattern reflected by the number of rabbit burrow excavations and sward height (Tables 1, 2).

Table 1. Species richness and number of Orthoptera adults for each species and nymphs on the low and high transects of the south and north slopes of Furze Hill in relation to sward height, bare earth, and lagomorph grazing.

Species/habitat characteristic	So	uth	No	Total	
	Low	High	Low	High	
Pseudochorthippus parallelus	348	75	214	151	788
Chorthippus brunneus	93	182	36	74	385
Roeseliana roeselii	7	0	4	0	11
Chorthippus albomarginatus	2	0	1	2	5
Conocephalus fuscus	3	0	1	0	4
Pholidoptera griseoaptera	1	0	0	0	1
Tetrix subulata	0	1	0	0	1
Total adults	454	258	256	227	1195
Total nymphs (all species)	988	1107	622	483	3200
Nymphs (% of total Orthoptera)	69	81	71	68	-
Mean species richness	4.0 ± 0	2.5 ± 0.5	3.5 ± 0.5	3.0 ± 0	-
Mean sward height (mm) \pm s.e.	204 ± 0	103 ± 5	251 ± 18	188 ± 47	186 ± 22
Mean bare earth frequency (%)	20 ± 20	95 ± 5	5 ± 5	50 ± 0	30 ± 15
No. lagomorph droppings	138	321	2	73	534
No. rabbit burrow excavations	3	28	2	31	64

Table 2. Results of the 2-way ANOVA analysis (F value displayed) with factor significance (p) and interaction.

Parameters	Elevation		Aspect		Interaction	
	F	р	F	р	F	р
Nymphs (all species)	0.2	0.69	52.4	< 0.01	3.8	0.12
Chorthippus brunneus	12.0	0.03	20.5	0.01	0.3	0.62
Pseudochorthippus parallelus	5.2	0.08	0.0	0.97	2.1	0.22
Overall species richness	8.0	0.04	0.0	1.00	2.2	0.21
Sward height	12.4	0.02	7.5	0.05	1.2	0.34
Lagomorph droppings	41.1	< 0.01	86.7	< 0.01	0.4	0.58
Rabbit burrow excavations	15.8	0.02	0.0	0.93	0.0	0.93

Discussion

The total of seven species recorded on Furze Hill is comparable to other small hills in the east of England, such as Hungry Hill at Lound Lakes (7 species; Gardiner 2021). Species richness of Orthoptera was affected by hill elevation but not by aspect, with fewer species on the high transects. On Furze Hill, *C. brunneus* abundance was significantly affected by elevation and aspect, as the species is more tolerant of short swards (<10 cm) with bare earth on the high slope of the south face than *P. parallelus*. *Pseudochorthippus parallelus* was also affected, although elevation and aspect had a lesser influence on abundance (Table 2). Nymphs (of all species) were significantly more numerous on the south slope compared to the north, which reiterates the well-studied effect of south-facing slopes being of higher favorability for Orthoptera due to the warm microclimate and high exposure to solar radiation (Voisin 1990, Weiss et al. 2013). Specifically, nymphs formed a high percentage of total Orthoptera on the south-facing high slope, perhaps due to the extremely low sward height and presence of two soil slippage areas with cliffed sand, which may have been oviposition and early instar development sites unsuitable for adults due to the absence of taller vegetation for feeding and shelter.

The habitat preferences of Orthoptera may relate to the choice of oviposition site, food preferences, vegetation height, and grassland management regimes (Clarke 1948, Gardiner 2006, 2009). Waloff (1950) stated that *C. brunneus* and *P. parallelus* lay their egg pods in the superficial layers of the soil. Bare earth is the usual egg-laying site for *P. parallelus*, although this species has been found to oviposit into grass-covered soil (Waloff 1950). Exposed soil may offer other benefits for grasshoppers by providing sites where they can bask (Key 2000), as exposed soil is often much warmer than surrounding vegetation. The high slopes of Furze Hill had a high occurrence of bare earth in the short sward (Fig. 2), where *C. brunneus* may lay its eggs.

Nymphs were evenly distributed between low and high slopes and seemingly more tolerant of shorter swards (<10 cm) with bare earth than adults that required taller vegetation. Early instar grasshopper nymphs of *C. brunneus* and *P. parallelus* are often found in short grassland near oviposition sites, as on Furze Hill's southfacing high slope with soil slippage areas, before moving to taller swards (10–20 cm height) as they mature for feeding and reproduction (Clarke 1948, Richards and Waloff 1954). Adults may then return to bare earth and sparse swards for egg-laying (Richards and Waloff 1954), such as those established by rabbit grazing on the high slopes of Furze Hill. It appeared that *C. brunneus* adults seemed able to utilize the summit's bare earth for basking and oviposition as they did on Hungry Hill at Lound Lakes (Gardiner 2021).

It is important to remember that microclimate may be critical for the development of insect populations (Marshall and Haes 1988). South-facing slopes act as hot 'sun traps' favorable for Orthoptera (Voisin 1990, Gardiner and Dover 2008, Weiss et al. 2013). However, short swards established by lagomorph grazing have excessively hot temperatures (>40°C) similar to hav meadows after cutting (Gardiner and Hassall 2009), which are likely to be favorable for grasshoppers inhabiting warmer vegetation such as C. brunneus (Marshall and Haes 1988) but may restrict taller grassland species such as O. viridulus, which was generally absent from the heavily rabbit-grazed summit of Hungry Hill at Lound Lakes (Gardiner 2021). Intense lagomorph grazing pressure also largely excluded R. roeselii, C. fuscus, and P. griseoaptera on Hungry Hill, as these species were found on the low slopes and pastures (Gardiner 2021). The latter two tettigonids were absent from heavily rabbit-grazed higher slopes at Furze Hill, which reduced the assemblage species richness. The geology of hills may also influence their micro-topography, the sand and gravel summit of Furze Hill creating ideal acid grassland that is accessible for rabbit grazing and digging. This disturbance leads to patchy, open swards, which are ideal for C. brunneus and P. parallelus.

On Cleeve Hill in Gloucestershire (UK), several species were found in soil slippage areas that had created a warm microclimate where stripe-winged grasshopper *Stenobothrus lineatus* (Panzer, 1796) was observed in abundance along with *C. brunneus* and *P. parallelus* (Gardiner 2011). Most grasshoppers were found in sheltered hollows or 'amphitheaters' where a warmer, less windy microclimate may be present (Gardiner 2011). On Furze Hill, the two slippage areas on the upper south slope had a prevalence of bare earth and cliff that likely provided a warm soil microclimate and egg-laying opportunities for adults (Fig. 3), particularly *C. brunneus*, which was in significantly higher abundance on the upper slope of the south face. Lagomorph grazing and digging by rabbits probably exacerbates the erosion of vegetation cover and permeates the proliferation of exposed soil.

Other pressure on Furze Hill included trampling by humans around the footpaths that cross the summit. During the 2020 Covid-19 lockdowns, there was noticeably higher trampling pressure (pre-Covid estimate <10 walkers/hour; during this study >20 walkers per hour) on the summit grasslands that formed part of the north and south high slopes in this study. Undoubtedly, this created bare earth in addition to lagomorph grazing and disturbed orthopterans. The significance of this is likely to be minimal compared to the population of rabbits on the hill, and it is unlikely



Fig. 2. South slope zonation from summit acid grassland with sheep's sorrel *Rumex acetosella* (left, red color sward) and abundant field grasshopper *Chorthippus brunneus* into lower, taller grassland (right) at Furze Hill. Photo credit: Tim Gardiner.



Fig. 3. Bare earth and short vegetation in a slope slippage 'amphitheater' utilized by grasshopper nymphs, field grasshopper *Chorthippus brunneus* adults, and slender groundhopper *Tetrix subulata* on a rabbit-grazed hilltop at Furze Hill. Photo credit: Tim Gardiner.

that the presence of enhanced human trampling in response to permitted daily exercise during lockdowns introduced error into the results of this study.

The main source of error in the current survey was the accuracy of the lagomorph dropping counts. Droppings may have been easier to locate in shorter, rabbit-grazed vegetation and would also have dried and been less likely to decay in such situations compared to the taller and moister vegetation present on the lower slopes. Therefore, to provide further evidence of rabbit grazing, the number of burrow excavations was also recorded. This confirmed that rabbit activity was indeed greater on the higher slopes, the digging providing valuable extra bare earth on the upper slope and summit of Furze Hill.

In conclusion, the effects of lagomorph grazing (mostly by rabbits) on a small hill in Essex were quite marked, with the low sward height on the high slopes being favorable for the short sward species *C. brunneus* and, to a lesser extent, *P. parallelus*. Adults of both species were found in abundance on the higher slopes, perhaps utilizing the short swards and bare earth as basking habitat. A meta-analysis of the current study combined with the Lound Lakes data (Gardiner 2021) illustrates the lower species richness on rabbit-grazed hill summits, the absence of species such as *R. roeselii* and *P. griseoaptera*, and the abundance of *C. brunneus* and *P. parallelus* (Table 3). Future studies should focus on determining whether rabbit grazing merely expands favorable habitat for species such as *C. brunneus* or whether bare earth is an attractant for adults moving away from nymphal habitats.

The high slopes also support priority butterfly species such as

Table 3. Meta-analysis matrix with Orthoptera species present in relation to aspect and elevation on rabbit-grazed hillsides from the current study combined with Gardiner (2021). Species in bold are abundant in that scenario.

Elevation	As	Aspect				
	North-facing	South-facing				
High	Ca Cb Cf Ov Pp	Ca Cb Cf Ov Pp Ts				
Low	Ca Cb Cf Ov Pp Rr	Ca Cb Cf Ov Pg Pp Rr				

Species key:

small heath *Coenonympha pamphilus* (Linnaeus, 1758), which is included within the 24 species of butterfly recorded on Furze Hill (41% of the UK's 59 species). The diversity of butterflies is another example of where a mosaic of bare earth, tall grass, and scrub/ wood edge habitat provides the greatest conservation benefit, particularly in a localized area such as Furze Hill. The mosaic of rabbit-grazed semi-improved grassland on a hill, wet basal pastures along a stream, and mature hedgerows means that the full range of successional stages is present in an undulating landscape of value to invertebrates. Where overgrazing from rabbits is a particular problem, it may be necessary to install fencing to prevent them from accessing more species-rich grassland at the base of hills.

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Ca Chorthippus albomarginatus; Cb Chorthippus brunneus; Cf Conocephalus fuscus Ov Omocestus viridulus; Pg Pholidoptera griseoaptera; Pp Pseudochorthippus parallelus Rr Roeseliana roeselii; Ts Tetrix subulata

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